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Hypoxic life of intertidal acorn barnacles

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Abstract Oxygen levels were monitored within the mantle cavities of three barnacle species (*Chthamalus stellatus*, *Semibalanus balanoides*, *Elminius modestus*), using optode microsensors. Conditions were always hypoxic, even when barnacles were actively using the prosoma and cirri to pump aerated seawater into the mantle cavity. Mantle fluid oxygen concentrations were extremely variable; behaviour and oxygen concentrations were not closely coupled. Ventilation of the mantle cavity depended partially on external water flow, with higher and more stable mantle fluid oxygen concentrations being sustained when the water around barnacles was agitated. During emersion, barnacles initially pumped seawater between the mantle cavity and the cone above the opercular plates to achieve ventilation. As water was lost it was replaced by air bubbles, eventually resulting in an air-filled mantle cavity. In *S. balanoides* and *E. modestus*, once the mantle cavity was filled with air, the barnacle usually used up the oxygen within the bubble within 2–3 h and did not regain oxic conditions until the barnacle was reimmersed in seawater. In *C. stellatus*, the air bubble was repeatedly refreshed for many hours by pneumostome formation. In response to low environmental salinity, all three species closed the opercular plates firmly and rapidly used up oxygen within the mantle fluid.

Introduction

Balanomorph barnacles of the cirripede order Sessilia are a diverse group as far as details of anatomy and behaviour are concerned (Anderson 1994). Intertidal balanomorphs from rocky shores in NW Europe include two chthamalid species, *Chthamalus montagui* Southward that lives high on the shore, particularly on exposed coasts, and *Chthamalus stellatus* (Poli) that is predominantly a middle shore barnacle but overlaps with *C. montagui*. The commonest middle shore barnacle is the balanoid *Semibalanus balanoides* (L.), though the introduced balanoid *Elminius modestus* Darwin overlaps and competes with it on sheltered shores, and also extends into the shallow sublittoral. Finally, *Balanus crenatus* Bruguière extends from the lower shore into the shallow sublittoral. *S. balanoides*, *E. modestus* and *B. crenatus* all penetrate estuaries, where they can encounter strong tidal fluctuations in environmental salinity (Davenport 1976). All barnacles living above low water spring tide level are emersed for part of the tidal cycle on at least some occasions, with emersion frequency and duration being greater the higher the position on the shore.

As with most filter-feeding animals, respiratory and feeding mechanisms are intertwined in barnacles. For respiration alone, barnacles pump water through the mantle cavity by a musculo-hydraulic system. The opercular plates part and rhythmical movements of the prosoma and furled cirri move water in and out of the mantle cavity. During feeding the cirri are either rhythmically extended and withdrawn with each respiratory pulsation (presumably enhancing respiratory exchange), or, in some species, they may be extended into external water currents for periods of time to act as plankton nets. During feeding in some species (including *S. balanoides* and *E. modestus*) the cirri may beat without withdrawal (fast beat; Crisp and Southward 1961). In those circumstances there appears to be no pumping of water through the mantle cavity, but the cirri effectively fan water across the opercular opening. In barnacles, respiratory exchange is regulated during periods of altered pH and, to a lesser extent oxygen tension, by modification of the duration of activity bursts and not by altering the frequency of the cirral beat (Southward and Crisp 1965).

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The barnacle mantle cavity is lined with epithelium that is assumed to be a respiratory exchange surface; this is reinforced by folded parts (branchiae) of the lining suspended within the mantle cavity from the opercular terga. In addition, it is probable that the cirri themselves act as exchange surfaces as they are well supplied with haemolymph. However, as Anderson (1994) points out, the relative importance of these structures is unknown; even the branchiae may be primarily expandable haemolymph circulation reservoirs rather than gills, while chitin is known to be a substantial impediment to oxygen diffusion (Krogh 1919), so uptake by the cirri may be limited.

Surprisingly little has been published about barnacle respiration; however, it is known that respiratory pigments are apparently absent from haemolymph (Waite and Walker 1988). There is limited evidence that haemoglobin (Southward 1963) or perhaps myoglobin (J. Wittenberg and C. Mangum, personal communication) may be present in certain muscular tissues of some barnacle species. It is known that the respiration of at least some barnacle species is depressed by low ambient oxygen concentrations (Prasada Rao and Ganapati 1968), and that the relationship between activity and respiration is not straightforward (Anderson and Southward 1987). It is also clear that at least some intertidal barnacle species (*S. balanoides*, *C. stellatus*) take air into the mantle cavity when emersed (Grainger and Newell 1965) to permit aerial respiration with minimal risk of desiccation. Grainger and Newell (1965) reported that the aerial uptake of oxygen in *S. balanoides* was depressed by about 72–76% compared with aquatic oxygen uptake at the same temperature. This contrasts with a study of the upper shore Chilean chthamalid *Jehlius cirratus* (Darwin) that reports minimal reduction (ca. 17%) when emersed (Simpfendörfer et al. 1995).

A priori, the ventilation system of balanomorph barnacles appears to be inherently inefficient. Essentially, water exchange is driven by a reciprocating piston pump, with the prosoma and cirri representing the "piston". Given that the prosoma and cirri do not form a tight seal with the lips of the opercular plates, it would appear that the bi-directional pumping action will inevitably mix inhaled and exhaled water. This contrasts with the more efficient arrangement in other intertidal filter-feeders such as bivalve molluscs and ascidians, in which the respiratory flow is uni-directional and the exhaled water is separated from the inhalant stream. In addition, all intertidal barnacles feature alternating periods of activity when pumping takes place, and inactivity when pumping is absent and the opercular plates largely closed. During periods of inactivity, which may be sustained for a few seconds or several minutes (depending upon species and circumstances), the tissues of the barnacles concerned are in contact with small volumes of seawater; it would seem inevitable that hypoxic conditions ensue.

Study of oxygen levels in the mantle cavity of individual barnacles has been difficult thus far because of technological constraints. Here, we use opto-chemical microsensors (Klimant et al. 1995) to test the general hypothesis that barnacles' tissues function under hypoxic conditions for much of the animal's life. Three species (*E. modestus*, *S. balanoides* and *C. stellatus*) were investigated, and the effects of water flow, emersion and salinity upon conditions within the mantle cavity were studied.

Materials and methods

Collection of barnacles

Specimens of *Chthamalus stellatus* and *Semibalanus balanoides* (5.4–10.2 mm and 5.2–8.8 mm, respectively) were collected from an exposed rocky shore at Garretstown (51°38′N; 8°33′W) on the south coast of Ireland. Sections of rock with barnacles attached were removed during low tide and returned to the laboratory. *Elminius modestus* (6.4–9.6 mm) were collected from the shore of the estuary at Douglas harbour (51°52′N; 8°22′W), a site that features marked fluctuations in salinity. Specimens were collected on small rocks or on the shells of mussels (*Mytilus edulis* L.). All specimens were returned to the laboratory where they were stored in aerated seawater (maximum storage time was 3 days). They were emersed (16–20°C) for 1–2 h prior to experimentation. During emersion they were held in damp conditions. Experiments were conducted at laboratory temperatures of 16–20°C, under conditions of mixed natural and fluorescent light.

Measurement of mantle cavity oxygen tension

The rocks and mussel shells on which individual barnacles were attached were placed in a vessel containing aerated seawater (unless otherwise dictated by experimental protocol). Oxygen measurements were carried out using optical fibre microsensors and the MICROX 1 oxygen measuring system (PreSens Precision Sensing, Germany). These microoptodes measure luminescence of an immobilised luminophore mounted in a fine optical fibre (<50 µm diameter). The luminescence is quenched by molecular oxygen, and there is a predictable relationship between the two quantities. There is no oxygen consumption by the probe, and oxygen records are unaffected by microbending of the fibre tip or the turbidity, refractive index, or coloration of the solution being sampled. The full response time is short (<5 s) whatever the temperature (Klimant et al. 1995; Holst et al. 1997). These features make detailed monitoring of the oxygen content of small water volumes feasible. During operation, recordings of oxygen content (as percent air saturation) are made at 1 s intervals, and data sets are continuously transmitted via the serial interface of a PC, allowing instant recording and storage using dedicated data handling and storage software designed for use with the MICROX 1. Two-point calibration of optodes was by immersion in air-saturated and oxygen-free water (obtained by bubbling oxygen-free nitrogen through it) (Irwin and Davenport 2002).

During experiments, each optode was housed within a protective steel needle so that only a short length of optode fibre (ca. 2–3 mm) projected from the tip. The steel needle was positioned using a micromanipulator (Sutter Instrument Company), and the position of the optode fibre was observed beneath a binocular microscope mounted above the vessel in which barnacles (on stones or mussel shells) were attached (Fig. 1).

Optodes were used to measure oxygen levels close to and within the mantle cavity of barnacles, and were positioned to ensure that pumping movements or cirral extension were unaffected by the presence of the optode fibre. The basic principle underlying the measurements was that, if a low level of oxygen was recorded in air or water within the mantle cavity, then this implied that at least

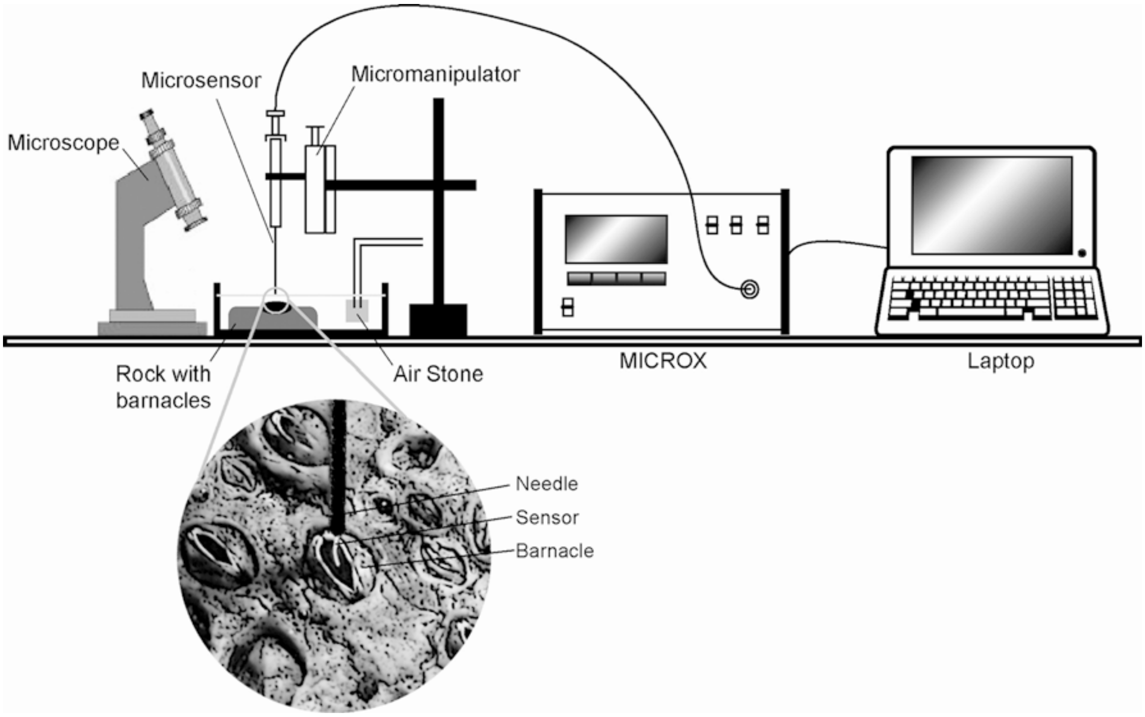


Fig. 1 Schematic detail of experimental arrangement

some tissues had to be functioning at that oxygen level or lower. When barnacles were pumping water past the optode, the levels recorded represented the prevailing mix of inhaled and exhaled water. Optodes function equally well in air or water, so monitoring of oxygen content of gas bubbles within the mantle cavity was also feasible.

In considering the results presented below it should be recognised that the optode system records oxygen concentrations in the water in contact with the optode tip (which does not itself affect that concentration). The tip was mounted within the mantle cavity, but the precise position varied from animal to animal, so it would be closer to respiring tissues in some animals than in others. In addition, the highly variable behaviour of barnacles (Crisp and Southward 1961; Davenport 1976) meant that water could be flowing into or out of the mantle cavity past the optode tip, or not flowing at all. When the opercular plates are closed, there may or may not be movements of the prosoma, while intermittent parting of the opercular lips is also common. This complexity meant, for example, that opening of the opercular plates could be associated with a *decrease* in recorded oxygen tension as deoxygenated water from deep within the mantle cavity was expelled past the optode. Conversely, retraction of the prosoma and closure of the opercular plates could be associated with a *rise* in oxygen tension as a slug of oxygenated water was taken in.

Experimental protocol

An inherent problem with experiments upon barnacles is that individual barnacle behaviour is extremely variable in terms of patterns of beating (see Anderson 1994 for review), even under similar environmental conditions. In consequence, though all of the experiments were performed on at least three specimens of the same species, individuality of response inevitably restricts statistical analysis.

First, barnacles were placed in aerated seawater and allowed to open and initiate pumping. Aeration was stopped, and a calibrated optode was manipulated into the region of the opercular opening and then progressively moved into the mantle cavity. Meanwhile notes on behaviour were made, allowing correlation of elements of behaviour with recorded oxygen concentrations. It should be noted that, in all experiments where aeration was switched on and off, the oxygen content of the bulk water surrounding the barnacles remained at 100% air saturation; aeration was used to control water flow, not water oxygen content.

Second, the effect of water movement on oxygen concentration was studied by alternately aerating the seawater around the barnacles vigorously and turning the aeration off to produce conditions of still water (ca. 10-min intervals). The vessels used were large enough (1 l) to ensure that the respiration of the barnacles made no discernible impact on the oxygen content of the seawater during the periods when aeration ceased.

Third, the effect of emersion on mantle cavity conditions was studied. To do this, water was siphoned from the holding vessel until the barnacle under investigation was emersed. During this process, and subsequently, the behaviour of the animal was closely observed and notes were made. Particular attention was devoted to determining when air was taken into the mantle cavity and when "pneumostomes" (Grainger and Newell 1965) were present/absent between the opercular lips. After a period of up to 20 h, seawater was siphoned back into the vessel and behaviour/oxygen content was recorded.

Fourth, on separate specimens of *E. modestus*, *S. balanoides* and *C. stellatus* the following procedure was carried out. Individual barnacles were placed in small 1 l vessels of aerated seawater (35 PSU) mounted in large empty trays. Once open and pumping, their mantle cavity oxygen content was monitored. Aerated freshwater was then allowed to flow into the seawater, causing it to overflow into the outer dish and reduce the salinity of the water surrounding the barnacle. Salinity was monitored using a portable Goldberg refractometer. When salinity levels had fallen sufficiently to induce opercular valve closure (Davenport 1976) the freshwater flow was cut off and mantle cavity oxygen concentration was monitored for up to 20 h. After this period, full seawater (35 PSU) was allowed to flow into the experimental vessel to displace the water of reduced salinity. Mantle fluid oxygen content and barnacle behaviour were monitored as the barnacles resumed activity.

Results

Correlation of elements of behaviour with recorded oxygen concentrations

Oxygen levels were measured inside the mantle cavities of three species of barnacle (*Eliminius modestus*, *Semibalanus balanoides* and *Chthamalus stellatus*) in flowing aerated seawater. Though the seawater was maintained at 100% air saturation, oxygen levels inside the mantle cavities of barnacles were always < 100% air saturation, often fluctuating to far lower levels. There was much individual variation, reflecting closing/pumping patterns. In addition, moving the optode deeper into the mantle cavity invariably resulted in recording of lower oxygen concentrations. A sample 2-h record for each species is shown in Fig. 2.

Details of barnacle behaviour observed by binocular microscope were correlated with simultaneous records of oxygen levels within the mantle cavity (examples given in Fig. 3). Primary behaviours recorded were: (1) opercular plates closed and (2) opercular plates open, with intermittent active pumping using cirri. The main pattern that emerged was that closure of the opercular plates was usually associated with dips in the oxygen concentration records for all three species, irrespective of the oxygen level at which the barnacle was operating.

Effect of water movement on oxygen concentration

For *E. modestus* under static (no external flow) conditions oxygen levels were seen to fluctuate dramatically as the opercular plates opened and closed. When the seawater surrounding the barnacle was flowing oxygen levels fluctuated far less (Fig. 4). This figure demonstrates that opercular valve closure was often (though not invariably) associated with higher oxygen concentrations at the optode tip. We interpret this as closure being associated with inhalation of oxygenated water, which subsequently remains still within the mantle cavity, so that oxygen gradients build up within the mantle fluid. Only when activity and pumping restarts does the mantle fluid become mixed again.

Oxygen concentration inside the mantle cavity of a barnacle (*C. stellatus*) was recorded as flow in the surrounding seawater was alternately turned on and off (Fig. 5). Irrespective of behaviour, oxygen levels within the mantle cavity were observed to fall quickly during static periods and to rise towards 100% air saturation, when external seawater was flowing. The mean oxygen concentrations were significantly lower (Student's *t*-test:

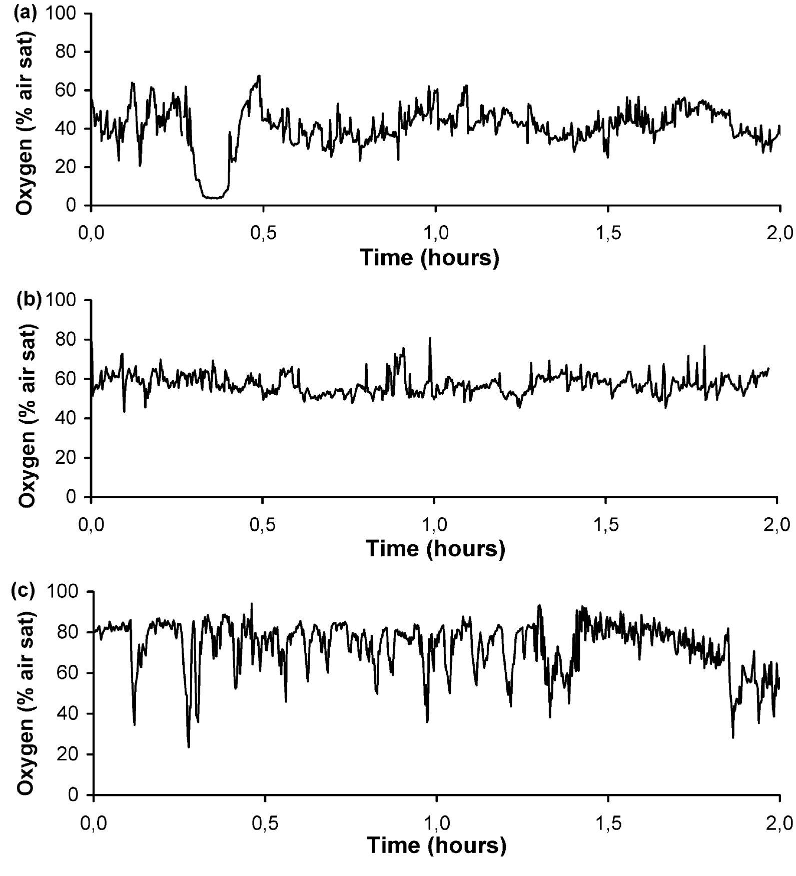


Fig. 2 Examples of oxygen concentration levels (% air saturation) in the mantle fluid of the barnacles **a** *Elminius modestus*, **b** *Semibalanus balanoides* and **c** *Chthamalus stellatus* in aerated seawater (100% air saturation) over a 2 h period during which the opercular plates were mostly open and the barnacles actively pumping

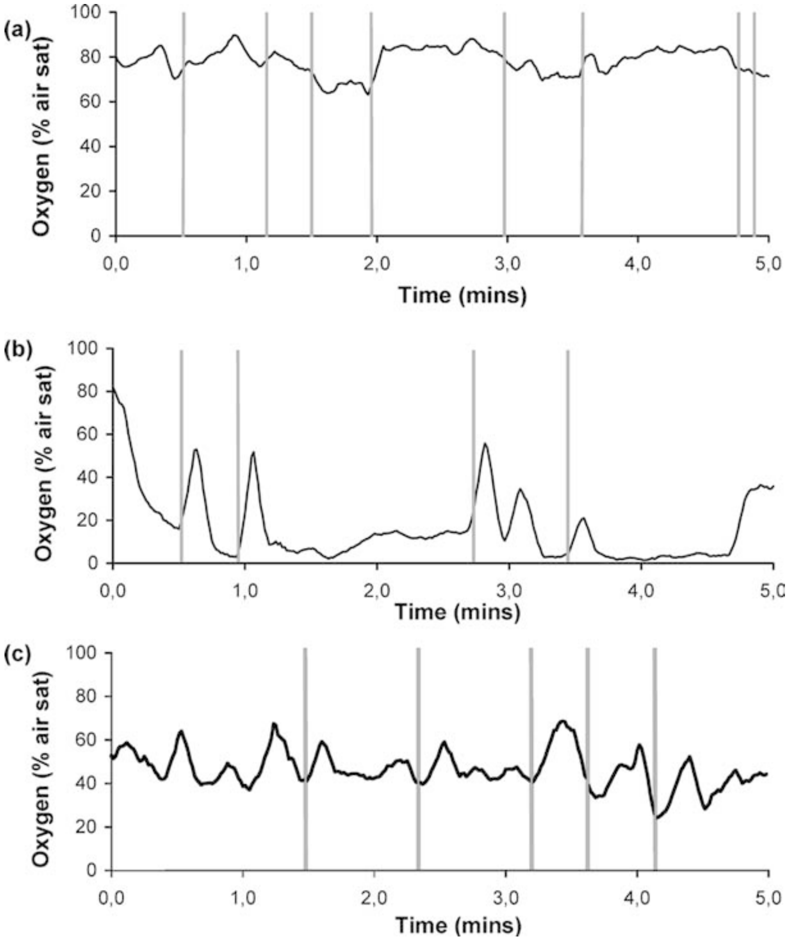


Fig. 3 Oxygen concentration (% air saturation) in the mantle fluid of the barnacles **a** *Elminius modestus*, **b** *Semibalanus balanoides* and **c** *Chthamalus stellatus* in aerated seawater (100% air saturation) over a 2 h period. *Vertical lines* represent brief closures of the opercular plates of the barnacle between periods of active pumping

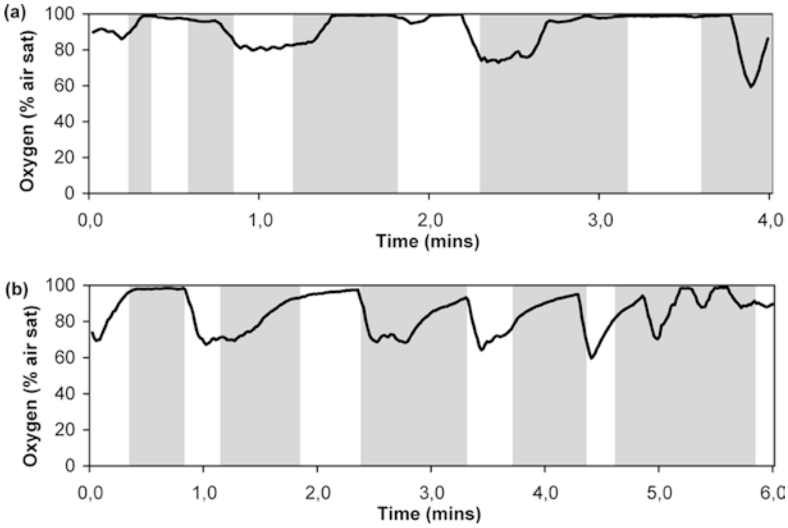


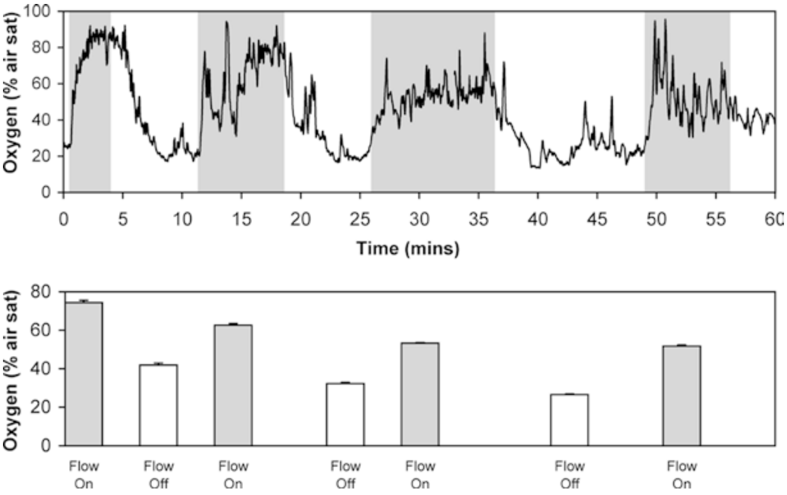
Fig. 4a, b *Elminius modestus*. Oxygen concentration (% air saturation) in the mantle fluid. *Grey shaded areas* represent periods when the opercular plates were *closed* and *white areas* represent periods when they were open: **a** barnacle held in flowing seawater conditions and **b** barnacle held in static seawater conditions

$t = 3.92$, $P < 0.05$) during static periods than during periods when seawater was flowing.

Effect of emersion on mantle cavity oxygen levels

Oxygen levels inside the mantle cavity of a barnacle (*C. stellatus*) during the period immediately following emersion are shown in Fig. 6. At the outset (time = 0.0 h) seawater had drained from the surface of the rock to which the barnacle was attached. Seawater was still retained within the cone above the opercular plates at this time, and the optode tip was monitoring the oxygen concentration of seawater within the mantle cavity. The shaded blocks on the record represent

Fig. 5 *Chthamalus stellatus*. Record of oxygen concentration (% air saturation) inside the mantle fluid over 1 h during which time the surrounding seawater was alternately flowing (*shaded grey*) and static (*white*). Histogram bars represent mean (± SE) oxygen concentrations (as % air saturation) during corresponding periods



periods during which the opercular plates of the barnacle were closed, and white blocks represent periods during which the barnacle was open. During open periods the cirri sometimes did not emerge, while at other times they were observed to emerge and beat in air. Both this pumping action and the action of closure of the opercular plates served to exchange water between the mantle cavity and the opercular cone, from which it gradually drained away. Additionally, air bubbles were actively taken up by the mantle cavity and excess water was subsequently released to the cone. At this time the optode sometimes recorded from water, sometimes from air. After about 0.45 h the barnacle closed the opercular plates over a large bubble within the mantle cavity (the optode tip was within the bubble); thereafter, the plates were very tightly closed, remaining moist on their outer surfaces. Oxygen levels within the trapped bubble declined steadily, but relatively slowly.

Oxygen levels recorded during 20 h of emersion for each species (three examples per species) are presented in Fig. 7. Much inter-individual variation was observed in oxygen levels during emersion. In *E. modestus* oxygen levels within the mantle cavity generally fell during the first few hours following the trapping of a final air bubble and remained at depressed levels until water was reintroduced around the barnacle. Most *S. balanoides* showed a similar pattern, but one specimen studied exhibited sustained high oxygen concentrations in its air bubble (Fig. 7b, top record), indicating more-or-less continuous connection with the atmosphere. By comparison, *C. stellatus* was observed to capture new air bubbles (by repeated pneumostome formation) for much longer periods after emersion (Fig. 7c). In all animals, on reimmersion, oxygen levels were observed to return slowly to levels typical of those observed pre-emersion (e.g. Fig. 8). Considerable inter-individual variability (irrespective of species) in the length of time taken for the return to normal oxygen levels was evident.

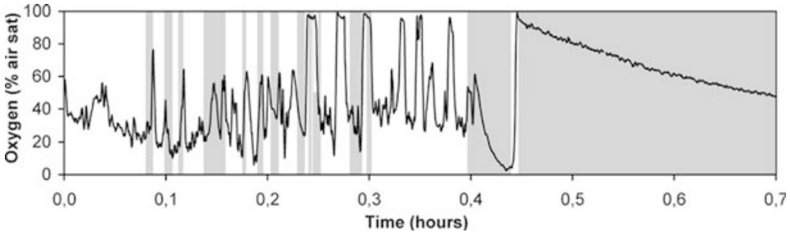
Effect of lowered salinity on mantle cavity conditions

When reduced salinity (7 PSU) was used to induce closure of the opercular plates of *E. modestus*, *S. balanoides* and *C. stellatus* the response of all species and individuals was similar and more predictable than when closure was induced by emersion (Fig. 9). On all occasions barnacles were seen to operate under hypoxic conditions for extended periods of closure. When full salinity (35 PSU) was restored to the surrounding seawater, oxygen concentrations returned to normal levels (e.g. Fig. 10), although variability was observed in the length of time between salinity restoration and first opercular plate opening.

Discussion

The results collected supported the general hypothesis that the tissues of sessilian barnacles are exposed to

Fig. 6 *Chthamalus stellatus*. Oxygen concentration (% air saturation) in the mantle cavity (fluid or air) during the period immediately following emersion at time 0. *White* and *grey shaded areas* represent periods when the opercular plates of the barnacle were open and closed, respectively



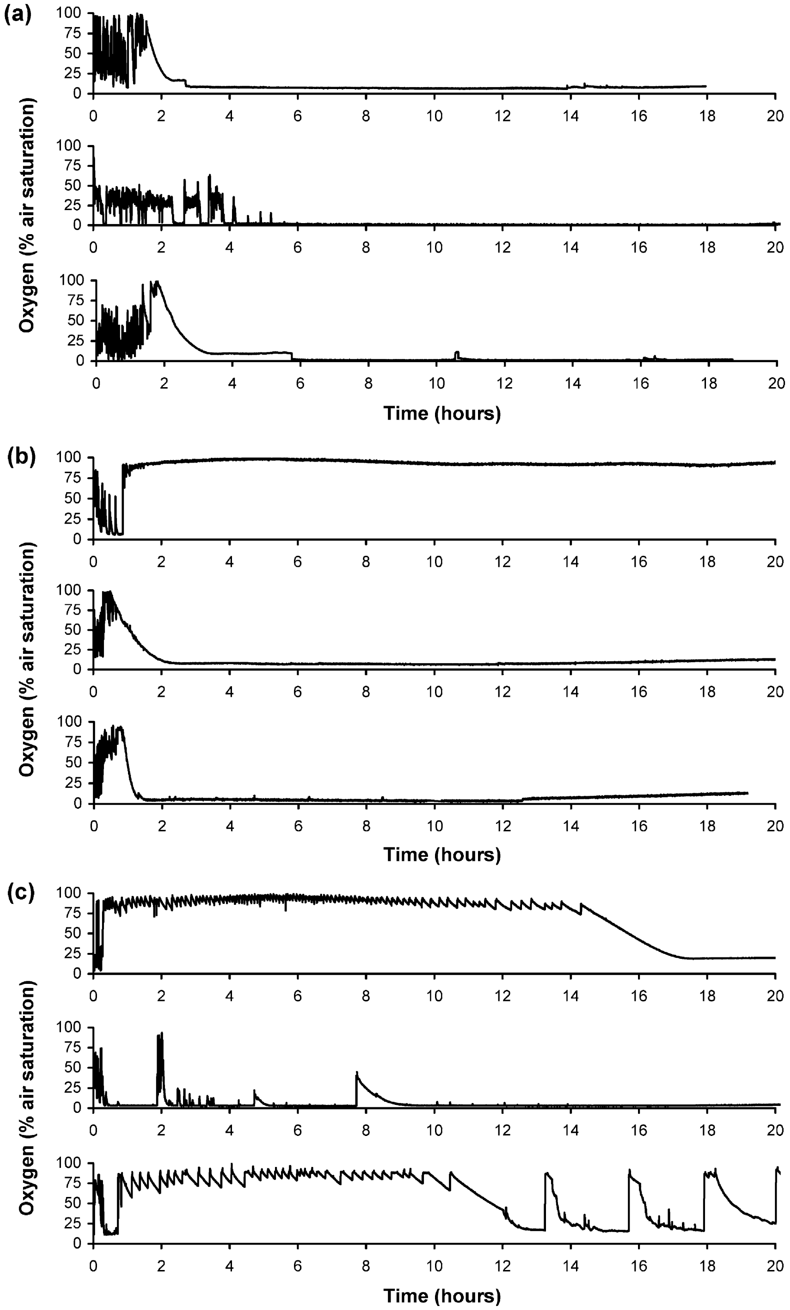


Fig. 7 Oxygen concentrations (% air saturation) in the mantle cavity (fluid or air) of three individuals each of **a** *Elminius modestus*, **b** *Semibalanus balanoides* and **c** *Chthamalus stellatus* during a 20 h period after water had left the surface of the rocks to which the barnacles were attached

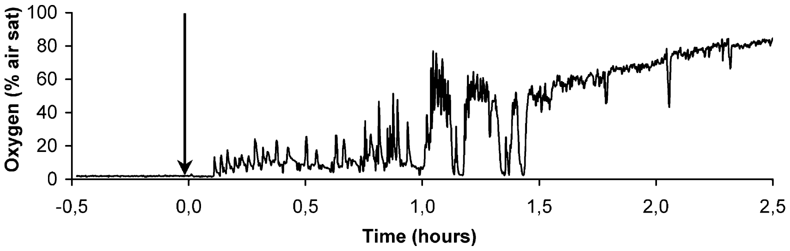
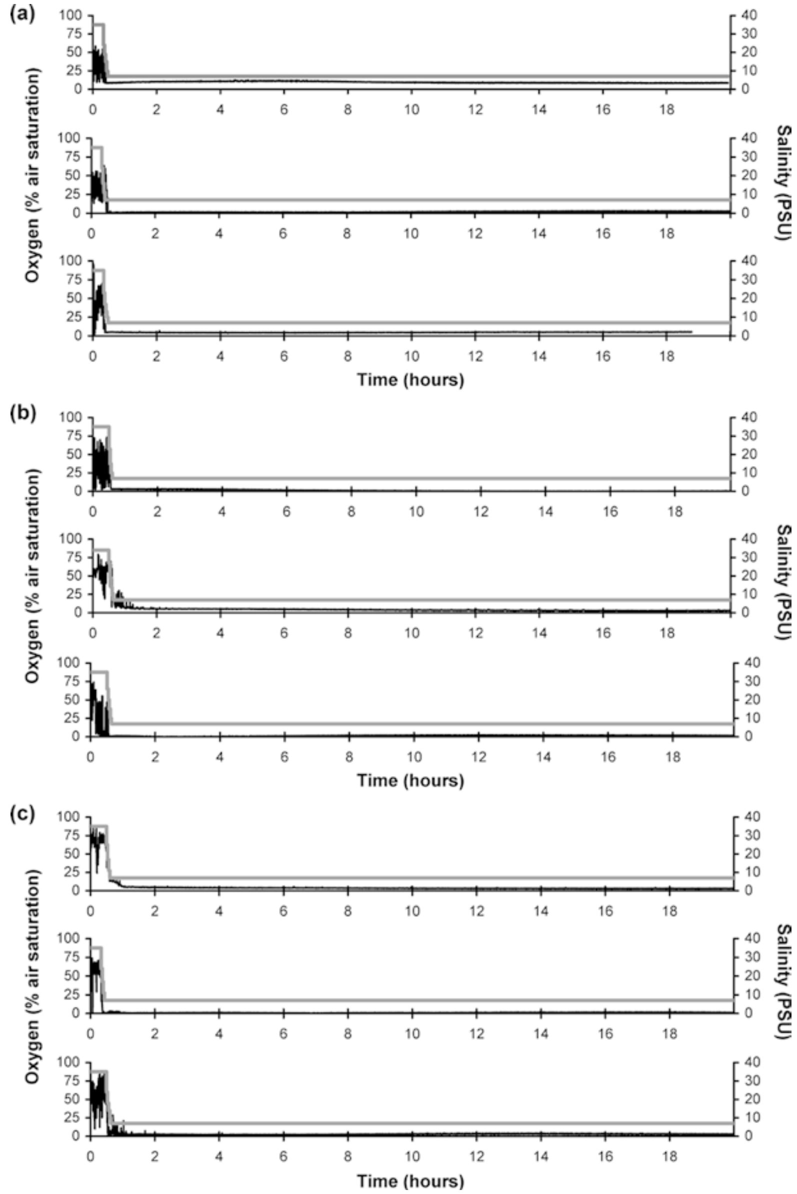


Fig. 8 *Elminius modestus*. Oxygen concentrations (% air saturation) in the mantle fluid during the period immediately preceding and during 2.5 h following the return of seawater over the rock on which the barnacle was attached. *Vertical arrow* indicates the time of reimmersion

hypoxic conditions during much of normal life. Even when pumping aerated water actively, all three species studied showed hypoxic mantle fluid oxygen concentrations often well below ambient levels. There were strong qualitative indications that there were steep concentration gradients and relatively poor mixing within the mantle cavity, suggesting that the tissues were operating at even lower oxygen tensions.

Fig. 9 Oxygen concentrations (% air saturation) in the mantle fluid of three individuals each of **a** *Elminius modestus*, **b** *Semibalanus balanoides* and **c** *Chthamalus stellatus* during a drop in salinity from 35 to 7 PSU. *Horizontal line* indicates salinity in seawater surrounding the rocks on which the barnacles were attached



Mantle fluid oxygen concentrations were extremely variable, and there was no evidence that behaviour and oxygen concentrations were closely coupled. The variability and gradients indicate that it is impossible to estimate the efficiency of extraction of oxygen from the ventilatory flow in barnacles. Against expectation, short periods of opercular plate closure were not automatically associated with declines in mantle fluid oxygen tension. This was certainly partly due to plate closure often being associated with inhalation of aerated water, but may also have resulted from a lack of mixing within the mantle cavity during periods of closure.

From the results obtained it is evident that ventilation of the mantle cavity is to some extent dependent on external water flow, with higher and more stable mantle fluid oxygen concentrations being sustained when the water around the barnacles is agitated. This appears to be another indication of the relative inefficiency of the reciprocating ventilation system of intertidal barnacles, though comparable data for the theoretically more efficient systems of bivalves and ascidians are currently unavailable.

When all three intertidal species were emersed there was a period of some minutes when water was pumped in and out of the mantle cavity, initially with water being exchanged between the mantle cavity and the cone formed by the upper parts of the wall plates. In the experimental configuration used throughout the present study the cone faced upwards, so it drained very slowly; in many (but not all) field situations the cone would point laterally or downwards, ensuring much more rapid loss of water. All three species eventually inhaled bubbles of air that became bigger as more and more water was lost. Finally a bubble large enough to fill the mantle cavity was present, and the opercular plates closed. During closure, oxygen levels

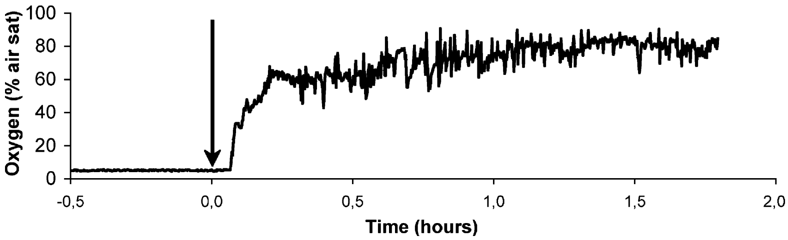


Fig. 10 *Elminius modestus*. Oxygen concentrations (% air saturation) in the mantle fluid during the period preceding and following the restoration of salinity from 7 to 35 PSU (*arrow*)

fell steadily, but much more slowly than was the case when closure took place with a water-filled cavity. This is to be expected since air contains approximately 40 times as much oxygen as an equivalent volume of air-saturated seawater (Denny 1993). In *Semibalanus balanoides* and *Elminius modestus* (which are middle shore barnacles), with a few exceptions, barnacles took in a "final" bubble of air, which became almost completely depleted of oxygen in 2–3 h. Thereafter, the barnacles remained quiescent with a near-anoxic mantle cavity until reimmersed in seawater. Patterns of behaviour were quite different in the higher shore *Chthamalus stellatus* that usually showed repeated pneumostome formation for many hours, so that air within the mantle cavity was repeatedly refreshed by inward diffusion of oxygen. However, after some 10–15 h, pneumostome formation became much less frequent or ceased. *C. stellatus* can be exposed to air for long periods during neap tide periods and has less water-permeable wall plates than the other two species. Presumably there is a trade off between the risk of desiccation posed by pneumostome formation and the energetic benefits of maintaining oxic conditions within the mantle cavity. All barnacle species tested resumed beating activity very soon after reimmersion in seawater. Consequently, mantle cavities showed a rapid return to oxic conditions, irrespective of the duration of emersion.

All three species showed a similar response to falling salinity; reduced activity followed by tight closure of the opercular plates, accompanied by rapid exhaustion of the oxygen within the mantle cavity. Intertidal barnacles are euryhaline osmoconformers and cannot allow their tissues to be flooded with water of salinity much below 15 PSU (Davenport 1976). *S. balanoides* and *E. modestus* encounter such low salinities in the estuarine parts of their distribution and show regular opercular plate closure to retain higher salinities around their tissues. However, it should be remembered that all intertidal barnacles (including the high shore *C. stellatus*) can be exposed to rainfall when emersed, even when they live on the open coast. Those barnacles with the wall plate cone facing upwards are likely to collect rainwater above the opercular plates so that there is a risk of low-salinity exposure when the opercular plates are opened.

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