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EFFECT OF WATER VELOCITY AND BENTHIC DIATOM MORPHOLOGY ON THE WATER CHEMISTRY EXPERIENCED BY POSTLARVAL ABALONE

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ABSTRACT The water bathing postlarval abalone often lies within the diffusive boundary layer (DBL) so its chemistry is greatly influenced by the metabolism of the biofilm on which the abalone feed. This study used microelectrodes to investigate the influence of water velocity and diatom morphology on dissolved oxygen and pH in the DBL. Decreasing water velocity increased the thickness of the DBL, thereby increasing the amplitude of changes in oxygen concentration. Over a film of the prostrate diatom *Nitzschia ovalis* Arnot, DBL thickness averaged 71, 139, 177, and 406 μm at water velocities of 78, 15, 7, and 1 mm s^{-1} respectively. Corresponding oxygen concentrations at the biofilm surface under moderate light (75 μE m^{-2} s^{-1}) and temperature (15°C) averaged 111%, 120%, 125%, and 151% of air saturation respectively, at the four velocities. The presence of a 1-mm tall diatom canopy (*Achnanthes longipes* Agardh) over a *Nitzschia ovalis* film thickened the DBL by 3-fold at 1 mm s^{-1} and 6-fold at ~80 mm s^{-1}. The thickened DBL and higher diatom biomass generated extreme conditions at the biofilm surface. Dissolved oxygen concentrations as high as 440% of air saturation, and pH as high as 9.8 were recorded beneath the canopy in moderate light (105 μE m^{-2} s^{-1}) and temperature (15°C) at a water velocity of 1 mm s^{-1}. Changes during darkness were less extreme, with 53% oxygen saturation and pH 7.7 the minima recorded. These measurements demonstrate the extreme water chemistry that can develop in the microhabitat of postlarval abalone. The changes will be amplified by the presence of filamentous diatoms, by increased light intensity, and by lack of water movement. Standard aeration will greatly reduce the extremes experienced by postlarvae by generating water movement sufficient to thin the DBL.

KEY WORDS: diffusive boundary layer, oxygen, pH, post-larvae, microelectrode, abalone, diatom

INTRODUCTION

Cultured abalone feed on a biofilm dominated by benthic diatoms for the first few months of their life. Films of benthic microalgae have photosynthetic rates up to several orders of magnitude higher on a volumetric basis than macroalgae or phytoplankton communities (Krause-Jensen & Sand-Jensen 1998). Benthic microalgae exchange gases with the water column by molecular diffusion through the diffusive boundary layer (DBL) generating steep gradients in dissolved oxygen and pH within a few mm of their growing surface (e.g., Revsbech 1989, Larkum et al. 2003). Microalgal films on hard, inert surfaces represent the most extreme case for oxygen accumulation, because the water chemistry overlying microalgal films on sediment can be ameliorated by exchange with the underlying matrix (Krause-Jensen & Sand-Jensen 1998).

A typical abalone culture situation involves establishment of a thin film of prostrate diatoms on plastic plates for larval settlement. Over a few months this biofilm develops progressively into a more complex film typically including stalked or filamentous diatom growth forms (Kawamura & Hirano 1992). The development of filamentous diatom films is significant because they may thicken the DBL, generating more extreme conditions at the surface where postlarval abalone reside. The only two studies of DBL conditions in relation to abalone postlarvae both measured oxygen above thin films of solitary diatoms from the genera *Nitzschia* or *Navicula* (Loipersberger 1995, Searcy-Bernal 1996). These authors documented maximum oxygen concentrations of around 200% saturation, which is much lower than concentrations measured within the DBL of thick, complex algal communities (e.g., Larkum et al. 2003).

Abalone settle as larvae about 0.25-mm long, and take several weeks to grow to a juvenile of ~2 mm shell length (SL) and ~0.6 mm shell height. Even at ~2 mm SL they are covered by a waterproof shell, which is elevated no more than a few hundred μm above the surface (Loipersberger 1995). There has been no investigation of whether postlarval abalone have mechanisms to access water from higher in the water column, thereby ameliorating the effects of the DBL. Without such mechanisms, postlarvae may suffer from the extreme oxygen conditions, as documented for 8–12 mm *Haliotis rufescens* (Elston 1983, Leitman 1992). The depletion of carbon dioxide by photosynthesis can also generate substantial fluctuations in pH within the DBL (e.g., Jones et al. 2000). Changes in pH are known to negatively affect juvenile abalone (Harris et al. 1999).

This paper adds to existing knowledge of the microenvironment of postlarval abalone by describing oxygen and pH conditions within the DBL above diatom films of contrasting morphology. Specifically it: (1) describes the impact on DBL thickness and oxygen/pH concentrations of adding a 1 mm tall diatom canopy (*Achnanthes longipes*) above a prostrate diatom film (*Nitzschia ovalis*); (2) describes the relationship between water velocity and DBL biophysical parameters; (3) models the relationship between light intensity and oxygen production for a simple diatom film and; (4) describes the modification of the boundary layer by postlarvae.

METHODS

Microelectrode Measurements Within the DBL

Oxygen and pH microprofiles were measured in the laboratory at 15 ± 0.6°C. The oxygen microelectrode (Revsbech 1989) had a tip diameter of 10 μm, a 90% response time of 1.9 sec and

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a stirring sensitivity of 0.9% over the range of water velocities used in this study. The glass pH electrode (Revsbech & Jørgensen 1986) received the pH signal over the length of a 400-μm tip that tapered from 10-μm (distal) to 40-μm (proximal) diameter. The sensor would integrate the pH signal in an unknown way over the 400-μm length of the sensor tip. Alignment of corresponding pH and oxygen microprofiles suggested that the pH value represented a point 100 μm from the distal end of the pH electrode tip. This value is reported, followed by upper and lower bounds representing either extreme of the 400-μm tip. The upper and lower bounds were tight around the estimated actual value (see Results) so the exact position of pH detection does not affect the interpretation of the data. When pH was profiled, the pH electrode was mounted vertically beside the oxygen sensor with its tip 5 mm "downstream" of the oxygen microelectrode tip, and 100 μm further from the surface. This minimized disturbance of the DBL by the larger pH electrode and allowed the oxygen electrode to register the substrate surface (see below). To obtain terminal pH values at the diatom growing surface, pH profiles were extrapolated downward through the last 200 μm to the surface, following the gradient in the final portion of the profile.

Profiling took place in a laminar flow chamber (Lorenzen et al. 1995) enclosed to exclude ambient light. Light intensity was controlled by use of a tungsten halogen lamp (Schott, Germany) and neutral density filters. Downwelling irradiance (E_d, 400–700 nm) was measured in the experimental setup by an underwater quantum irradiance sensor (LiCor LI-192SA, USA) and light meter (LiCor LI-1000, USA). Water velocity in the laminar flow chamber was measured from the travel times of neutrally buoyant particles flowing ~1 cm above the sample, using a horizontally-mounted dissecting microscope. DBL thickness was defined as the distance from the substrate surface to the point where the linear slope of the profile intersected with the oxygen concentration of the bulk medium (Jørgensen & Revsbech 1985).

The microelectrodes were mounted vertically in a motorized micromanipulator (Märtzhäuser/LOT-ORIEL, Germany). The oxygen microelectrode was connected to a pA-meter (PA2000, Unisense A/S, Denmark) and the pH electrode to a mV meter. Profiles were plotted and annotated on a 2-channel chart recorder and written to a PC equipped with an A/D-data acquisition card (Computer Boards Inc., USA) and a custom-built motor controller card. The rate of net photosynthesis (P) in mmoL 0_2 m^{-2} h^{-1} was calculated from the slope of the linear section of each oxygen microprofile (Jørgensen & Revsbech 1985) using the formula: $J(x) = -D_0 \delta C/\delta(x)$, where D_0 is the molecular diffusion coefficient of oxygen (www.unisense.com/support/pdf/gas_tables.pdf) and C is the concentration of oxygen (μM) at depth x (mm). Oxygen calibrations were made at experimental temperature and salinity at 0% saturation (2% sodium ascorbate solution at pH 12) and in air-saturated seawater. The oxygen microelectrode calibration is linear up the saturation level of pure oxygen (476% of air saturation). The pH microelectrode was calibrated with pH standards of 7.0, 8.0, 9.0, and 10.0 and the signal was linear over this range.

Oxygen profiling compared two diatom films (described in Results) at four water velocities, with four replicate late-exponential phase cultures of each diatom species. Subsequent pH and oxygen microprofiles were performed on selected cultures to demonstrate the extremes of pH encountered.

Net Photosynthesis (P) Versus Irradiance (E_d) Curves

For two *Nitzschia ovalis* cultures at late-exponential phase of growth, the P-E_d relationship was determined at 11 irradiance levels covering the range possible in the experimental setup described above. A P-E_d curve was fitted using the function of Platt et al. (1980) modified by the addition of a respiration term (R), and simplified in the absence of photo-inhibition to: $P = P_m [1 - \exp(-\alpha E_d/P_m)] + R$. α is the initial slope of the light curve before the onset of saturation and provides a measure of the efficiency with which the plant utilizes light at low irradiance. The irradiance at onset of photosynthesis saturation, E_k, was calculated as $E_k = P_m/\alpha$. The compensation irradiance, E_c, where the rate of photosynthesis equals the rate of respiration, was calculated by solving the P-E_d curve equation for E_d when $P = 0$. The P-E_d curve was fitted with a nonlinear Levenberg-Marquardt regression algorithm in Curve Expert 1.3.

Diatom Culture and Handling

Benthic diatoms (described in Results, nonaxenic) were cultured on 25 × 25 mm squares of overhead transparency film (103-μm thick) placed on the floor of 6-well tissue culture plates (Falcon). Growth medium was that of Jørgensen (1962) modified by the addition of 0.05 μg/L of vitamin B_{12}. Diatom density was quantified microscopically in 5 subsamples per sample. For microprofiling, the square of transparency film was transferred gently from the culture dish to a custom-made holder in the laminar flow chamber. The edges of the flexible plastic square slid into grooves in the U-shaped holder, creating a slight upward bow in the square. When an oxygen microelectrode touched the flexible plastic film, the signal dipped but the electrode remained intact, allowing profiles down to the surface of the plastic. Parafilm and agar were used as the diatom substrate for postlarval experiments described below, but like Loipersberger (1995), we found these less ideal than plastic as substrata for benthic diatom adhesion and growth. The permeability to oxygen of the overhead transparency film and Parafilm used was negligible—oxygen diffused through transparency film and Parafilm 6,800 and 210 times more slowly than through water.

Effect of Postlarvae on DBL

Films of *Nitzschia ovalis* or *Nitzschia longissima* Grunow were grown on agar (2% in seawater) or Parafilm, and then placed in a 60 mm diameter dish filled with seawater at 20 ± 2°C. Postlarval *Haliotis iris* Gmelin (1.4, 1.7, 1.9 mm SL) were immobilized by: (1) "caging" them on agar with several very fine pins made from drawn glass, pushed into the agar or (2) gluing the rear of the shell to a tiny patch of Parafilm cleared of diatoms using cyanoacrylate medical glue. Postlarvae remained largely active during this treatment. It is possible that the stress of handling and immobilization affected the metabolic rate and oxygen consumption of postlarvae, but we were concerned primarily with alteration of the DBL rather than the actual oxygen concentrations. Oxygen was profiled at various positions around and away from the postlarvae to make observations on the degree to which postlarvae disturb the DBL, and thereby alter the chemistry of their microenvironment.

RESULTS

Description of Diatom Films

Achnanthes longipes grows as a cluster of up to several large cells (31 μm × 13 μm × 16 μm) on the end of a thin stalk. A mature *Achnanthes* film somewhat resembles a forest canopy with stalks leading up to a layer of photosynthetic cells. The cultures used in this study had relatively long stalks for the species with the top of the *Achnanthes* canopy ~1 mm above the growing surface. *Nitzschia ovalis* is a small (8 μm × 5 μm × 5 μm) solitary diatom that forms a flat film 1–2 cells thick. Diatom density in the film of *Nitzschia ovalis* alone was $1.04 \pm 0.04 \times 10^6$ cells cm^{-2} (mean ± SE, $n = 4$). The *Achnanthes longipes* + *Nitzschia ovalis* films averaged $6.9 \pm 0.5 \times 10^5$ cells cm^{-2} of *Nitzschia* and $9.6 \pm 0.88 \times 10^3$ cells cm^{-2} of *Achnanthes*. The diatoms films contained no other algae, but did contain bacteria.

Effect of Diatom Morphology and Water Velocity on DBL

Average DBL thickness over a film of the prostrate diatom *Nitzschia ovalis* increased from 71 μm at an average water velocity of 78 mm s^{-1} to 406 μm at 1 mm s^{-1} (Fig. 1 and Fig. 2). Corresponding maximum measured oxygen concentrations averaged 109% to 148% saturation (Fig. 2B). The presence of a 1-mm tall canopy of the stalked diatom *Achnanthes longipes* above a *Nitzschia ovalis* film thickened the DBL by 3-fold at 1 mm s^{-1} and 6-fold at ~80 mm s^{-1} (Fig. 2A). The upper limit of the DBL fell around or below the top of the *Achnanthes* canopy at the three highest flows but the DBL was still substantially thickened by its presence. Corresponding maximum oxygen concentrations were higher as a result of the thicker DBL, averaging 120% and 214% saturation for 78 mm s^{-1} and 1 mm s^{-1} respectively, at 75 μE m^{-2} s^{-1} (Fig. 2B). Rates of net photosynthesis increased with increasing water velocity for *Nitzschia ovalis* but showed the opposite trend for *Achnanthes longipes* + *Nitzschia ovalis* (Fig. 2C).

More extreme oxygen supersaturation was measured in conjunction with pH profiling (Fig. 3). Oxygen concentrations up to 440% saturation and pH as high as 9.84 (lower and upper bounds 9.71–10.21—see methods) were recorded near the base of an *Achnanthes longipes* + *Nitzschia ovalis* film at 105 μE m^{-2} s^{-1} and ~1 mm s^{-1} water velocity. Cell densities were 7.4×10^3 and 7.8×10^4 cells cm^{-2} for *Achnanthes* and *Nitzschia* respectively. The extreme values were attributable to high rates of net photosynthesis from the film (4.43 mmol O_2 m^{-2} h^{-1}) combined with a thick DBL (1.4 mm). Changes during darkness were less extreme (Fig. 3), with 53% DO saturation and pH 7.70 (7.63–7.72) the minima recorded for a second film (cell densities of 1.2×10^4 and 6.4×10^4 cells cm^{-2} for *Achnanthes* and *Nitzschia* respectively). Net respiration in darkness was 0.2 and 0.6 mmol O_2 m^{-2} h^{-1} for these two films of *Achnanthes* + *Nitzschia*. The pH and oxygen extremes over early stationary phase cultures of *Nitzschia ovalis* were moderated by the thinner DBL (Fig. 3). Net respiration rate (0.37 mmol O_2 m^{-2} h^{-1}) was high relative to net photosynthesis (0.61 mmol O_2 m^{-2} h^{-1}) reflecting the elevated heterotrophic activity in these mature films.

Net Photosynthesis (P) Versus Irradiance (E_d) for Nitzschia ovalis

The maximal rate of net oxygen production at light saturation (P_m) was 4.24 mmol O_2 m^{-2} h^{-1}, and net respiration in darkness consumed 0.434 mmol O_2 m^{-2} h^{-1} (Fig. 4). The compensation irradiance (E_c), at which oxygen production was balanced by oxygen consumption, was 6.6 μE m^{-2} s^{-1}. The irradiance at the onset of photosynthesis saturation (E_k) was 62 μE m^{-2} s^{-1} but net photosynthesis increased up to 126 μE m^{-2} s^{-1} for culture 1 and 228 μE m^{-2} s^{-1} for culture 2 (Fig. 4). The density of the films characterized was 9.7 and 9.8×10^5 cells cm^{-2}.

Effect of Postlarvae on DBL

Postlarvae did alter the DBL and consequently the oxygen concentrations that they were exposed to, but their effect was relatively minor. Ciliary beating drove a water current across the front of the postlarva beneath the shell, entering in the vicinity of the gill. None of the postlarvae examined had the first respiratory pore, which develops at about 2 mm SL in *Haliotis iris*. Movements of the cephalic and epipodial tentacles, rotations of the shell, and the exhalent water current all produced fluctuations in oxygen concentrations at fixed points within the DBL. For 1.7–1.9 mm SL postlarvae, shell rotations combined

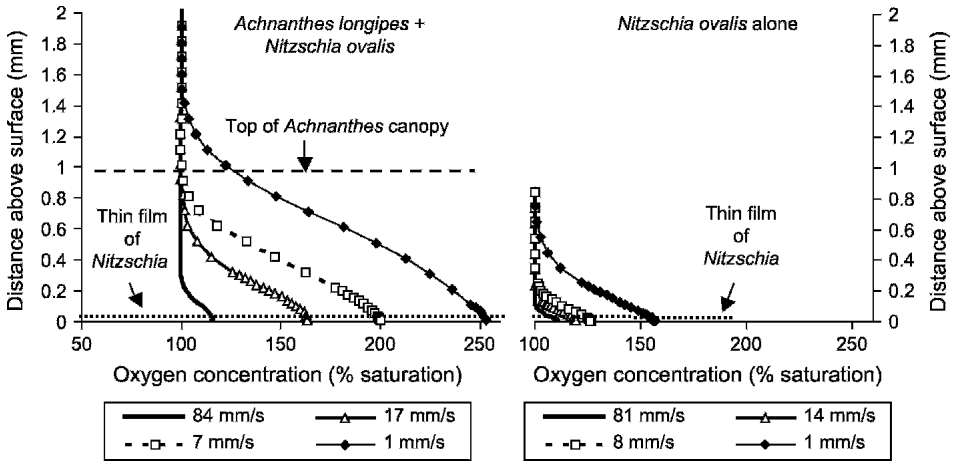

Figure 1. An example of oxygen microprofiles at a range of water velocities. Each data series represents a series of oxygen measurements moving down from the bulk seawater through the DBL to the substratum. The left graph is for a combined film of the stalked diatom *Achnanthes longipes* and the prostrate diatom *Nitzschia ovalis*, whereas the right graph is for a film of *Nitzschia ovalis* alone.

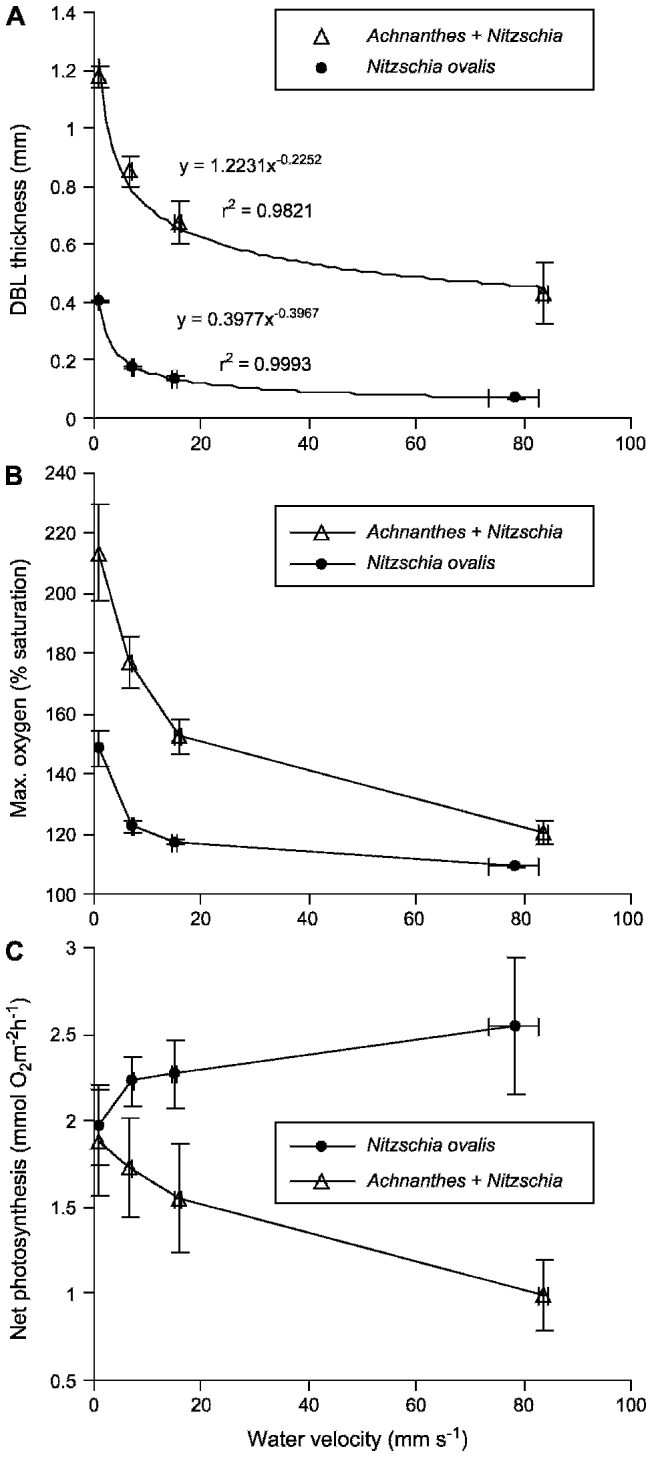

Figure 2. Relationship between water velocity and: (A) DBL thickness; (B) maximum measured oxygen concentration within each profile; and (C) rate of net photosynthesis. Data are mean ± SE, $n = 4$.

with tentacle waving disturbed water up to 2.2 mm above the surface, and exhalent water up to 0.5 mm. The maximum observed amplitude of these fluctuations in oxygen concentration was equivalent to moving 0.3 mm vertically through the DBL. The fluctuations occurred over a period of several seconds to a couple of minutes, so did not sustain a consistent difference in oxygen concentration.

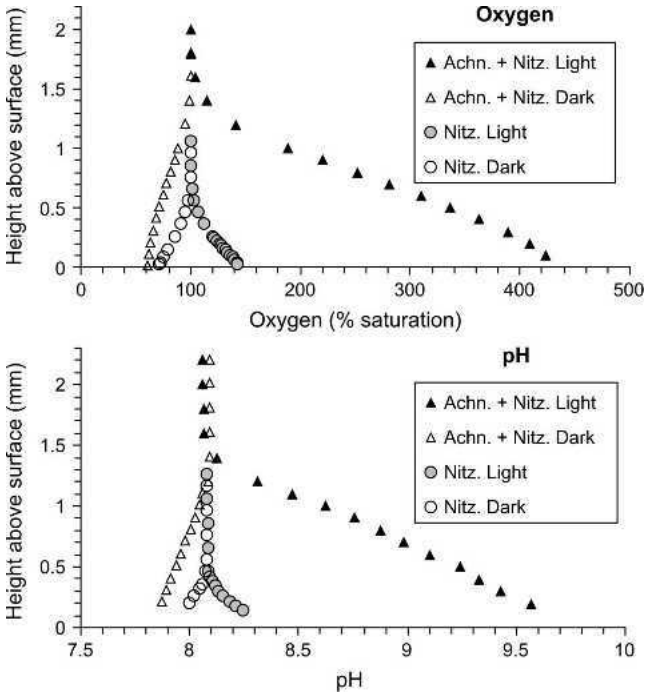

Figure 3. Profiles of oxygen (top) and pH (bottom) over film of *Achnanthes longipes* + *Nitzschia ovalis* (= Achn. + Nitz.) or *Nitzschia ovalis* (= Nitz.) alone, in darkness and in light (105 μE m^{-2} s^{-1}).

DISCUSSION

The addition of a 1-mm tall canopy of the stalked diatom, *Achnanthes longipes*, caused major changes in the water chemistry of the DBL. The presence of *Achnanthes* thickened the DBL, leading to more extreme oxygen concentrations in the zone occupied by postlarval abalone. At very low water velocities, oxygen concentrations ranged from 53% to 440% saturation, and pH from 7.7–9.8.

The *Achnanthes* + *Nitzschia* films used in this study were not extreme examples of microalgal biofilms. Much thicker and higher biomass films develop in abalone hatcheries and natural habitats given adequate time, light, and nutrients (e.g., Dodds et al. 1999, Jones et al. 2000). Nor were the light intensities in this study particularly high. Most profiling was done at 75 or 105 μE m^{-2} s^{-1}, which is ~5% of full sunlight intensity. Higher irradiance, thicker films, and more productive algal assemblages can create more extreme oxygen supersaturation. For example, Larkum et al. (2003) measured oxygen concentrations of 600% to 700% saturation in 1–2 mm thick biofilms growing on coral. The areal rates of photosynthesis recorded in the present study (Fig. 4) are low compared with many algal films (e.g., Dodds et al. 1999, Larkum et al. 2003) because of the relatively low biomass of our diatom films. The photosynthesis-irradiance relationship (Fig. 4) showed that *Nitzschia ovalis* was adapted to relatively low light intensity. The compensation irradiance was only 7 μE m^{-2} s^{-1} and the onset of saturation occurred at 62 μE m^{-2} s^{-1}.

The DBL thicknesses in this study (0.07–1.4 mm) are within the range reported in the literature (e.g., Jensen & Revsbech 1989, Kaspar 1992, Jones et al. 2000, Larkum et al. 2003). They are much thinner than those reported by Loipersberger (1995) who measured DBL thicknesses of 0.5–5 mm over single-cell-thick films of *Nitzschia* and *Navicula* spp. across velocities

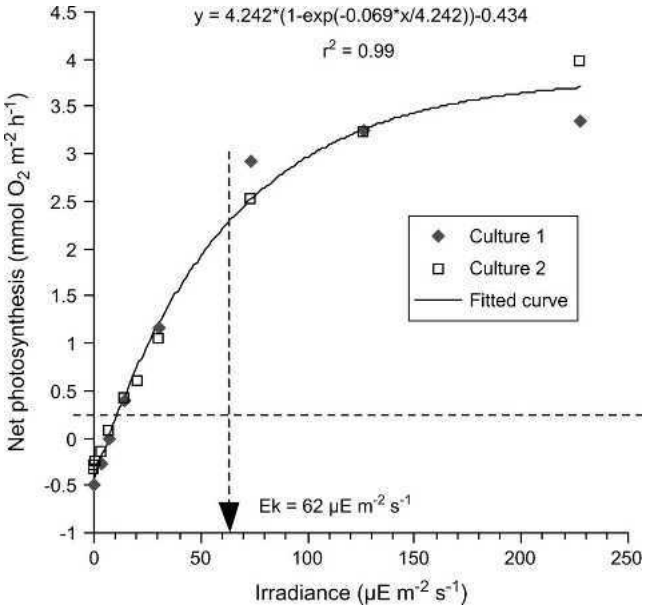

Figure 4. Net oxygen production as a function of downwelling irradiance for two cultures of *Nitzschia ovalis*. Positive production values represent net photosynthesis and negative values represent net respiration. The curve is fitted to the combined data from the two cultures as described in Methods. The dotted horizontal line represents the compensation point where net oxygen production is nil. E_k is the irradiance at the onset of saturation.

of 0–60 mm s^{-1}. Despite the difference in absolute DBL thicknesses, the shape of Loipersberger's decline in DBL thickness with increasing flow was similar to that found in the present study. The details of the experimental setup will influence DBL thickness. The small, thin squares of transparency film that we used may create a thinner DBL than larger or thicker substrates. Both studies used laminar flow to establish stable DBLs. Water movement in aerated abalone settlement tanks is turbulent so the use of laminar flow will probably overestimate DBL thickness in an aerated tank for a given water velocity.

The pH within the DBL reached about 9.8 in the most extreme case of an *Achnanthes* + *Nitzschia* film under very low flow at 105 µE m^{-2} s^{-1}. Similar extremes have been found in previous microelectrode studies with benthic diatoms and more complex algal films (e.g., Jensen & Revsbech 1989, Jones et al. 2000, Larkum et al. 2003). At these high pH values the availability of carbon dioxide and bicarbonate is likely to limit the rate of photosynthesis (e.g., Larkum et al. 2003). Both high and low pH values can affect the growth and survival of abalone. Growth of *Haliotis rubra* was reduced by 50% at pH values of 7.37 or 9.02, but survival was not affected above pH 7.0 (Harris et al. 1999). *Haliotis laevigata* were slightly more tolerant (Harris et al. 1999).

Oxygen and pH changes under darkness were mild compared with the extremes measured in the light, with minima of 53% oxygen saturation and pH 7.7. Rates of net respiration in darkness were typically only about 10% of recorded maximum net photosynthesis rates (Figs. 3 and 4). The stationary phase cultures of *Nitzschia ovalis* (Fig. 3) were an exception, where respiration rate in darkness was ~60% of net photosynthesis rate at 105 µE m^{-2} s^{-1}. The extent of oxygen depletion in darkness will depend on the nature of the community influencing the DBL. Lower minimum oxygen concentrations have been reported at the base of the DBL over *Nitzschia* sp. (30% to 40%, Searcy-Bernal 1996), coralline algae (13%, Kaspar 1992) and stony corals (near 0%, Shashar et al. 1993).

The increased photosynthetic rate of *Nitzschia ovalis* with increased velocity (Fig. 2C) probably relates to more efficient diffusion of solutes across the DBL. The *Achnanthes* + *Nitzschia* films showed the opposite pattern, probably because the *Achnanthes* cells fell increasingly above the DBL as water velocity thinned the DBL, and so released oxygen to the bulk seawater rather than contributing substantially to the DBL gradient.

Postlarval abalone (1.4–1.9 mm) appeared unable to markedly change their local water chemistry within the DBL. Body rotation and tentacle waving caused small disturbances of the DBL, but these fluctuations were short-lived, and of limited amplitude. Some thinning of the DBL is likely to occur because of the respiratory current, and the turbulence created by postlarvae as obstacles in the flow path. Even in combination, these factors will be insufficient for postlarvae to avoid extreme conditions near the base of a thick DBL.

The consequences of extreme oxygen supersaturation for postlarval and very small juvenile abalone remain unclear. The only preliminary tests done with postlarvae (unspecified size) found no mortality from oxygen concentrations that varied between 150% and 300% saturation for four days (Loipersberger 1996). Loipersberger also exposed 30-mm juveniles to 300% oxygen saturation for 22 days with nil mortality. This latter finding contrasts with other abalone data. Elston (1983) generated 150% to 200% oxygen saturation by algal photosynthesis and observed clinical and histological effects in 8–10 mm *Haliotis rufescens* within several hours of exposure. Leitman (1992) documented lethal and sublethal effects in 12 mm *Haliotis rufescens* from 120% to 143% oxygen saturation over several weeks. *Haliotis rubra* had reduced growth and survival at 120% saturation, whereas *Haliotis laevigata* did not (Harris et al. 2005).

Abalone postlarvae survive and grow well on favorable diatom species in small, static assays (e.g., Roberts et al. 1999) where boundary layers would be thick and extreme oxygen supersaturation is expected. Observations of increased growth and survival of postlarvae reared in darkness or very low light suggest a role for harmful DBL effects, but could also be explained by behavioral or nutritional factors (Searcy-Bernal et al. 2003, Gorrostieta-Hurtado & Searcy-Bernal 2004).

The challenge of coping with extreme water chemistry in the DBL is not limited to aquaculture situations, or to abalone. Oxygen and pH fluctuations as wide or wider than those described here have been described for natural biofilms from marine and freshwaters (e.g., Kaspar 1992, Jones et al. 2000; Larkum et al. 2003). Hence any benthic species with submillimetric juvenile stages may experience extreme oxygen concentrations particularly when water velocity is low or biofilms are thick. This could be a significant factor in the extremely high mortality rates of marine invertebrate postlarvae in natural habitats (e.g., Shepherd & Daume 1996).

Until the susceptibility of abalone postlarvae to high and low oxygen saturation is better known, judicious tank management can be used to minimize risks. The present study highlighted the impact of water velocity and filamentous diatoms on DBL thickness and water chemistry. Solitary, prostrate diatom species typically dominate early in diatom film development, with filamentous growth forms developing several weeks after

settlement (Kawamura & Hirano 1992). Filamentous diatoms like *Achnanthes longipes* grow poorly in lower light levels (Graham et al. 2005) so shading of tanks in the weeks after settlement, and regular flipping of plates, offer simple means of maintaining areas free of filamentous diatoms. At least some of the prostrate diatoms that are ideal as food for small postlarvae (Kawamura et al. 1998) remain productive at relatively low irradiance (Graham et al. 2005; Figure 4 of this study). To achieve nil net oxygen production, growers should target the compensation irradiance (E_c) of the algae in their system (taking into account the shading that occurs between plates). For *Nitzschia ovalis*, the E_c was only 7 $\mu E\ m^{-2}\ s^{-1}$ (Fig. 4).

This study illustrated the erosion of the DBL by water velocities of a few cm s^{-1} under laminar flow. Typical settlement tank aeration drives turbulent flow between settlement plates at velocities of several cm s^{-1}, and much higher velocities occur adjacent to rising air bubbles (pers. obs.). Increasing the water velocity further will have limited effect on the thickness of the DBL (Fig. 2). As soon as aeration ceases, the DBL will begin to thicken and water chemistry will become more extreme. Maintenance of normal vigorous aeration is therefore the simplest and most effective means of moderating water chemistry within the postlarval environment.

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