

## NOTE

## Microclimate of the brown alga *Feldmannia caespitula* interstitium under zero-flow conditions

Martina Pöhn, Kay Vopel\*, Eva Grünberger, Jörg Ott

Department of Marine Biology, Institute of Ecology and Conservation Biology, University of Vienna, Althanstr. 14, 1090 Vienna, Austria

**ABSTRACT:** The microclimate of the brown alga *Feldmannia caespitula* (J. Agardh) Knoepffler-Péguy interstitium was studied using microelectrode techniques. Zero water flow and irradiances of 170 and 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  cause steep  $\text{O}_2$  gradients peaking 3 to 4 mm below the outer surface of the tufts at 310 and 506% atmospheric saturation, respectively. The mean fluxes of  $\text{O}_2$  from the interstitium to the surrounding bulk water were  $87 \pm 21$  and  $262 \pm 68 \text{ nmol cm}^{-2} \text{h}^{-1}$  at low and high quantum flux density. Except for the outer 2 to 4 mm thick margin, the alga interstitium became anoxic within 52 min after abrupt darkening. The rate of dark oxygen uptake was  $52 \pm 5 \text{ nmol cm}^{-2} \text{h}^{-1}$ . The tufts were populated by 9 metazoan taxa: nematodes, harpacticoid copepods, ostracods, gastropods, bivalves, polychaetes, amphipods, isopods and halacarids. Our results suggest that the interstitium of fine-textured algal thalli is a microhabitat of variable water chemistry with temporary anoxia and hyperoxia in an otherwise relatively stable water column. Although the tufts are attractive for meiofauna by providing food and protection from currents and predators, rapid fluctuations in oxygen concentration probably cue temporal emigration of the algal infauna.

**KEY WORDS:** Phytal · *Feldmannia caespitula* · Micro-environment · Meiofauna · Oxygen concentration gradients · Oxygen deficiency

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Submerged macrophytes and epiphytic algae are usually populated by a diverse meiofauna whose abundance and composition is a function of the size, physiognomy, and distribution of the macrophytes and algae (Wieser 1959, Hagerman 1966, Ott 1967, Whatley & Wall 1975, Gunnill 1982). A more complex physiognomic structure correlates with higher abundance of the associated fauna (Hicks 1985, Hall & Bell 1988, Gee & Warwick 1994, Hull 1997). Finely structured epiphytic algae offer protection from currents, wave action, solar

irradiance, desiccation and fish or invertebrate predators (Hicks 1980, Coull & Wells 1983). They also supply food to meiofauna by providing attachment sites for microbiota or by enhancing accumulation of sediment and detritus (Lewis & Hollingworth 1982, Johnson & Scheibling 1987, Jarvis & Seed 1996). The colonisation of a structurally complex alga by meiofauna should not only depend on the alga's physiognomy, but also on chemical properties of the microhabitat. Water movement in the interstitium of fine-textured species decreases with increasing distance from the outer surface (Ott 1967) and, therefore, molecular diffusion rather than turbulence may dominate the distribution and transport of chemical constituents. Here we report on the variability of biochemical gradients in tufts of *Feldmannia caespitula* (J. Agardh) Knoepffler-Péguy under zero-flow and different light conditions.

**Material and method.** The study was carried out in a sheltered bay in the Gulf of Calvi (west coast of Corsica, France) in late September 1999. The upper sublittoral of the granitic rocky coast was covered with various algae, e.g. the red alga *Corallina* sp. (Coraliniaceae), the green alga *Cladophora prolifera* (Roth) Kützing 1843 (Cladophoraceae), and the brown alga *Feldmannia caespitula* (Ectocarpaceae). The latter alga grows in tufts (2 cm high) consisting of rarely branched filaments, which distally terminate in 1 to 2  $\mu\text{m}$  long colourless hairs (see also Knoepffler-Péguy 1970). *In situ* quantum flux density varied between 200 and 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  at a water depth of 1 m. The water temperature was about 25°C and the salinity ranged from 38 to 39. Detailed descriptions of the site and further information regarding wind and water currents are available from Bay (1984) and Djenedi (1985).

Four tufts of *Feldmannia caespitula* were collected by snorkelling from a rocky shore about 50 m from the scientific research station STARESO in 0.5 m water depth. The algae were stored in an outdoor

\*Corresponding author. Present address: Alfred Wegener Institute for Polar and Marine Research, Columbus Center, 27568 Bremerhaven, Germany.  
E-mail: kvopel@awi-bremerhaven.de

aquarium for 1 h, thereafter transferred to a laboratory aquarium (water temperature was 25 to 26°C, salinity 39) and illuminated at incident irradiances of 170 or 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for at least 1 h before and during measurements. Light intensities were measured with an underwater quantum irradiance sensor (UWQ-3486, Li-Cor, USA) connected to a DataLogger (LI-1000). The light source (Schott KL 1500) was positioned at an angle of 60° relative to the water surface. Different light intensities were obtained by varying the distance between light source and water surface.

Multiple oxygen microprofiles were recorded along the vertical axes of the tufts using microelectrodes (ME 11025, MasCom, Germany) attached to a motor-driven micromanipulator (Märzhäuser, Germany) and secured to a stable iron frame. The sensors, with a tip diameter of <10  $\mu\text{m}$  and a response time of <2 s, were positioned perpendicular to the water surface and moved vertically in 200  $\mu\text{m}$  increments over a distance of 1 cm. The tip of the sensor was placed at the outer surface of the tuft, which served as the reference depth for vertical positioning. The position of the sensor tip was observed by means of a dissecting microscope. The sensor current, measured by a miniaturised picoampere meter mounted directly on the shaft of the microsensors (MasCom GmbH, Germany), was converted to a mV signal using a 2 channel-indication-amplifier and digitised by an analogue-to-digital converter (DI 220, Dataq Instruments, Inc., USA) for PC data acquisition. The sensors were calibrated at 25°C (experimental temperature), using the output current in the overlying water and in nitrogen-flushed water for air saturation and zero oxygen, respectively. Redox potential was measured with a redox microelectrode (ME 14000, MasCom, Germany; tip diameter <20  $\mu\text{m}$ ) and a calomel reference electrode (REF 401, Radiometer Copenhagen, Denmark). The performance of the redox microelectrode was checked using a Redox Buffer Solution (DIN 38404, Mettler Toledo, Germany).

Areal net photosynthesis is equal to the diffusive oxygen fluxes out of the photosynthetic part of the tuft (Jensen & Revsbech 1989). Total respiration in the dark is defined as the diffusional  $\text{O}_2$  flux into the algae. The fluxes,  $J(x)$ , were calculated from the steady-state  $\text{O}_2$  profiles by Fick's first law of diffusion (Revsbech & Jørgensen 1986):  $J(x) = D_0 \times dC/dx$ , where  $dC/dx$  is the slope of the  $\text{O}_2$  profile at depth  $x$ , and  $D_0$  is the molecular diffusion coefficient of  $\text{O}_2$  in the water. In our case  $D_0 = 2.242$  and  $2.299 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$  at 25 and 26°C, respectively (Broecker & Peng 1974). The concentration gradients were estimated from the linear part of the oxygen gradient nearest the tuft-water interface. All values are given as means  $\pm$  standard deviation.

For faunistic analyses a total of 10 algae tufts (mean volume: 2.5  $\text{cm}^3$ ) were collected at noon by slipping a

plastic bag over the algae. After 2 h storage in an aquarium outdoors, 5 tufts were transferred to a 4% formaldehyde seawater solution; the other 5 tufts were fixed 2 h after sunset. The tufts were washed, the water was sieved through a 63  $\mu\text{m}$  mesh, and the metazoans were sorted quantitatively and identified under a dissecting microscope (maximal 16 $\times$  magnification).

**Results and discussion.** The concentration of oxygen in the interstitial water of *Feldmannia caespitula* tufts changed with quantum flux intensities and distance from the outer surface of the alga ('relative depth' along the vertical axes of the tufts). Zero-flow conditions and constant illumination result in steep  $[\text{O}_2]$  gradients based on the steady state of oxygenic photosynthesis, molecular diffusion, and respiration of the alga and associated bacteria and meiofauna. A quantum flux of 170 (Figs. 1 & 2A) and 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 3A) caused an oxygen supersaturation of the interstitium with maximum concentrations of ca 310 and 506% atmospheric saturation at relative depths of ~3.6 and 2.8 mm, respectively. During illumination, oxygen diffuses from the outer margin of the tufts to the surrounding water and to the inner part of the alga, where concentrations decreased to atmospheric saturation values at a relative depth of about 8 mm (Fig. 3A). The rates of areal net photosynthesis amounted to  $86.8 \pm 21.1$  and  $262.0 \pm 68.4 \text{ nmol cm}^{-2} \text{ h}^{-1}$  at a light intensity of 170 and 1500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively. During darkness, oxygen diffuses from surrounding bulk water to the outer 2 to 4 mm thick margin of the tufts at a rate of  $52.1 \pm 5.0 \text{ nmol cm}^{-2} \text{ h}^{-1}$ . The

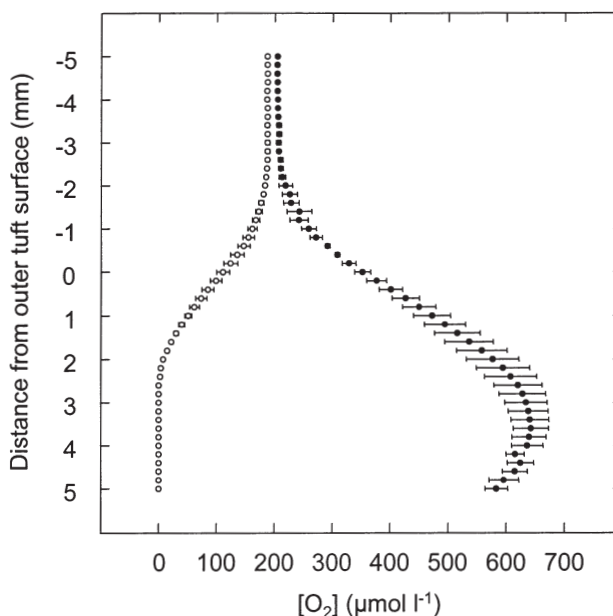


Fig. 1. Average steady-state  $[\text{O}_2]$  profile (means  $\pm$  SD,  $n = 5$ ) in the interstitium of a *Feldmannia caespitula* tuft incubated at quantum flux of 170  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (●) and darkness (○)

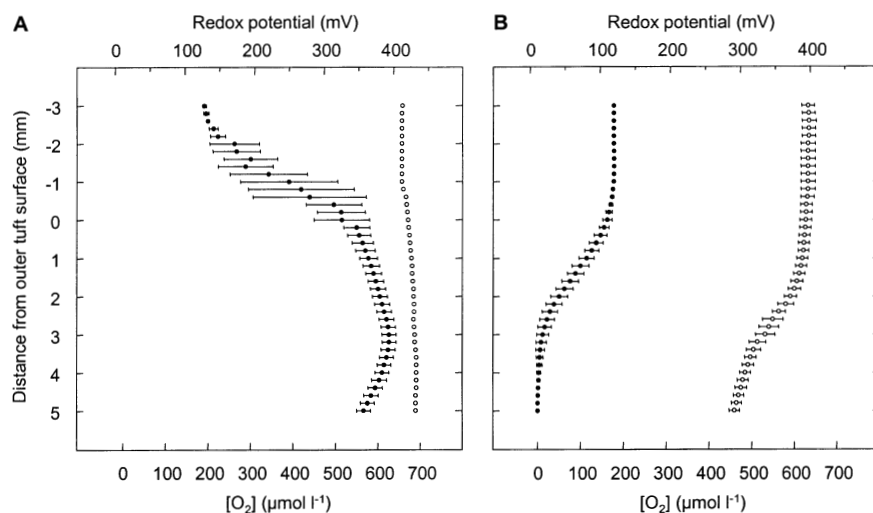


Fig. 2. Average steady-state gradient of  $[O_2]$  (●) and redox potential (○) (means  $\pm$  SD,  $n = 4$ ) in a *Feldmannia caespitula* tuft incubated in (A) light ( $170 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and (B) dark

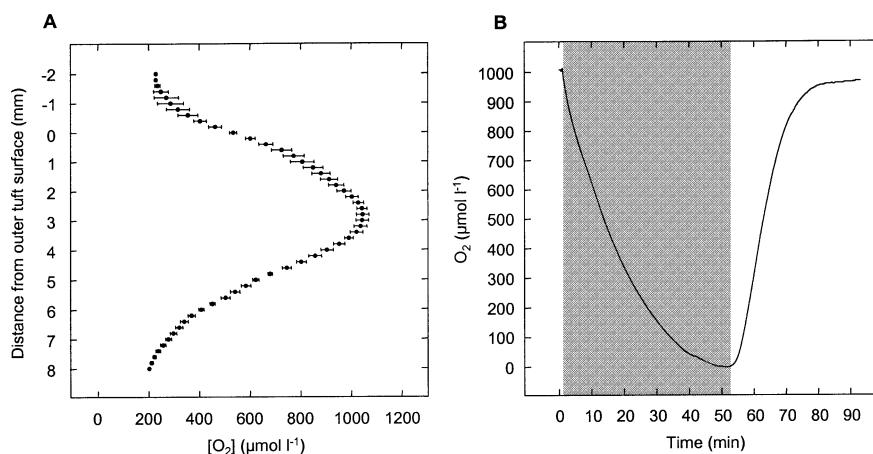


Fig. 3. (A) Average steady-state profile of  $[O_2]$  (means  $\pm$  SD,  $n = 4$ ) in the interstitium of a *Feldmannia caespitula* tuft incubated at a quantum flux density of  $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and (B)  $[O_2]$  at 3.4 mm below the outer surface as a function of time during instantaneous light-dark and dark-light shifts

redox potential of the interstitial water remained constant at about +415 mV down to 0.8 mm above the outer edge of the algae and at +432 mV downwards (Fig. 2A); during darkness the values dropped to +292 mV at 5 mm relative depth (Fig. 2B). Continuous recordings during an instantaneous light/dark shift showed that the oxygen content of the interstitial water 3.4 mm below the outer surface (Fig. 3A) decreased from 480% atmospheric saturation to zero values within 52 min (Fig. 3B). Original conditions were restored 37 min after the light was switched on again. Oxidised conditions were not replaced by reduced conditions as usually happens in many shallow-water sedimentary systems. There is, however, a potential for reduced

conditions and probably for the occurrence of sulphide: minimal redox values of  $-366 \text{ mV}$  were measured in the interstitial water of the most inner part of the tufts after more than 10 h incubation in stagnant water at daylight (Fig. 4).

Nine metazoan taxa populate the algal interstitium: nematodes, harpacticoid copepods, polychaetes, ostracods, gastropods, bivalves, amphipods, halacarids and isopods. Pooled samples taken during the day and at night (5 tufts each) yielded a total of 157 and 88 individuals, respectively. Nematodes, harpacticoid copepods and polychaetes averaged 89% (day) and 77% (night) of total metazoan abundance (Table 1). Harpacticoids amounted up to 91% of the arthropods. Gammarids, isopods and halacarids were only found during the day.

The shape and the dynamics of the  $[O_2]$  profiles resemble those found in shallow-water sedimentary systems, where microalgae and cyanobacteria mainly contribute to the benthic oxygen production (Revsbech et al. 1980). The transport of oxygen between the alga interstitium and the surrounding bulk water was limited by molecular diffusion across a diffusive boundary layer (DBL) which extended 1.3 mm above the outer surface of the tufts (calculated from gradients shown in Figs. 1–3). The thickness is in accordance with values calculated for marine sedi-

ments (Revsbech & Jørgensen 1983). Here high oxygen saturation values are also restricted to a thin subsurface layer and the maximum penetration depth of oxygen usually varies with the intensity of incident light (Revsbech et al. 1980, Epping & Jørgensen 1996). In *Feldmannia caespitula* tufts the rates of areal net photosynthesis are much lower, and total dark respiration is higher compared to values estimated for shallow water sediments (Revsbech et al. 1981, Jensen & Revsbech 1989, Epping & Jørgensen 1996). The alga infauna may contribute to the transport of oxygen between the interstitium and the surrounding water by creating turbulence. A single copepod swimming close to the outer margin of the tuft, for example, caused small-scale vari-

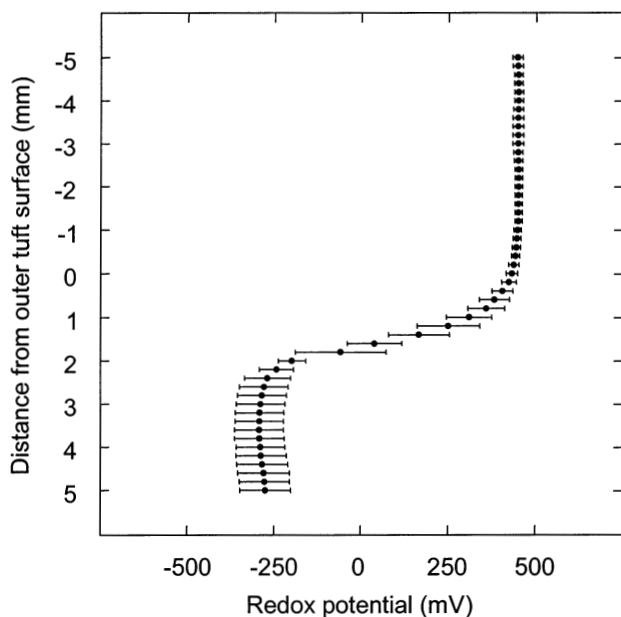


Fig. 4. Average steady-state gradient (means  $\pm$  SD,  $n = 3$ ) of redox potential in a *Feldmannia caespitula* tuft interstitium in darkness. Prior to the measurement the alga was incubated for 10 h in stagnant water at daylight

Table 1. Abundance of metazoan taxa found in *Feldmannia caespitula* tufts during day and night (pooled data from 5 tufts in each case). The mean volume of a tuft was  $2.5 \text{ cm}^3$

Metazoan taxa	Abundance (ind./5 tufts)	
	Day	Night
Nematoda	43	26
Bivalvia	4	2
Gastropoda	4	4
Polychaeta Errantia	49	22
Polychaeta Sedentaria	7	4
Harpacticoida	40	28
Ostracoda	4	2
Gammaridae	3	0
Isopoda	1	0
Acari	2	0
Total fauna	157	88

ability of replicate measurements, as shown by higher standard deviations of mean concentration values in Fig. 2A, but did not affect the alga interstitium. Similar fluctuations have been observed in the water immediately above the sediment surface due to local disturbance by faunal activity (Revsbech et al. 1980).

Atilla & Fleeger (2000) used different artificial substrates to underline the importance of structural complexity in the colonisation of phytal habitats. The relationship between associated fauna and algae, however, is not only attributed to factors associated with

the physiognomy of the algae, but also to their biological activity as well as the chemical characteristics of the microhabitat. The tuft-like thalli of *Feldmannia caespitula*, despite a small volume of about  $2.5 \text{ cm}^3$ , clearly offer living space of high complexity. Dense filaments provide protection from predation and currents and reduce the flow. Sterile trichomes, which overtop the alga's surface, increase this effect. Reduced flow contributes to particle settlement and thus supports the accumulation of food. For these reasons the algae attract meiofauna in an environment surrounded by rough wave action and rocks. Oxygen deficiency during darkness, on the other hand, can make the interstitium unattractive for invertebrates. Animals are forced to move to the outer parts, where competition increases, or even enter the pelagic realm. Oxygen supersaturation, as measured in at least 70% of the alga tufts during illumination, is another critical factor and probably a cue for animal migration. High  $[\text{O}_2]$  combined with UV-radiation may lead to the production of  $\text{H}_2\text{O}_2$ , which is also known to reduce the aerobic metabolism of marine invertebrates (Abele-Oeschger et al. 1994, 1997).

Our microelectrode measurements show the oxygen concentrations along the vertical axes of the tufts and, therefore, are not suitable for a reconstruction of a 3-D distribution of oxygen. A 3-D picture of oxygen concentration, however, would be necessary to prove whether or not the rate of photosynthesis in the outer margin of the basal parts is affected by light absorption and shading, which would allow horizontal migration of meiofauna without the need to pass the oxygen supersaturated upper boundary.

Previous studies have shown that the phytal, benthic and pelagic zones should not be considered as separate entities since they continually share components (Hicks 1986, Walters & Bell 1986, Walters 1988). Migration is one mechanism for this interaction and influences the structure of the populations in the different habitats. Migrating fauna in shallow-water areas move a significant amount of energy from the benthic to the pelagic realm and increase the exchange of nutrients (Walters & Bell 1986). Light is presumed to be the dominant environmental factor of meiofauna migration (Cronin 1982), and the relative change of light intensity is probably the stimulus for migration in copepods (Forward et al. 1984, Stearns & Forward 1984). Light also changes the water chemistry in the phytal zone, where the oxygen content depends on photosynthetic activity. Water chemistry has until now only been considered to influence migration and distribution in sediments (Meyers et al. 1987), whereas it has been largely neglected in the phytal zone.

Although our pooled data are not suitable to prove significant differences in abundance during day and

night, a lower total number of nematodes, harpacticoid copepods and polychaetes in the samples taken 2 h after sunset does provide an indication for nocturnal migration. Future experiments on the chemotactic response of the meiofauna can provide conclusive evidence for the hypothesis of chemical control of meiofauna migration.

The rapid response measured under zero-flow conditions suggests that the tufts of *Feldmannia caespitula* are islands of high variability in [O<sub>2</sub>] (anoxia and hyperoxia) within an otherwise relatively stable water column. We are aware that the zero-flow conditions are unrealistic and extremes of anoxia and hyperoxia may not occur in nature. It has, however, been demonstrated that even coarsely branched algae reduce water movement by at least 2 orders of magnitude (Ott 1967). Within dense algal growth in protected bays conditions may approach those simulated in our experiments, with amplitudes of oxygen concentrations greatly exceeding those in the ambient water. This structurally complex habitat offers some advantages (i.e. protection against predators, food) for associated meiofauna, but the respiratory microenvironment (steep and rapid changing gradients) means an unpredictable stress.

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