# OXYGEN MICROENVIRONMENT OF CORALLINE ALGAL TUFTS AND THEIR ASSOCIATED EPIPHYTIC ANIMALS

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ABSTRACT

Separate subhabitats are distinguishable in tufts of *Corallina officinalis*, including the surface of the algae itself and the interspace (areas of water) within the algal tufts. The oxygen microenvironment of each of these was investigated in laboratory investigations using oxygen microelectrodes to test the hypothesis that oxygen gradients form adjacent to the seaweed surface and that the oxygen concentration of the seawater between the branches of individual plants differs from that of the surrounding water body due the tuft forming nature of this seaweed. Regions of hyperoxia (up to 250% of saturation) were detected at the surface of *Corallina* branches in static conditions, with steep declining gradients of oxygen concentration through the diffusive boundary layer in the vertical plane to 100% of saturation a distance almost 2mm from the surface. Oxygen concentration at the surface did not vary with position along individual branches, or with position on any one branch segment. Concentrations were significantly higher on main branches than on peripheral branches of individual plants. Water flow was the dominant factor controlling the depth and oxygen supply of diffusive boundary layers and in moving water oxygen levels did not achieve such high saturation levels and the boundary layer was thinner. On a larger scale, oxygen concentrations in the interspace of *C. officinalis* tufts were highly variable and commonly in excess of air saturation. The oxygen environment was both temporally and spatially dynamic, and very rapid changes in oxygen concentration were observed in response to changing flow conditions. Despite the ranges of oxygen concentrations, and often hyperoxic conditions described, a thriving epiphytic community of animals smaller than 2mm, dominated by harpacticoid copepods and marine mites is associated with this extreme and dynamic environment.

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Cite as follows: Irwin, Sandra and Davenport, John 2010 Oxygen microenvironment of coralline algal tufts and their associated epiphytic animals. *Biology and Environment: Proceedings of the Royal Irish Academy* **110**B, 185–193. DOI: 10.3318/BIOE.2010.110.3.185.

Received 20 January 2010. Accepted 23 February 2010. Published 22 November 2010.

## INTRODUCTION

Diffusive boundary layers are defined as 'the distance from the surface to where the concentration of the dissolved substance is ±10% of the concentration in the ambient medium' (Jørgensen and Des Marais 1990), and are commonly of the order of a few millimetres in thickness. These have been widely studied at the sediment–water interface in aquatic systems (Jørgensen and Des Marais 1990; Wenzhöfer *et al.* 2001; Røy *et al.* 2002; Roberts and McMinn 2004) and to a lesser extent at the interface of water and other structures (Searcy-Bernal 1996; Shashar *et al.* 1996; Røy *et al.* 2002; Hurd *et al.* 2006).

Kaspar (1992) reported on oxygen conditions on surfaces of encrusting coralline algae, and demonstrated that the thickness of the diffusive boundary layer was between 0.2mm and 2.5mm and was affected by the presence of a surface biofilm and prevailing flow conditions. Diffusive boundary layers have also been described around algal tufts and colony-forming marine algae, where oxygen concentrations within the colony differ from those in the surrounding water body (Ploug *et al.* 1999; Pöhn *et al.* 2001). Oxygen gradients within diffusive boundary layers around marine seaweeds are supplied by local photosynthesis and respiration (Kohler-Rink and Kühl 2000; Pöhn *et al.* 2001). Although marine algae live in extremes of light exposure, in tuft-forming species effective light exposure may be reduced in all but the uppermost branches of dense canopies of macroalgae through self-shading, which causes photosynthetic rate to decrease with increasing depth through tufts of macroalgae (Vergara *et al.* 1998), making these an interesting group to study.

The calcareous red alga *Corallina officinalis*, common in intertidal pools of Irish coastal shores, forms dense tufts of fronds that are sensitive to desiccation and thrives in crevices and pools on exposed shores. Due to their structural complexity, coralline algae offer particularly good refuge from predation and desiccation (Coull and Wells

1983; Davenport *et al.* 1999). *C. officinalis* provides food and protection to a diverse community of invertebrates including amphipods, isopods, bryozoans, polychaetes, copepods, ostracods and foraminifers (Dommasnes 1968; Goss-Custard *et al.* 1979; Hicks and Coull 1983; Grahame and Hanna 1989; Hull 1997). The polychaete *Spirorbis corallinae* is also found, almost exclusively, on this alga (Goss-Custard *et al.* 1979; Crisp and Mwaiseje 1989).

Faunal species associated with *C. officinalis* vary in their ability to withstand extremes of oxygen. Hypoxia tolerance has been extensively investigated in marine invertebrates, while tolerance to hyperoxia has received considerably less attention (McMahon and Russel-Hunter 1978). Hypoxia-tolerance is species-specific, and although it transcends taxonomic categories (Mangum and Van Winkle 1973), it generally follows the order foraminifers > bivalves > polychaetes > crustaceans, with some exceptions (Kohler-Rink and Kühl 2000). Many animals react to hypoxia using behavioural responses, commonly avoidance (Diaz and Rosenberg 1995; Wannamaker and Rice 2000). Sessile species show functional metabolic adaptations to low oxygen stress ranging from oxygen conformity through regulation of oxygen uptake to anaerobiosis (McMahon and Russel-Hunter 1978; Burnett and Stickle 2001). Consequently, macroalgae in intertidal rock pools, including *C. officinalis*, support thriving epiphytic communities despite being exposed to rapid large-scale fluctuations in both oxygen and carbon dioxide related to tidal and diurnal cycles (Truchot 1980). Extremes in oxygen concentration in the poorly mixed waters of residual intertidal pools have been widely described (Goss-Custard *et al.* 1979; Morris and Taylor 1983) and are controlled principally by biological processes. Investigations of oxygen environments on a smaller scale have been limited by the availability of equipment capable of measuring oxygen with high spatial resolution. In the absence of such information this study set out to describe the oxygen environment on the surface of coralline algae where sessile epiphytic animals attach and through coralline tufts where mobile epiphytic animals live, and to provide details of the fauna inhabiting *C. officinalis* on a sheltered shore in south-western Ireland.

## MATERIALS AND METHODS

### SAMPLE COLLECTION

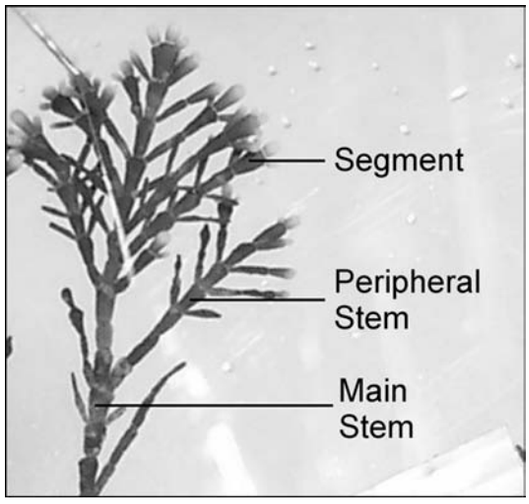
Sampling was carried out during the spring of 2003 at Bullen's Bay, a sheltered shore on the south coast of Ireland (51°48′ N, 08°33′ W), in the lee of the Old Head of Kinsale, where the articulated *Corallina officinalis* (Order: Corallinales, Family: Corallinaceae) is a dominant feature of intertidal rock pools. For surface measurements of oxygen concentration at the seaweed surface and within tufts, entire *C. officinalis* plants were collected together with the rocks to which they were attached, and stored in a similar manner. For investigations of faunal assemblages an open ended cylinder (120ml, diameter 6cm) was used to cut through the *C. officinalis* to the rock surface, thus trapping all associated fauna, and a metal scraper was used to remove the plant and associated substrate. Samples were sieved to collect animals, which were preserved in 70% ethanol in seawater. Individual animals were removed and identified to higher taxon level using a binocular microscope. Animals were photographed using a digital camera attached to the trinocular port of a microscope eyepiece tube, and maximum and minimum axes measured using SigmaScanPro, Version 5.0.0.

### OXYGEN MEASUREMENT

Oxygen measurement was carried out using oxygen microsensors with a tip diameter less than 50μm (MICROX, PreSens GmbH, Germany) housed in steel needles, as described in Irwin and Davenport (2002). These are optical chemical sensors, or micro-optodes, with glass fibre sensor tips housed in steel syringe needles. Unlike traditional amperometric oxygen electrodes, oxygen micro-optodes consume no oxygen during measurement and the signal is independent of flow velocity, bending of the fibre or optical properties of the sample. The micro-optodes were calibrated at 0% and 100% air saturation in advance of measurement, and connected to a PC which used MICROX 1 v2.01 to log oxygen concentration at one second intervals. Calibration of the micro-optodes against a precise gas mixing device (mechanical Vosthofpump, 0.1% accuracy) shows that a two-point calibration procedure (0% and 100% air saturation) describes the calibration curve sufficiently in the range from 0% to 100% oxygen (% volume) (0% to 500% air saturation) with no significant offset to be considered (Holst *et al.* 2000; Irwin and Davenport 2002). All measurements were performed in seawater at 16.0°C–16.5°C at an irradiance of 27.8μmol photon $m^{-2}$ $s^{-1}$, similar to the conditions experienced by the alga *in situ* at the time of collection (light was measured using a Meterman 631 light meter).

For measurement of oxygen concentrations at the surface of *C. officinalis* fronds, individual

branched sections were removed from plants and secured at the base of a Perspex experimental flume (400ml) containing seawater (seawater was pumped ashore at a site on the south coast of Ireland, 51°49′ N 08°00′ W, and subsequently filtered through 1μm filters and UV sterilised; the salinity was 34). Seawater flow through the flume was unidirectional and was controlled using a centrifugal seawater pump with inverter control (PDH 0.57 Gear Pump, Centrifugal Pump Services Limited, UK). This pumped water from a constant temperature seawater source tank via a flow meter (0.3–3.0l $m^{-1}$, Aqua Systems Limited, UK) through the flume, from where it was returned by gravity to the source tank. The cross-sectional area of the flume was $8cm^2$ and the flow velocity through the experimental chamber when the pump was turned on was 2.1cm $s^{-1}$. The micro-optode was positioned above the piece of *C. officinalis* and manipulated into the required position using a micromanipulator. That the sensor tip was in contact with the surface was verified by viewing the set-up through a binocular microscope. Oxygen concentrations were measured at various points on the surface of six replicate fronds, at different positions on each segment along the length of both the main stem and one peripheral stem per replicate in both static and flowing conditions (Pl. I). Oxygen concentration gradients were measured at the centre of the first segment of the main branch of six fronds under both static and flowing conditions by taking measures of oxygen concentration at intervals of 0.2mm in the vertical plane as the sensor tip was moved away from the seaweed surface.




**Pl. I—Frond of *Corallina officinalis* showing the main stem, peripheral stems and individual segments.**

To describe oxygen profiles developed through tufts of *C. officinalis*, small rocks on which tufts were attached were placed in a 2l tank filled with seawater (100% air saturation) in daylight, and allowed to settle for one hour before measurements were taken. For measurement in static conditions these were allowed to rest without supplementary aeration, and in many cases the bulk seawater above the tuft of seaweed had oxygen concentrations in excess of 100% air saturation when measuring commenced. For measurements in stirred conditions, aeration and water movement were provided by a small air pump. Replicate measurements were carried out on eight different tufts in both static and mixed seawater. The probe was positioned a few centimetres into the tuft of *C. officinalis*, depending on tuft size, and measurements taken at intervals of 1mm as the probe was moved outward through the tuft. Measurements were standardised according to the edge of the tuft, hence the different lengths of the resulting traces.

### DATA ANALYSIS

As data were logged at one second intervals, the micro-optode was allowed to record in each position for one minute, and all values quoted represent the mean of at least 40 measurements in the centre of each minute's recording. Differences between oxygen concentrations at different points on algae surfaces under static and flowing conditions were investigated using a two-way ANOVA. One-way ANOVA was performed to detect significant differences between oxygen concentrations at the surface of different segments along the length of the main branch. Paired *t*-tests were used to investigate differences in oxygen concentration at different positions on segments.

## RESULTS

### SURFACE OXYGEN CONCENTRATIONS

Oxygen concentrations considerably in excess of ambient seawater were observed adjacent to the fronds of *Corallina officinalis* under illumination. Measured oxygen concentrations at the surface of main branches of *C. officinalis* plants ranged from 135.0% to 453.5% air saturation in static water. At a flow rate of 2.1cm $s^{-1}$ the range of oxygen concentrations was reduced to between 124.5% and 288.4% air saturation. On peripheral branches the range of oxygen concentrations under static conditions was from 137.0% to 424.6% air saturation, and under flowing conditions was from 120.7% to

202.3% air saturation. Despite similarities in the observed ranges in oxygen concentration, two-way ANOVA revealed a significant difference between oxygen concentrations measured under static and flowing conditions ($F_{3,1} = 163.7$, $P < 0.01$), and also a significant difference between those measured on main branches and peripheral branches of *C. officinalis* fronds ($F_{3,1} = 23.1$, $P < 0.01$). There was a significant interaction between flow rate and branch type ($F_{3,1} = 14.9$, $P < 0.01$). The difference between oxygen concentrations on main and side branches was more evident under static conditions (Fig. 1). No difference was found between oxygen concentrations at the surface of the frond between the top (broad) end and the bottom (narrow) end of individual segments in either static or flowing conditions (Static: $t = 0.01$, df = 19; Flow: $t = 0.17$, df = 33). When oxygen concentration was measured at the surface of fronds at different segments along the length of one branch (main branch) no significant variation was observed between segments ($F_{55,6} = 2.13$, $P > 0.05$).

Measures of oxygen concentration under varying conditions of flow were made following an acclimation period to relevant experimental conditions. Oxygen concentration remained relatively constant at the surface under flowing conditions, and increased rapidly immediately flow was turned off, levelling off at a consistent higher level in under two minutes. Traces produced during three replicate measurements are shown in Fig. 2.

## OXYGEN CONCENTRATION GRADIENTS

Steep oxygen microgradients were present adjacent to the algae surface under static conditions

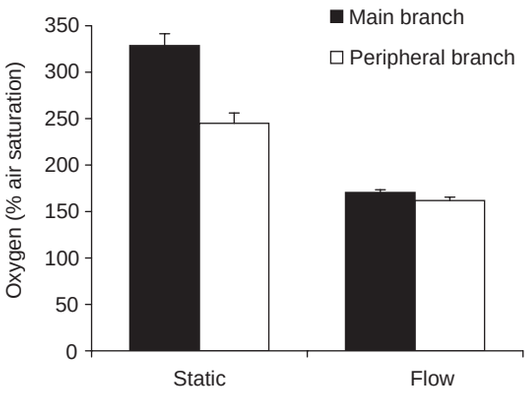



**Fig. 1—Mean (±SE) oxygen concentrations (% air saturation) at the algae surface (main branches and peripheral branches) of *Corallina officinalis* under static and flowing conditions.**

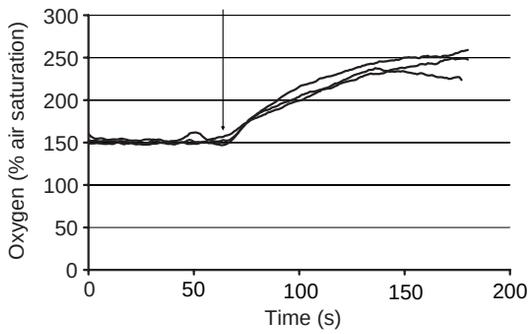



**Fig. 2—Oxygen concentration at the tissue surface on a main stem of *Corallina officinalis* as a function of time, following cessation of flow in the surrounding water body (arrowed).**

and at a flow rate of 2.1cm $s^{-1}$, decreasing from the elevated levels at the surface to the saturation levels of the surrounding water body. The maximum diffusive boundary layer thickness was observed in static water and was a little over 1mm thick. This was reduced significantly in flowing water, where elevated oxygen concentrations were observed only within 0.5mm of the algae surface (Fig. 3). Bulk water oxygen saturation levels remained stable at distances greater than 2.0mm and 0.5mm in static and flow conditions respectively. Measured oxygen concentrations at the surface of the seaweed were significantly higher under static conditions (mean 249.4% air saturation) than under flow conditions (155.4% air saturation) and oxygen concentrations within the boundary layer were more variable at any given distance in static water.

## OXYGEN CONCENTRATIONS IN TUFTS

On a larger scale, oxygen concentrations in the interspace of *C. officinalis* tufts under illumination were not homogenous, even when water flow was present through the tuft. Oxygen concentrations considerably above 100% air saturation were observed within the tufts. Under static conditions in a 2-litre vessel the oxygen concentration, measured at intervals of 1mm in the outermost 3cm of tufts, ranged from 98% to 281% air saturation (Fig. 4a). The highest oxygen concentrations under these conditions were generally observed near the periphery of the tuft. While water flow through the algal tuft served to decrease variability in oxygen concentration, measured levels nonetheless showed considerable variation within a narrower range, from 73.4% to 169.1% air saturation (Fig. 4b).

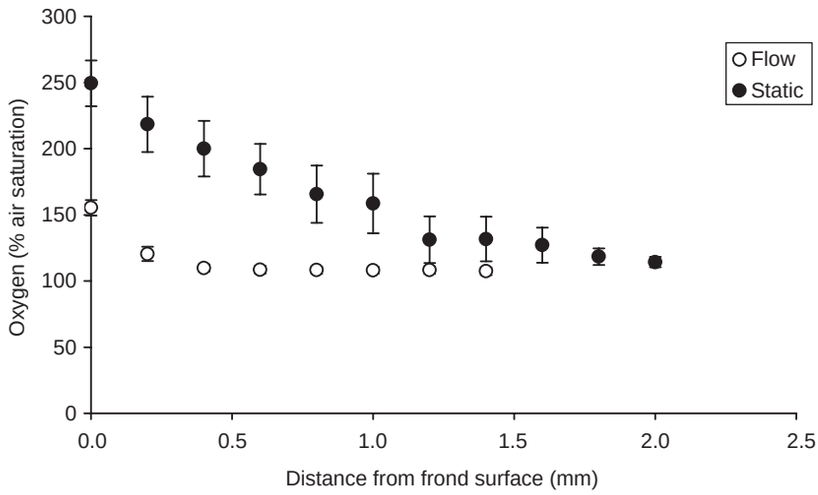



**Fig. 3—Vertical oxygen microprofiles adjacent to fronds of *Corallina officinalis* in static and flow conditions (2.1cm $s^{-1}$). Mean ± SE, $n = 6$.**

### EPIPHYTIC ANIMALS

One hundred and ninety animals from *C. officinalis* fronds ($n = 4$) were identified and measured. The epiphytic animal assemblage was dominated by harpacticoid copepods (39.5% of total individuals) and marine mites (20.5%). Together these two taxa comprised 60% of the total individuals (Table 1). Gammarid and caprellid amphipods made up 10.5% and foraminiferans 7.9%. The remainder was comprised of members of various life history stages of a selection of taxa. These included polychaetes and nemertean worms, a polychaete larva, ostracods, isopods, cyprid larvae, hermit crab larvae and a *Mytilus edulis* spat.

The longest measured maximum axis of the harpacticoid copepods was 1.1mm, and the shortest was 0.3mm. The marine mites ranged, in terms of maximum axis length, from 0.2mm to 1.2mm. With the exception of some of the hermit crab larvae, both mean maximum and mean minimum diameters of all animals measured were less than 2mm, with the majority being less than 1mm. Apart from the hermit crab larvae, gammarid amphipods, calanoid copepods and bivalves were among the largest specimens collected and the foraminifera were the smallest (Table 1). While not all animals measured had body dimensions smaller than the measured diffusive boundary layer, a high proportion of them were of a size small enough to confine them to living entirely within this microhabitat while attached to the seaweed surface. All animals sampled from *C. officinalis* were within such a size range that they would be entirely exposed to the oxygen microenvironment in the interspace of algal tufts.

## DISCUSSION

### SURFACE OXYGEN CONCENTRATIONS

The maximum recorded single oxygen measurement at the surface of *Corallina officinalis* fronds in this study was 453.5% air saturation in static seawater under illumination, with an average of 249.4% air saturation. Elevated oxygen concentrations are commonly reported where photosynthetic activity produces oxygen that does not immediately diffuse into the surrounding water body (Shashar *et al.* 1996; Rink *et al.* 1998; Pöhn *et al.* 2001; Irwin and Davenport 2002; Hurd *et al.* 2006), and are reported to peak between 200% and 300% air saturation at the surface of plants and animals in seawater (Kaspar 1992; Searcy-Bernal 1996). Oxygen concentrations were significantly lower on peripheral branches than on main branches of *C. officinalis*, a phenomenon not previously reported, and possibly related to either diffusion from the peripheral branches or differences in photosynthetic capacity of the different areas. No differences were observed between oxygen levels at different parts of individual segments, or between segments on the same branch of the seaweed. The oxygen microenvironment at the algal surface was dynamic in response to changing flow conditions, with concentrations at the surface demonstrating rapid predictable responses to the introduction of flow. As new technologies emerge that allow the

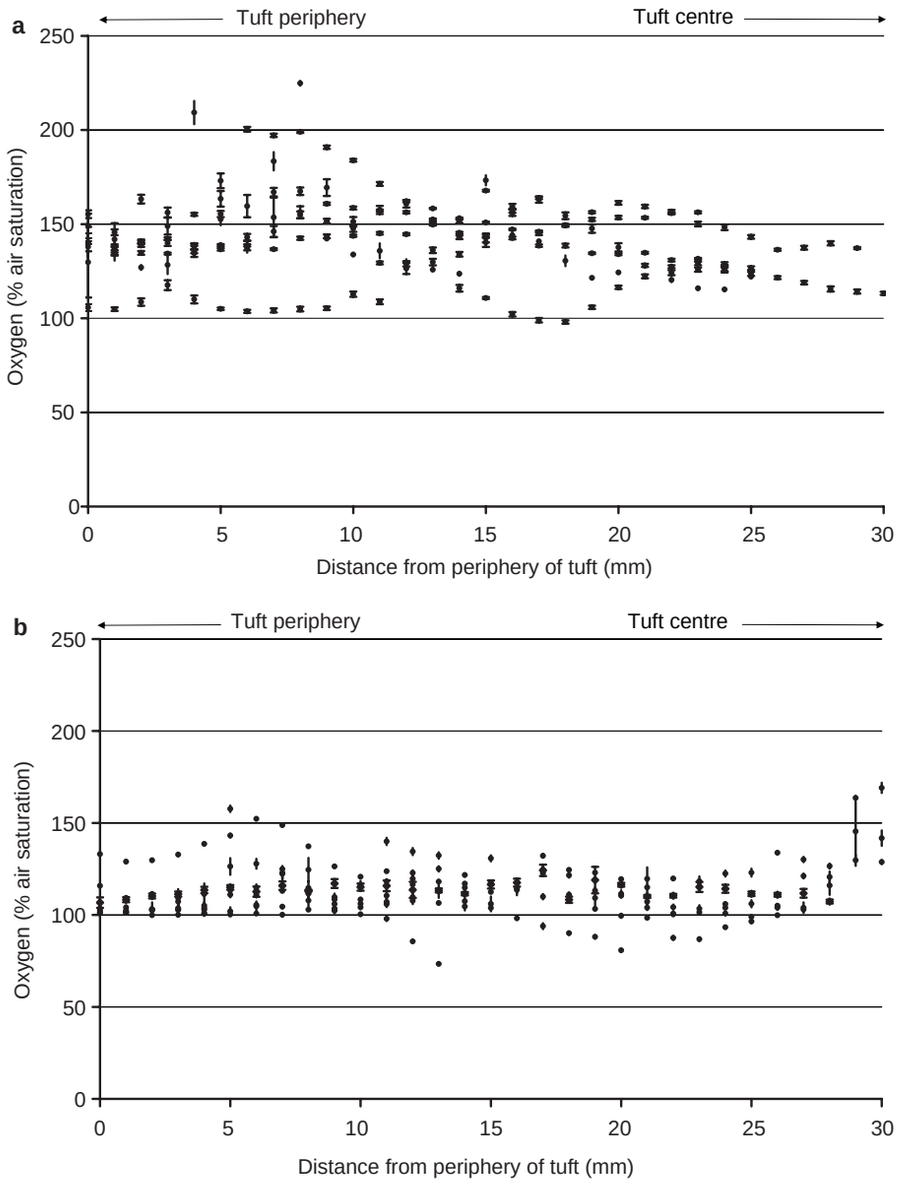



**Fig. 4—Patterns of oxygen concentration (% air saturation) within the outer 3cm of tufts of *Corallina officinalis* attached to rocks under (a) static conditions and (b) flowing conditions.**

description of oxygen microenvironments at such a small scale, the speed at which oxygen microenvironments fluctuate in biological systems is becoming apparent (Searcy-Bernal 1996; Ploug *et al.* 1999; Irwin and Davenport 2002; Miller and Dunton 2007).

## OXYGEN CONCENTRATION GRADIENTS

Oxygen microenvironments adjacent to *C. officinalis* main branches were typically maintained to distances of 1–2mm above the seaweed surface in static conditions and <0.5mm in flow conditions. Steep oxygen gradients were described through the diffusive boundary layer between the elevated oxygen concentrations measured at the algae surface and the oxygen saturated surrounding water body, when oxygen was measured at narrow intervals in the vertical plane. Frictional forces between the water surface and the algal frond at submillimetre scale are responsible for these boundary layers within which flow velocity decreases towards zero at the interface between the water and the solid object. Diffusive boundary layers of the order measured in this study are typically reported adjacent to solid objects in water bodies (Searcy-Bernal 1996; Shashar *et al.* 1996; Kohler-Rink and Kühl 2000). Local conditions

**Table 1—Mean (±SE) maximum and minimum axis and numbers of epiphytic animals on *Corallina officinalis*.**

| | *No. of individuals* | *Minimum axis (mm)* | *Maximum axis (mm)* |
|---|---|---|---|
| Harpacticoid copepod | 75 | 0.27 (0.01) | 0.57 (0.02) |
| Marine mite | 39 | 0.22 (0.02) | 0.42 (0.03) |
| Foraminifera | 15 | 0.27 (0.02) | 0.32 (0.03) |
| Gammarid | 13 | 1.00 (0.11) | 1.61 (0.16) |
| Nemertean | 8 | 0.19 (0.15) | 1.54 (0.33) |
| Caprellid | 7 | 0.49 (0.06) | 0.90 (0.06) |
| Ostracods | 5 | 0.43 (0.05) | 0.59 (0.05) |
| Bivalve | 4 | 1.24 (0.41) | 1.85 (0.68) |
| Balanomorph larva | 4 | 0.23 (0.07) | 0.46 (0.16) |
| Polychaetes | 4 | 0.32 (0.05) | 0.96 (0.16) |
| Gastropod | 3 | 0.97 (0.34) | 1.88 (0.78) |
| Hermit crab larva | 3 | 1.60 (0.30) | 2.13 (0.29) |
| Calanoid copepod | 2 | 0.28 (0.02) | 1.53 (0.11) |
| Isopod | 2 | 0.40 (0.07) | 0.70 (0.15) |
| *Littorina* veliger | 2 | 0.61 (0.08) | 0.77 (0.08) |
| Juvenile limpet | 1 | 0.82 | 0.92 |
| *Mytilus edulis* larva | 1 | 1.00 | 1.55 |
| Polychaete larva | 1 | 0.45 | 0.59 |
| Crustacean zoea | 1 | 0.54 | 0.76 |

of flow were seen to affect both the oxygen concentration measured at the algae surface and the height above the frond at which oxygen concentration approached equilibrium with that of the surrounding water body. In this study mean oxygen concentration at the algae surface was reduced from 249.4% to 155.4% air saturation when flow was introduced to the surrounding water body. This supports previous findings related to oxygen microenvironments around static objects in water bodies (Kaspar 1992; Searcy-Bernal 1996; Gardella and Edmunds 1999). The thickness of the diffusive boundary layer was also reduced under flowing conditions, a widely reported phenomenon in studies of this kind (Zhang and Bishop 1994; Shashar *et al.* 1996; Irwin and Davenport 2002). The third observed effect of flow in the main water body was to increase uniformity in oxygen concentrations measured through the diffusive boundary layer adjacent to the algal surface relative to those measured in static conditions.

## OXYGEN CONCENTRATIONS IN TUFTS

Separate subhabitats within *C. officinalis* tufts are distinguishable, including the algae surface discussed above, and also the interspace within the algal tufts (Crisp and Mwaiseje 1989). In terms of space occupancy by the faunal community, these are not exclusive habitats as many animals are alternately mobile and attached, while many species occupy both subhabitats simultaneously. While the interspace available on *C. officinalis* is relatively small, Crisp and Mwaiseje (1989) suggest that the presence of spirorbid tubes may keep open the space between the semi-rigid branches. Oxygen concentrations within tide pools are known to fluctuate through diurnal and tidal cycle to levels significantly higher than saturation. In intertidal pools in south-western Ireland levels as much as 200% air saturation have been recorded (Goss-Custard *et al.* 1979). The exchange of oxygen produced by photosynthesis from the algae surface to the interspace and subsequently between the tuft and the surrounding water body occurs by molecular diffusion. We investigated whether in poorly mixed water bodies limitation of this diffusion gives rise to areas of hyperoxia in the interspace of algal tufts. Under static conditions oxygen concentrations in excess of 200% air saturation were recorded in the interspace of *C. officinalis* tufts. No trend in oxygen concentration between the periphery and the centre of tufts was observed, and areas of hyperoxia were randomly distributed within the tuft interspace.

When flow was introduced to the surrounding water body such extremes of hyperoxia were not observed within the tufts. Oxygen concentrations ranged from below 100% to 150% air

saturation and varied spatially within the tuft interspace within this range, suggesting that the impact of metabolic processes on the oxygen environment is reduced under these conditions. Overall, oxygen concentration in and around *C. officinalis* tufts will be influenced by a combination of distance from photosynthetic frond, illumination, shading, water flow and shelter from flow and shading from light provided by tuft material.

### EPIPHYTIC ANIMALS

Small animals (<1mm) such as harpacticoid copepods and marine mites, were abundant on *C. officinalis*. The assemblage comprised both juveniles and adults of many species, with some species represented by just the juveniles (the adults of the species living elsewhere). This assemblage is typical of that described on *C. officinalis* (Crisp and Mwaiseje 1989). The dominant animal groups in the tufts of *C. officinalis* examined were copepods (predominantly harpacticoids), marine mites (Acarina), amphipods (including the Caprellidae) and Foraminifera. Early life stages of many marine invertebrate species were present, including barnacle cypris larvae, *Mytilus edulis* spat and *Littorina* veligers. It must be noted that the samples used in this study represent only the fauna of *C. officinalis* from rock pools on a sheltered shore. It is worth bearing in mind that the faunal community is dynamic, both spatially and temporally (Goss-Custard *et al.* 1979; Hull 1997; Davenport *et al.* 1999), and that the distribution of fauna is regulated to some degree by physical factors, with marked differences reported in the abundance of animals at different areas, even within a single pool (Grahame and Hanna 1989). The dominance of copepods in this study is an effect of season on the temporal partitioning of epiphytic animals. Although copepods are a major faunal group on many subtidal red algae, highest numbers are commonly reported over the winter (Hicks 1971).

The fauna found in this study were typically of the order of 0.5mm thick with the exception of the amphipods collected. *C. officinalis* is notable in hosting small epiphytic specimens as the relatively small interstitial space between the branches, though somewhat increased by the presence of spirorbids, limits the maximum size of animals found living there. Where members of larger species are found on *C. officinalis* only small specimens are recorded (Dommasnes 1969). The three major contributing groups to the faunal assemblage in this study had mean maximum and minimum lengths within a size range similar to the thickness of the diffusive boundary layers described. The results of oxygen microenvironment investigations in this study clearly demonstrate that these animals, when on the surface of *C. officinalis*, are exposed to an extreme and dynamic oxygen environment. *C. officinalis* is a common inhabitant of poorly mixed intertidal pools, where it experiences negligible flow rate through its tufts for significant lengths of time. Under these conditions the diffusive boundary layer can be as deep as 2mm, thus exceeding the maximum axis of all but the largest epiphytic animals.

## ACKNOWLEDGEMENTS

This work was funded by a basic research grant from the Irish Research Council for Science, Engineering and Technology (IRCSET). We thank Bob McNamara and Helen Gurney-Smith for assistance with experimental work.

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