

NOTE

Oxygen conditions on surfaces of coralline red algae

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ABSTRACT: Oxygen profiles above coralline algal surfaces were measured with micro-electrodes. At flow velocities of 1 to 3 cm s⁻¹ in the mixed layer, the diffusive boundary layer was 0.1 to 0.2 mm on algae which were frequently grazed by limpets and chitons. It extended to 0.5 mm above surfaces on which a microbial film had developed after 16 d without grazing. When the mixed layer above grazed algae was not stirred the diffusive boundary layer reached 2.5 mm. The lowest O₂ concentration on the algal surface was 11 % of air saturation (*Lithothamnion* sp. dark, unstirred), and the highest concentration was 397 % of air saturation (*Lithothamnion*, light, unstirred). With a flow velocity of 1 to 3 cm s⁻¹ in the mixed layer, the corresponding range was 53 to 211 % of air saturation. The O₂ consumption rate was 0.8 mmol m⁻² h⁻¹. O₂ production rates at light saturation were 3.2 mmol m⁻² h⁻¹ (*Corallina* sp.) and 10.4 mmol m⁻² h⁻¹ (*Lithothamnion*). For a *Lithothamnion* sp. the compensation point was at 10 µmol quanta m⁻² s⁻¹, and the photosynthetic O₂ production was saturated at 50 to 100 µmol quanta m⁻² s⁻¹. The biofilm which developed in the absence of grazers increased the O₂ consumption of the surfaces, but no anaerobiosis was observed on coralline surfaces under any of the conditions tested.

Coralline algae (Rhodophyta, Corallinaceae) can be found in the photic subtidal of most rocky sea coasts (Johansen 1981). Despite their slow growth, corallines compete successfully for large proportions of the hard substratum under a wide variety of environmental conditions. Intensive grazing appears to be important for the prevention of overgrowth and thus for the long-term survival of coralline algae in many natural habitats (Steneck 1986). Limpets, chitons, abalone, sea urchins and finfish are among the herbivores capable of keeping the coralline surface clean.

The coralline algae provide food and shelter for the newly-settled larvae and juveniles of at least some of

their regular grazers, thus acting as their nursery ground (Garland et al. 1985). Coralline surfaces are uniquely able to induce the planktonic larvae of abalone (*Haliotis*) to settle and metamorphose (Morse & Morse 1984). There appear to be mutual benefits in the coralline-grazer association: grazers keep the corallines free from soft algal colonizers, and the corallines provide a suitable habitat for larval settlement.

The ecologically significant inducers of abalone larval settlement are organic substances which are often assumed to originate from the corallines (Morse & Morse 1984). However, coralline surfaces are colonized by bacteria, despite the frequent and intensive scouring (Lewis et al. 1985, Johnson et al. 1991). These bacteria may affect the larval settlement of abalone and possibly other grazers (e.g. sea urchins; Pearce & Scheibling 1990) by producing and/or degrading settlement-inducing molecules (Kaspar et al. 1989, Johnson et al. 1991).

The metabolism of newly-settled larvae, post-larvae, juveniles and microbial colonizers on the coralline surfaces is affected by the oxygen concentration in the diffusive boundary layer (DBL) between the surface and the mixed water above the surface (Revsbech & Jørgensen 1986). The oxygen concentration is the result of oxygen consumption and production rates by the algae/microbes/grazers community and of the diffusion rate across the DBL. This paper describes the oxygen conditions on the coralline surfaces as affected by respiration, photosynthesis, water movement and grazing.

Materials and methods. Fist-size stones which were colonized by coralline algae (*Lithothamnion* sp. and *Corallina* sp.), foliose red and brown algae and the associated fauna (e.g. chitons, limpets) were collected on 24 February and 3 March 1991 at 0.5 to 1.5 m depth

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from Limfjorden near the Rønbjerg field station of the University of Århus, Denmark. The stones were kept submerged in seawater and brought to the laboratory where they were placed in aquaria containing aerated seawater (27 ‰ salinity, 18 to 21 °C) and exposed to natural light fluctuations.

Oxygen measurements were started after a 2 wk adaptation period. Individual stones were placed in an aquarium under the same conditions as above. A micromanipulator was used to lower a microelectrode with guard cathode (Revsbech 1989) vertically onto the coralline surfaces. The signal was measured with a picoammeter and recorded with a strip chart recorder. Further details are given by Revsbech & Jørgensen (1986). Aeration at a constant rate provided for water flow velocities of 1 to 3 cm s⁻¹ and oxygen concentrations at equilibrium with air in the mixed layer near the electrode. The aquarium was wrapped in black plastic for dark incubations. A TCT-W Type FL fibreoptics light source (Lyngså, Saeby, Denmark) was used for light incubations. Light measurements were done with a Model LI-185A quantum photometer and a LI-190S quantum sensor (LI-COR Inc, Lincoln, Nebraska).

The effect of grazing was determined on a stone which was kept in a separate aquarium without grazers for 16 d before the first oxygen profiles were taken. Five limpets (1 to 2 cm diameter) were then placed on the stone overnight, and on the following day the measurements were repeated above areas of the surface which had been grazed clean by the limpets.

The diffusive boundary layer (DBL) was defined as the area between the coralline surface and the distance from this surface at which the oxygen concentration first reached equilibrium with air (Jørgensen & Revsbech 1985). The flux of oxygen through the DBL was calculated from the linear portion of the oxygen gradient, using Fick's first law of diffusion (Revsbech & Jørgensen 1986). The profiles were measured in at least 4 replicates within a few mm of each other. Standard deviations were less than 13 % of the mean for all measurements. They are given in Fig. 1 but left out for clarity in the other figures.

Results and discussion. Under dark and stirred conditions the oxygen concentration at 4 sites on a *Corallina* sp. surface was 93 to 98 % of air saturation. On a *Lithothamnion* sp. surface the range was 53 to 95 % when stirred and 11 to 69 % when unstirred (13 measurements). The lowest oxygen concentrations were at the bottom of conceptacles where the DBL was likely to be thickest (Jørgensen & Des Marais 1990).

The thickness of the DBL is a major controlling factor of the oxygen concentration on the coralline algal

surface. At water flow velocities of 1 to 3 cm s⁻¹ in the mixed layer the DBL was 0.1 to 0.2 mm (Figs. 1, 2 & 3). Under similar conditions, DBL thicknesses of 0.2 to >1 mm over sediments (Jørgensen & Revsbech 1985) and 0.16 to 0.59 mm over an algal mat (Jørgensen & Des Marais 1990) have been reported. The thinner DBL over corallines is not surprising in view of their smooth, well-defined surface which is normally kept free of colonizers by frequent grazing and sloughing of the epithallium (Johnson & Mann 1986, Steneck 1986). Under stirred conditions, the coralline surface provided for a relatively thin DBL and thus a small diffusive barrier. After stirring had been stopped, the DBL expanded to 2.5 mm (Fig. 2). On a *Lithothamnion* sp. surface which had not been grazed for 16 d the DBL extended to 0.5 mm due to the development of a biofilm consisting of detritus, microalgae, protozoans, nematodes and bacteria (Fig. 3).

The demand for oxygen by the coralline algae is the second important factor controlling the oxygen conditions on the algal surface. The O₂ uptake rate under stirred conditions was 0.8 mmol m⁻² h⁻¹ (calculated from 'dark', 'stirred' and 'after grazing' profiles in Figs. 1, 2 & 3 respectively). This compared with 0.1 mmol m⁻² h⁻¹ in a deep-sea sediment (Reimers & Smith 1986), 0.5 to 1.8 mmol m⁻² h⁻¹ in a saltmarsh (Schwinghamer et al. 1991), 1.1 to 3.8 mmol m⁻² h⁻¹ in coastal sediment (Hopkinson & Wetzel 1982, Revsbech & Jørgensen 1986) and 2.7 to 5.3 mmol m⁻² h⁻¹ in a microbial mat of a hypersaline pond (Revsbech et al. 1983). Thus, the coralline algae had a relatively low demand for oxygen.

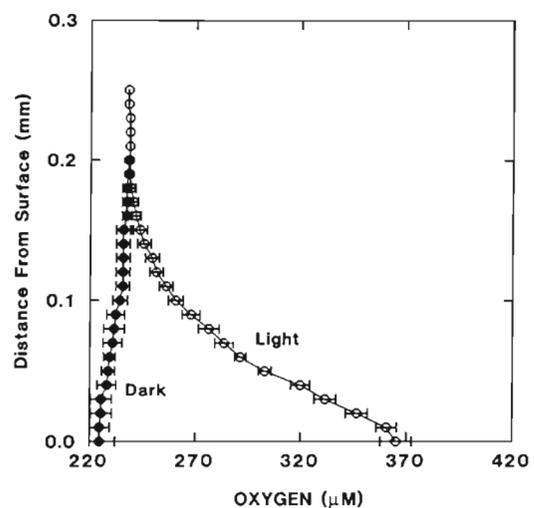


Fig. 1 Oxygen profiles above a *Lithothamnion* sp. surface under dark and light (100 µmol quanta m⁻² s⁻¹) conditions. This surface was frequently grazed by chitons and limpets. Each point represents mean of 5 measurements; bars indicate ± 1 SD

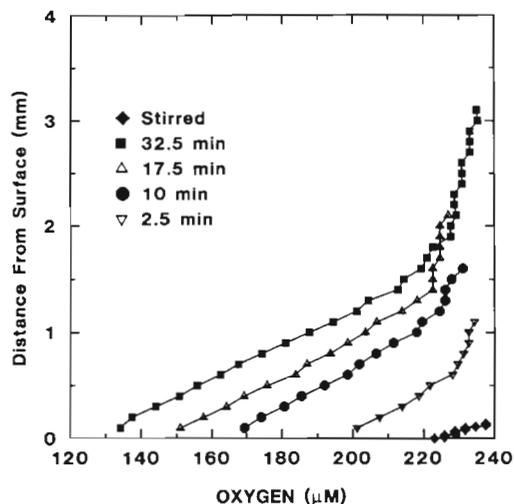


Fig. 2. Dark oxygen profiles in the DBL above a *Lithothamnion* sp. surface at various times after stirring was stopped. Each point represents 4 measurements. Profiles for 17.5 and 32.5 min are not significantly different

The low oxygen demand, together with a thin DBL, resulted in aerobic conditions on the naturally grazed algal surfaces as well as under conditions favouring oxygen depletion (higher experimental temperature than *in situ* temperature, no turbulence, increased biofilm thickness due to lack of grazing). The results suggest that small organisms (e.g. invertebrate larvae or bacteria) living in the DBL above the coralline surface may not require an anaerobic energy metabolism. However, it is conceivable that invertebrate larvae, whose diameter is similar to that of conceptacles and the thickness of the DBL, come under oxygen stress in sheltered pockets such as conceptacles.

Incubation of the corallines under light caused the oxygen concentration to increase above the equilibrium with air (Fig. 1). At light saturation, surface oxygen concentrations at 10 sites above a *Lithothamnion* sp. were 119 to 211 % (stirred) and 245 to 397 % (unstirred) of air saturation. The highest oxygen concentrations were above young vegetative tissue near the fringes of thalli. The net oxygen production calculated from the profile in Fig. 1 was $10.4 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$. Under similar conditions, a *Corallina* sp. produced oxygen at $3.2 \text{ mmol m}^{-2} \text{ h}^{-1}$. Wanders (1976) measured 4.7 to $10.6 \text{ mmol m}^{-2} \text{ h}^{-1}$ for coralline crusts and $20 \text{ mmol m}^{-2} \text{ h}^{-1}$ for a dense foliose algal turf. A cyanobacterial mat produced oxygen at $37 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Revsbech & Jørgensen 1986). For a eucaryotic algal mat $47 \text{ mmol m}^{-2} \text{ h}^{-1}$ has been reported (Revsbech & Ward 1983). Our results confirm the relatively low photosynthetic oxygen production by corallines. Despite their slow growth, corallines are widespread and often dominate the

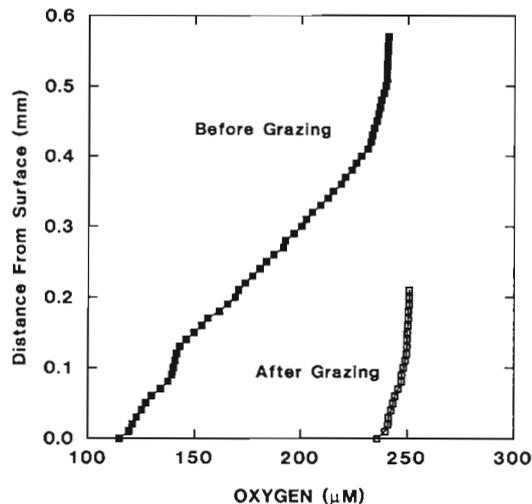


Fig. 3. Dark oxygen profiles in the DBL above a *Lithothamnion* sp. surface before and after grazing of the biofilm which had developed over a 16 d period during which grazers (limpets) had been removed. Each point represents the mean of 5 measurements

subtidal vegetation (Johansen 1981). Their success may depend largely on the frequent sloughing of their surface (Johnson & Mann 1986) and the grazing by a range of invertebrates whose larvae settle preferentially on corallines (see Johnson et al. 1991, Steneck 1986).

The *Lithothamnion* sp. used in this work had a compensation point of $10 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$, and its photosynthetic oxygen production reached light saturation between 50 and $100 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ (Fig. 4). These results are similar to those reported for other corallines adapted to low light and temperatures (Adey 1973).

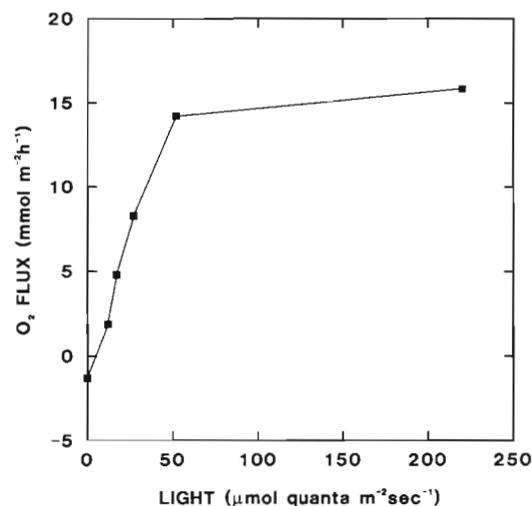


Fig. 4. Oxygen flux across the DBL above a *Lithothamnion* sp. surface at various light intensities

A biofilm developed on the coralline surface within a short time after the grazers had been removed (Figs. 1 & 3). Such a biofilm may prevent the physical contact necessary between invertebrate larvae and the settlement inducers on coralline surfaces (Morse & Morse 1984), or it may alter the postulated role of bacteria in larval settlement. Due to the extended diffusional barrier it may also lead to an increased concentration of soluble settlement inducers near the surface. The testing of such hypotheses will provide further insight into the interactions between invertebrate larvae and their preferred settlement substrata and produce valuable knowledge for the hatchery-based rearing of juveniles.

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LITERATURE CITED

- Adey, W. H. (1973). Temperature control of reproduction and productivity in a subarctic coralline alga. *Phycologia* 12: 111-118
- Garland, C. D., Cooke, S. L., Grant, J. F., McMeekin, T. A. (1985). Ingestion of the bacteria on and the cuticle of crustose (non-articulated) coralline algae by post-larval and juvenile abalone (*Haliotis ruber* Leach) from Tasmanian waters. *J. exp. mar. Biol. Ecol.* 91: 137-149
- Hopkinson, C. S., Wetzel, R. L. (1982). In situ measurements of nutrient and oxygen fluxes in a coastal marine benthic community. *Mar. Ecol. Prog. Ser.* 10: 29-35
- Johansen, H. W. (1981). Coralline algae, a first synthesis. CRC Press, Boca Raton
- Johnson, C. R., Muir, D. G., Reysenbach, A. L. (1991). Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* 74: 281-294
- Johnson, C. R., Mann, K. H. (1986). The crustose coralline alga, *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *J. exp. mar. Biol. Ecol.* 96: 127-146
- Jørgensen, B. B., Revsbech, N. P. (1985). Diffusive boundary layers and the oxygen uptake of sediments and detritus. *Limnol. Oceanogr.* 30: 111-122
- Jørgensen, B. B., Des Marais, D. J. (1990). The diffusive boundary layer of sediments: oxygen microgradients over a microbial mat. *Limnol. Oceanogr.* 35: 1343-1355
- Kaspar, H. F., Mountfort, D. O., Pybus, V., Gillespie, P. A. (1989). Degradation of gamma-aminobutyric acid by marine bacteria. In: Miyachi, S., Karube, I., Ishida, Y. (eds.) Current topics in marine biotechnology. The Japanese Society for Marine Biotechnology, Tokyo, p. 421-422
- Lewis, T. E., Garland, C. D., McMeekin, T. A. (1985). The bacterial biota on crustose (nonarticulated) coralline algae from Tasmanian waters. *Microb. Ecol.* 11: 221-230
- Morse, A. N. C., Morse, D. E. (1984). Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. *J. exp. mar. Biol. Ecol.* 75: 191-215
- Pearce, C. M., Scheibling, R. E. (1990). Induction of metamorphosis of larvae of the green sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. *Biol. Bull. mar. biol. Lab., Woods Hole* 179: 304-311
- Reimers, C. E., Smith, K. L. Jr (1986). Reconciling measured and predicted fluxes of oxygen across the deep sea sediment-water interface. *Limnol. Oceanogr.* 31: 305-318
- Revsbech, N. P. (1989). An oxygen microelectrode with a guard cathode. *Limnol. Oceanogr.* 34: 474-478
- Revsbech, N. P., Jørgensen, B. B. (1986). Microelectrodes: their use in microbial ecology. In: Marshall, K. C. (ed.) Advances in microbial ecology, Vol. IX. Plenum, New York, p. 293-352
- Revsbech, N. P., Jørgensen, B. B., Blackburn, T. H., Cohen, Y. (1983). Microelectrode studies of the photosynthesis and O₂, H₂S, and pH profiles of a microbial mat. *Limnol. Oceanogr.* 28: 1062-1074
- Revsbech, N. P., Ward, D. M. (1983). Oxygen microelectrode that is insensitive to medium chemical composition: use in an acid microbial mat dominated by *Cyanidium caldarium*. *Appl. environ. Microbiol.* 45: 755-759
- Schwinghamer, P., Kepkay, P. E., Foda, A. (1991). Oxygen flux and community biomass structure associated with benthic photosynthesis and detritus deposition. *J. exp. mar. Biol. Ecol.* 147: 9-35
- Steneck, R. S. (1986). The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Ann. Rev. Ecol. Syst.* 17: 273-303
- Wanders, J. B. W. (1976). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: Primary productivity in the coral reef. *Aquat. Bot.* 2: 235-270

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