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# COMPARATIVE EFFECTS OF PRESSURE, TEMPERATURE AND OXYGEN TENSION ON PHOTOSYNTHETIC AND RESPIRATORY RATES IN *PORPHYRA UMBILICALIS* (L.) J. Ag.*

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**Abstract**

Influences of hydrostatic pressure (600 atm), temperature (5°, 15° & 30° C) and $O_2$ concentration (3 410 % of air saturation) of the outer medium were studied on the rate of $O_2$ exchange of *Porphyra umbilicalis* collected from Heligoland (North Sea). The $O_2$ tension acted antagonistically to the pressure effects. The pressure influenced rates of respiration and apparent photosynthesis decreased gradually with a decrease in the $O_2$ concentration and *vice versa;* the effects on photosynthesis, however, were lesser than those on respiration. The $O_2$ concentration of 30 % was found to be critical, at higher values respiration of the pressure affected algae increased whereas at lower values it decreased as compared to control. At $O_2$ concentrations lower than 15 %, the rate of $O_2$ exchange decreased very sharply. The pressure influences were retarded by higher and intensified by lower temperatures.

## Introduction

Oxygen enters in the ocean at air-water interface. It is generated by autotrophic marine algae during photosynthesis and is consumed in the oxidation of dead organic material and respiration of living organisms. The steady state concentration of dissolved $O_2$ at any depth of the ocean is, therefore, determined by the rates of its supply and consumption. In deep oceanic water the $O_2$ concentration is often very low because a considerable part of it is lost during the long way taken by the huge masses of polar water sinking to the oceanic depth (Table 1). Apart from hydrostatic pressure another very important abiotic factor with which deep sea organisms are confronted is low $O_2$ concentration. Resistance of pressure by marine invertebrates was found to be higher in a medium not fully air saturated, and it decreased with increasing $O_2$ concentration to about air saturation or higher values (Theede & Ponat, 1970). Variations in $O_2$ tension also exert a considerable influence on the resistance of marine algae to high hydrostatic pressure. The pressure resistance manifested by *Ulva lactuca* decreased slowly with the rising $O_2$ concentration above air saturation value and decreased sharply when the oxygen concentration was below 10 % of air saturation (Shameel, 1973). Rate of respiration in seaweeds is directly proportional to $O_2$ concentration of the outer medium (Nath, 1967). Therefore it appeared very interesting to investigate the effects of these parameters at different temperatures on a red seaweed *P. umbilicalis* whose barobiology has not been studied.

*Dedicated to the memory of my teacher, Prof. Fritz Gessner on his 5th death anniversary on 20. 12. 1977, who inspired in me the interest for barobiology of seaweeds.

TABLE 1. Oxygen deficiency in deep oceanic waters (after Dana Report No. 12, 1937 and IIOE Final Cruise Report, Vol. 12, Woods Hole, 1965).

| Ocean or Sea | Position of measurement | | Depth of measurement (m) | $O_2$ concentration (% of air saturation) |
|---|---|---|---|---|
| Atlantic Ocean | 7°30 N | 79°19 W | 2500 | 28.9 |
| | 25°11′N | 20°57 W | 4000 | 44.9 |
| Banda Sea | 4°08′S | 123°00′E | 4900 | 27.6 |
| | 5°52′S | 131°14 E | 7000 | 29.0 |
| Indian Ocean | 21°31 N | 64°06′E | 3200 | 35.9 |
| | 4°26′N | 85°21′E | 3500 | 38.1 |
| Pacific Ocean | 7°10′N | 78°15′W | 2000 | 25.2 |
| | 7°16′N | 78°30′W | 3500 | 31.7 |
| S. Chinese Sea | 19°18′N | 120°13′E | 2000 | 30.2 |
| | 15°22′N | 115°20′E | 4000 | 33.3 |

## Materials and Methods

*Porphyra umbilicalis* (L.) J. Ag. was collected from Heligoland, North Sea, where it inhabits the uppermost intertidal zone. Discs of 20 mm diameter were cut from healthy and non-reproductive thalli, which were freed from all sorts of epiphytes and epizoons. They were kept at 5°C in artificial sea water medium (Table 2), made after a modification of Ohno (1976) having a salinity of 32.8 °/oo S and a pH of 7.5, and were cultured as reported earlier (Shameel, 1977a). After 2 weeks' adaptation the discs were kept in PVC tubes, 6.5 ml in volume, containing sea water medium with a particular oxygen concentration and were subjected to hydrostatic pressure of 600 atm for 5 hours. Three sets of experiments were conducted at 5°, 15° and 30°C. Immediately after release of pressure the rates of respiration and photosynthesis were measured in the air saturated artificial sea water at 5°C. The methods of pressure treatment and measurement of the rate of $O_2$ exchange were the same as described previously (Shameel, 1973). The Metric Convension has adopted $N/m^2$ as the standard unit for expressing hydrostatic pressure, but the author still considers the use of atm as the most suitable pressure unit in barobiology. The value 1.000 atm indicates the absolute pressure at sea level for dry air at 45° latitude at 15°C, and this definition has been used here and is recommended for future studies.

For the preparation of sea water with low oxygen concentration $N_2$ gas and for higher concentration $O_2$ gas was used. A big measuring cylinder was filled with artificial sea water, at the top 2 big corks were placed, which completely fitted the inner diameter

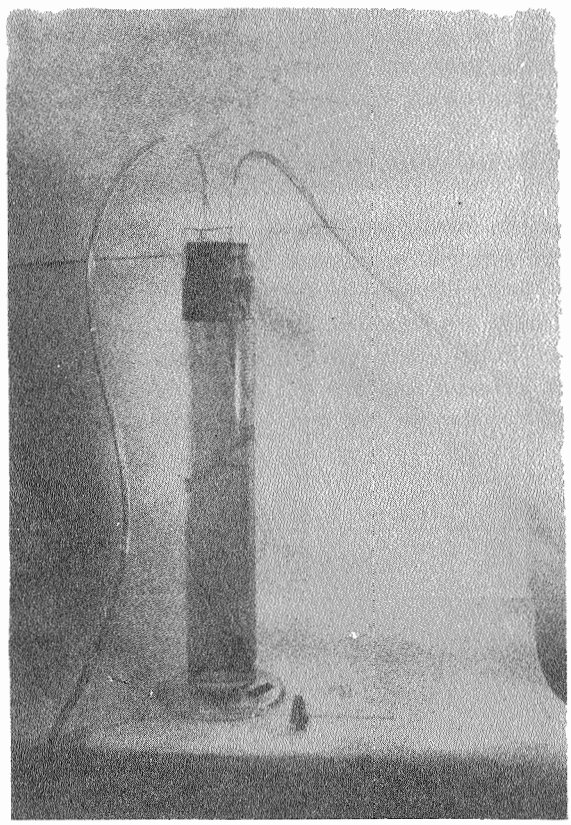

Fig. 1. Arrangement for the preparation of sea water with different $O_2$ concentrations.

of the cylinder but could still move up and down with the sliding of the water level (Fig. 1). The corks were painted from all sides with boat paint to avoid evaporation of water as well as to prevent gaseous exchange with the atmosphere. The corks were bored with two holes to pass 2 plastic tubings, one of which serving as the water outlet and the other was used to bubble $N_2$ or $O_2$ gas in order to get the desired decrease or increase in the $O_2$ concentration of sea water. By this method a particular $O_2$ concentration could be easily maintaned for at least 24 hours. The use of paraffin layer while bubbling gas above sea water level as advocated by Theede & Ponat (1970) has a great disadvantage of producing an emulsion of paraffin and water, which disturbs the measurement of the rates of respiration and photosynthesis. The $O_2$ content of the sea water was determined from the tables of Grasshoff (1976) in percent of air saturation at a particular temperature and salinity. The value 100 % oxygen saturation indicates the amount of $O_2$ dissolved in sea water of a particular salinity after equilibrium with atmospheric air of 100 % relative humidity, at 1 atm at a particular temperature. This definition has been used due to some practical considerations.

## Results and Discussion

The results obtained in terms of mg $O_2$ /g dry weight/ hour were compared with those of the controls and expressed in terms of control percentages. They were arithmetic means of 8 independent values; standard deviation was less than 5 % in each case.

1. Influences on the rate of respiration

With a decrease in the oxygen concentration of sea water the pressure influenced rate of respiration of the thalli of *Porphyra umbilicalis* decreased constantly (Fig. 2). There appears to be a direct relationship between $O_2$ supply of the outer medium and the rate of respiration under the influence of hydrostatic pressure. Gessner & Hammer (1962) observed that the leaf-blade of *Rhyncholacis macrocarpa* respires 5 - 10 times more than the thick leaf-stalk, and due to the lack of intercellular spaces in Podostemonaceae they concluded that the rate of $O_2$ diffusion acts as a reducing factor. Gessner

**TABLE 2. Composition of the artificial sea water.**

| No. | Salt added | Quantity/ l |
|---|---|---|
| 1 | $AlCl_3 . 6H_2O$ | 3.000 mg |
| 2 | $CaCl_2$ | 700.000 mg |
| 3 | $CuCl_2 . 6H_2O$ | 0.024 mg |
| 4 | $CuSO_4 . 5H_2O$ | 0.005 mg |
| 5 | EDTA-2Na | 6.000 mg |
| 6 | $FeCl_3 . 6H_2O$ | 0.772 mg |
| 7 | $H_3BO_3$ | 30.000 mg |
| 8 | KBr | 100.000 mg |
| 9 | KCl | 600.000 mg |
| 10 | $LiNO_3$ | 0.700 mg |
| 11 | $MgCl_2 . 6H_2O$ | 11.000 g |
| 12 | $MnCl_2 . 4H_2O$ | 0.864 mg |
| 13 | NaCl | 23.500 g |
| 14 | NaF | 3.000 mg |
| 15 | $NaHCO_3$ | 420.000 mg |
| 16 | $Na_2HPO_4 . 12H_2O$ | 10.000 mg |
| 17 | $Na_2MoO_4 . 2H_2O$ | 0.050 mg |
| 18 | $NaNO_3$ | 20.000 mg |
| 19 | $Na_2SO_4 . 10H_2O$ | 4.000 g |
| 20 | $SrCl_2 . 6H_2O$ | 40.000 mg |
| 21 | $ZnCl_2$ | 0.061 mg |

& Pannier (1958a, b) have shown that a proportional decrease in the relative rates of respiration appears in fresh water algae and marine plants with a decrease in $O_2$ tension, and the respiration of phytoplankton associations increases with the rising $O_2$ tension. Nath (1967), however, observed a direct proportionality between $O_2$ supply and $O_2$ utilization in different seaweeds. From all these observations it becomes evident that high hydrostatic pressure causes a quick diffusion of $O_2$ in the inner part of the thalli, due to which the rate of respiration increases with the rise of $O_2$ concentration in the outer medium.

The $O_2$ concentration of 30 % air saturation appeared to be very critical. If $O_2$ content of the sea water rose from this value the pressure affected rate of respiration increased from the control, and if $O_2$ concentration declined from this point the rate of respiration of the pressure treated thalli decreased from that of the control specimens (Fig. 2). It is probably due to the reason that the oxidation of certain very sensitive chemical groups of enzymes, proteins and other macromolecules increases with the abundance of oxygen and decreases with its deficiency. The substances which are sensitive towards $O_2$ are SH-enzymes, SH-containing co-enzymes and flavoproteins, lipids and ascorbic acid (Davies & Davies, 1965; Theede *et al.*, 1969).

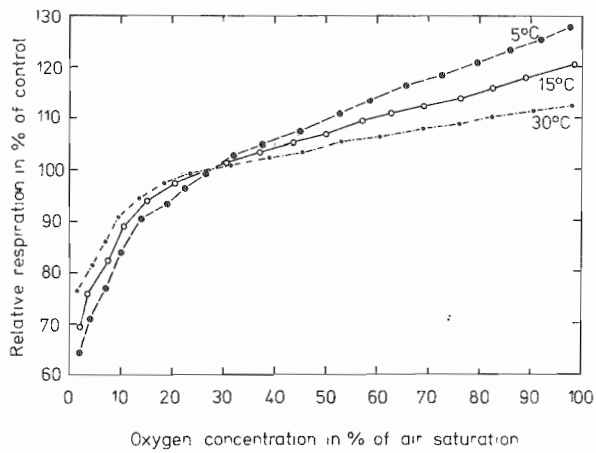


Fig. 2. Respiratory rate in *Porphyra umbilicalis* immediately after exposure to hydrostatic pressure of 600 atm for 5 hours at different temperatures and $O_2$ tensions lower than air saturation, measured in air saturated artificial sea water at 5°C.

It appears that at high hydrostatic pressure and high oxygen concentration the metabolism of the organism is disturbed. The increased rate of respiration of the pressure treated alga may be considered as an index of injury and disturbance in its metabolism. Therefore, greater the disturbance and injury higher would be the increase in the rate of respiration as compared with that of the control algae, which has been termed as "algal fever of respiration" (Shameel, 1973). As a matter of fact high hydrostatic pressure profoundly influences the rate of respiration in different seaweeds (Table 3). From these observations it may be conjectured that there exist two components of aerobic respira-

**TABLE 3. Influences of high hydrostatic pressure on respiratory rates observed in different groups of seaweeds.**

| Seaweed | Pressure (atm) | Duration (hour) | Observer |
|---|---|---|---|
| Chlorophyta: | | | |
| *Caulerpa prolifera* | 100 - 800 | 4 - 6 | Shameel, 1973 |
| *Ulva lactuca* | 50 - 800 | 5 | Fontaine, 1929 |
| *Ulva lactuca* | 10 - 800 | 5 - 10 | Shameel, 1973 |
| *Valonia macrophysa* | 100 - 800 | 6 | Shameel, 1973 |
| Phaeophyta: | | | |
| *Fucus vesiculosus* | 10 - 800 | 6 - 10 | Shameel, 1973 |
| *Laminaria saccharina* | 600 | 4 | Shameel, 1973 |
| Rhodophyta: | | | |
| *Delesseria sanguinea* | 10 - 800 | 1 - 10 | Shameel, 1973 |
| *Membranoptera alata* | 100 - 800 | 6 | Shameel, 1973 |
| *Phycodrys sinuosa* | 100 - 800 | 5 - 6 | Shameel, 1973 |

tion and one of them is more sensitive to hydrostatic pressure than the other. There is still a lack of understanding of effects of light on oxidative metabolism in photoautotrophic algal cells. More information is needed to explain this obscure but fundamental phenomenon. Detailed analytical investigations are required to clarify the pressure sensitivity of respiration.

### 2. Influences on the rate of photosynthesis

Respiration and photosynthesis are so closely linked that an ecofactor which influences one system exercises a remarkable effect on the other. Application of hydrostatic pressure affects photosynthesis in a way analogous to that of respiration. It was observed that the rate of apparent photosynthesis of pressure treated thalli of *Porphyra umbilicalis* gradually decreased with the declining oxygen concentration of sea water medium (Fig. 3). The influence of hydrostatic pressure appears to depend on the partial pressure of $O_2$ in the entire experimental range, and there seems to be a direct relation ship between $O_2$ supply of the outer medium and the rate of photosynthesis under the influence of pressure. The influence on the rate of photosynthesis was lesser than respiration, and the rate of photosynthesis of pressure treated algae at all the investigated $O_2$ concentrations remained lower than those of the control specimens. The photosynthesis of dinoflagellates has also been found to be reversibly inhibited at a pressure of upto 400 atm (Marchand, 1968). Decrease in photosynthesis indicates that high hydrostatic pressure not only causes the structural changes in the protoplasm but also affects and disturbs the normal course of metabolism.

High hydrostatic pressure directly affects photosynthesis and therefore different aspects of this process has been studied in several marine algae (Table 4). The measurement of absolute rate of photosynthesis has always been difficult and all the studies made were on apparent photosynthesis. It is usually assumed that respiration is independent of photosynthetic $O_2$ evolution. This assumption leads sometimes to quite erroneous results. The magnitude of a change in evolution of $O_2$ can not be known. Therefore, it is necessary to understand the effect of light on respiration during photosynthesis.

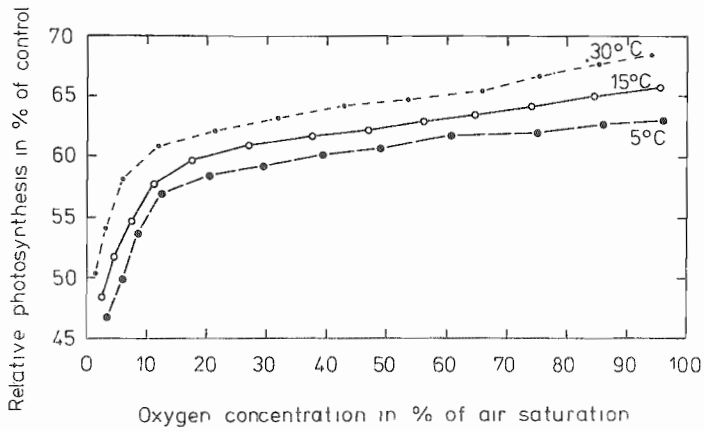


Fig. 3. Photosynthetic rate in *Porphyra umbilicalis* immediately after exposure to 600 atm pressure at different temperatures and $O_2$ tensions lower than air saturation, measured in air saturated artificial sea water at 5°C and 7000 lux light intensity.

The oxygen liberating process is less sensitive to hydrostatic pressure than steady-rate photosynthesis. It indicates that water splitting may be mainly a photochemical process as compared to the steady-rate limiting enzymatic dark reactions. Increased $O_2$ activity under pressure may also interfere with steady-rate $O_2$ evolution through a form of the Warburg effect (Vidaver, 1969). As a matter of fact the $O_2$ evolving systems of seaweeds remain unaffected by high hydrostatic pressure, the inhibition of $O_2$ evolution results from subsequent dark reactions.

3. Interrelationship of pressure and temperature

The parameters of hydrostatic pressure and temperature exhibit a very clear interrelation in their joint influences on the rates of respiration and photosynthesis under different $O_2$ tension (Figs. 2 & 3). Pressure effects are retarded by higher temperatures and intensified by lower ones; the changes produced in the rates of respiration and photosynthesis of pressure treated thalli of *Porphyra umbilicalis* are maximum at 5°C and minimum at 30°C. Similar observations regarding the antagonistic effects of temperature and hydrostatic pressure on different biological reactions have been made in different seaweeds (Shameel, 1978). In exhibiting pressure and temperature optima several seaweeds respond to the application of hydrostatic pressure in the same way as many other enzyme mediated biological processes (Shameel, 1974). Temperature generally tends to oppose the pressure inhibition and rise of pressure antagonises the inhibitory effect of high temperature.

TABLE 4. Influences of hydrostatic pressure observed on the different aspects of photosynthesis in marine algae.

| Photosynthetic reaction | Marine alga | Pressure (atm) | Duration (hour) | Observer |
|---|---|---|---|---|
| a-spike | *Porphyra perforata* | 70 - 1430 | – | Vidaver, 1969 |
| | *Ulva lobata* | 70 - 1430 | – | Vidaver, 1969 |
| $O_2$-gush | *Porphyra perforata* | 70 - 1430 | – | Vidaver, 1969 |
| | *Ulva lobata* | 70 - 1430 | – | Vidaver, 1969 |
| Photosynthetic energy transfer | *Porphyra perforata* | 1200 | – | Schreiber & Vidaver, 1973b |
| | *Ulva lobata* | 340 - 1020 | – | Chandler & Vidaver, 1971 |
| Photosynthetic enhancement | *Porphyra perforata* | 340 - 1160 | – | Vidaver, 1969 |
| | *Ulva lobata* | 535 | – | Vidaver & Chandler, 1969 |
| Photosanthetic rate | *Caulerpa prolifera* | 100 - 800 | 4 - 6 | Shameel, 1973 |
| | *Delesseria sanguinea* | 10 - 800 | 1 - 10 | Shameel, 1973 |
| | *Fucus vesiculosus* | 10 - 800 | 6 - 10 | Shameel, 1973 |
| | *Membranoptera alata* | 100 - 800 | 6 | Shameel, 1973 |
| | *Phycodrys sinuosa* | 100 - 800 | 5 - 6 | Shameel, 1973 |
| | *Ulva lactuca* | 10 - 800 | 5 - 10 | Shameel, 1973 |
| | *Valonia macrophysa* | 100 - 800 | 6 | Shameel, 1973 |
| Primary photosyn. processes | *Porphyra perforata* | 500 - 1400 | – | Schreiber & Vidaver, 1973a |
| | *Ulva lobata* | 400 - 1300 | – | Schreiber & Vidaver, 1973a |
| Steady oxygen evolution rate | *Porphyra perforata* | 170 - 1230 | – | Vidaver, 1969 |
| | *Ulva lobata* | 170 - 1230 | – | Vidaver, 1969 |

Reactions of different metabolic systems are not affected to the same extent by changes in pressure and temperature. It may be elaborated in the case of photosynthesis. Through the reduction of NADP and the esterification of ADP with inorganic $PO_4'''$ to form ATP the light energy is transformed to chemical energy, which is further incorporated in the biosynthesis of trioses:

$$\begin{aligned} \text{RuMP} + \text{ATP} &\rightleftharpoons \text{RuDP} + \text{ADP}^* \\ \text{RuDP} + \text{CO}_2 &\rightleftharpoons \text{PGA} \\ \text{PGA} + [\text{NADPH} + \text{H}^+] + \text{ATP} &\rightleftharpoons \text{C}_3\text{H}_6\text{O}_3 + \text{NADP} + \text{ADP} \end{aligned}$$

The $CO_2$ concentration, amount of RuMP available, rates of phosphorylation and NADP reduction are the factors influencing the above reactions. The $CO_2$ concentration at excess amount is not rate limiting. The rate of reactions of the pentose monophosphate shunt depends on ATP and NADPH + $H^+$ and determines the availability of RuMP (Metzner, 1973). Rate of photosynthesis is determined by the rates of NADP reduction and ADP esterification, when light is not in excess. In light saturation the photosynthetic rates are dependent on hydrostatic pressure as well as temperature, but light reactions are the major components of photosynthetic apparatus and are most likely to be affected by changes in hydrostatic pressure and temperature.

## 4. Interrelationship of pressure and $O_2$ tension

During the investigation of combined effects of pressure and temperature at $O_2$ concentrations lower than air saturation the 15°C temperature appeared to be intermediate and was selected for the study of the effects at $O_2$ concentrations higher than air saturation in combination with pressure. The results are shown in Fig. 4. Oxygen

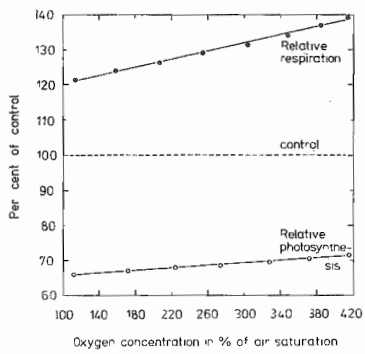


Fig. 4. Photosynthetic and respiratory rates in *Porphyra umbilicalis* immediately after exposure to hydrostatic pressure of 600 atm for 5 hours at 15°C and different $O_2$ tensions higher than air saturation, measured in air saturated artificial sea water at 5°C; photosyn. measurements under 7000 lux light intensity.

*PGA = phosphoglyceric acid, RuDP or RuMP = ribulose di- or mono-phosphate.

**TABLE 5. Combined effects of hydrostatic pressure and $O_2$ tension observed on different biological reactions of marine organisms.**

| Biological reaction | Marine organism | Pressure (atm) | Duration (hour) | Observer |
|---|---|---|---|---|
| Movement of cilia | *Cyprina islandica* | 700 | 1 | Theede & Ponat, 1970 |
| | *Mytilus edulis* | 700 | 1 | Theede & Ponat, 1970 |
| Pressure tolerance | *Cyprina islandica* | 300 - 900 | 1 | Schlieper, 1972 |
| Photosynthetic rate | *Ulva lactuca* | 600 | 5 | Shameel, 1973 |
| Respiratory rate | *Ulva lactuca* | 600 | 5 | Shameel, 1973 |
| Rate of survival | *Cyprina islandica* | 700 | 1 | Theede & Ponat, 1970 |
| | *Iodtea baltica* | 500 | 1 | Theede & Ponat, 1970 |

content of the outer medium appears to act antagonistically to the influences of pressure. Higher the $O_2$ concentration in percent of air saturation lesser is the effect of pressure on the rates of respiration and photosynthesis and *vice versa*. The $O_2$ concentration of 15 % air saturation appears to be another very critical point (Figs. 2 & 3). Below this value i.e. at very low $O_2$ contents the pressure effects are quite sever and the rates of respiration and photosynthesis decrease very sharply. This strong decrease in gas exchange is due to PGA which oxidizes NADPH + $H^+$ thereby reducing the PGA pool and oxidation of NADPH + $H^+$. The carboxylation of RuDP produces more PGA, which decreases RuMP concentration. ATP is essential for the maintenance of protoplasmic gel structures and the insufficient rate of ATP synthesis causes a decrease of pressure resistance.

Variations in $O_2$ tension exert a profound influence on the resistance to pressure by marine organisms. Correlation between pressure resistance and $O_2$ tension are of special significance in barobiology. Detailed analyses of the combined effects of these parameters have been made on different biological reactions (Table 5). Pressure resistance was found to decrease with the rising $O_2$ tension to about air saturation or higher, and the cellular pressure tolerance is lowest when the $O_2$ content of the sea water exceeds the normal air saturation equilibrium. The primary reason for this decrease of pressure resistance is oxidation and inhibition of SH-enzymes, fatty acid-CoA, SH-containing flavoproteins and lipids of cell membranes and ascorbic acid under high hydrostatic pressure (Haugard, 1968). Growth of microorganisms is inhibited and certain enzymes are inactivated by high pressure oxygen (ZoBell & Kim, 1972). The catalases, coenzymes, dehydrogenases, esterases, oxidases and other regulators or enzyme systems of marine organisms are highly susceptible to HPO (Shameel. 1975). More investigations on the biochemical aspects of this problem are badly needed.

## 5. Concluding remarks.

All types of chemical and biochemical reactions, which render volume changes, are strongly affected by hydrostatic pressure. This significant physico-chemical parameter of the hydrosphere, the largest biotope known, has had a role in the work of a few investigators of seaweed biology. The complex effects of pressure on the physiology in general and specifically on metablism of marine algae are far from understood. Hydrostatic pressure, like other physical parameters offers promise as a useful tool in the resolution of biosynthetic and physiological problems of seaweeds (Shameel, 1977b). Many of these problems have yet to be exploited very seriously and there is a considerable scope for seaweed biologists once the intial step has been taken. It is hoped that future studies would elaborate the usefulness of pressure application as a routine laboratory tool of research and an interest may be stimulated in other seaweed laboratories as well in order to render efforts in the study of this least investigated environmental parameter of our planet.

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