Modelling the contribution of benthic microbial mats to net primary production in Lake Hoare, McMurdo Dry Valleys

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Abstract: A model was used to simulate primary production of benthic microbial mats in Lake Hoare, southern Victoria Land, Antarctica, and to compare potential benthic to planktonic production. Photosynthetic and respiratory characteristics of mats from five depths in the lake were extrapolated across depth, surface area and time, to estimate whole-lake, annual net primary production. Variation in under-ice light regimes resulting from changes in ice thickness and transparency, and light extinction in the water column was examined, and an uncertainty analysis of key model parameters performed. Daily mat production estimates were 0.98–37.83 mg C m⁻² d⁻¹, depending on depth and PAR, whereas in situ production of phytoplankton averaged 15% of this. Annual patterns of mat production achieved maximum rates of 15–16 g C m⁻² y⁻¹ at 10 m depth when ≥5% of ambient PAR was transmitted through the ice covering the lake; observed transmittance values were usually ≤5%. Increasing underwater PAR had little effect above 5–7% transmittance, as photosynthesis became saturated at this level. Uncertainties in estimates of maximum photosynthetic rate (Pmax), initial slope of photosynthetic-light response (α) and maximum respiration rate (Rmax) explained 72–99% of uncertainty in model behaviour; Pmax was increasingly important at high light levels whereas α was more important at low light levels, however Rmax exerted the greatest influence under most conditions.

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Introduction

Mat-forming, benthic microbial communities are common in a wide range of aquatic ecosystems throughout the world, but are especially abundant where disturbance pressures are low and environmental conditions are extreme, such as saline lakes and geothermal springs (Stal 1995). Under such conditions the ability of stress-tolerant microbes to slowly accumulate numbers and biomass appears to explain their dominance. Microbial mats also dominate the biomass and productivity of ponds, streams, and lakes of the McMurdo Sound region of Antarctica (Vincent et al. 1993a, Hawes & Howard-Williams 1998, Hawes & Schwarz 1999, 2000). These habitats provide a high stress-low disturbance regime; typically stressful conditions include combinations of low temperature, high pH, seasonal freezing, frequent desiccation, high salinity, continuous high or low irradiance and long periods of darkness. However, these stresses are offset by the absence of vascular plants, vertebrate animals, crustaceans and insects so that competition and grazing pressures from organisms commonly present in temperate aquatic systems are absent (Vincent 1988, Hawes & Howard-Williams 1998).

Many studies have examined the composition, distribution and metabolic characteristics of these communities (Wharton et al. 1983, 1989, Hawes et al. 1993, 1999, Hawes & Howard-Williams 1998, Hawes & Schwarz 1999, 2000), and simulation models have been developed to explore patterns of behaviour and calculate rates of production (Moorhead et al. 1997b, Hawes et al. 2001). However, while localized high biomass and correspondingly high levels of activity have been documented, the contributions of benthic mat communities to whole-lake primary production have not been quantified. Here we use a mathematical model to estimate production of benthic mats in Lake Hoare, Taylor Valley, Antarctica, and compare these estimates to observed patterns of phytoplankton production. In addition, recent data on climate variability in the Taylor Valley has shown that irradiance, one of the primary drivers of productivity, varies from year-to-year due to changes in lake ice thickness and depth (Doran et al. 2002). We therefore conducted an uncertainty analysis of the model by varying the values of key model parameters and evaluating the subsequent impacts of these variations on estimated patterns of net primary production.

Location and environmental characteristics

Study site

The McMurdo Dry Valleys are located in eastern Antarctica (76°30’–78°30’S, 160°–164°E), and represent the largest ice-free region of the continent (c. 4800 km²; Matsumoto...
The most persistent aquatic ecosystems in the McMurdo Dry Valleys are a number of lakes that receive water from seasonal melting of nearby glaciers. Most of these lakes have closed basins and are covered by a permanent ice cover of approximately 3–5 m thickness (Andersen et al. 1993, Chinn 1993, Wharton et al. 1993). This ice cover reduces light penetration, restricts gas exchange, and limits sediment input (Simmons et al. 1993, Wharton et al. 1993). This cover also eliminates currents caused by the wind and so decreases mixing (Matsumoto 1993, Wharton et al. 1993, Spaulding et al. 1997). Most lakes also have strong salinity gradients and low but stable temperature profiles that further contribute to stratification of the water column (Spigel & Priscu 1998). Thus stable stratification imposes conditions on benthic mats that can vary sharply with depth, and in turn, influence patterns of primary production (Hawes & Schwarz 1999, 2000).

Lake Hoare (77°38′S, 162°53′E) is located in Taylor Valley. It is 4.2 km long, 1.0 km wide, and 34 m deep at its deepest point (Spigel & Priscu 1998). The lake is dammed to the north-east by the Canada Glacier, which provides an inflow of glacial meltwater (Wharton et al. 1993). Other sources of inflow come from Andersen Creek, which enters the north-east corner of Lake Hoare, and drainage from Lake Chad in the south-east. Lake Chad receives water from the Seuress Glacier, and recently has become a contiguous part of Lake Hoare as the depths of these two lakes increased over the past decade (Spaulding et al. 1997). No outflows from Lake Hoare exist, so water loss is restricted to sublimation of ice and evaporation of meltwater during summer (Wharton et al. 1993, Doran et al. 1994). Lake Hoare was chosen as the focus for the present study because it is one of the lakes that have been continuously monitored by the McMurdo Long-Term Ecological Research (LTER) program (1993–present), and it has been the site of intensive studies on benthic mat communities (Hawes & Schwarz 2000, Hawes et al. 2001).

**Microbial mats**

Photosynthetic microbial mats exist at the sediment water interface throughout Lake Hoare, except at depths below 26 m, at which point the water becomes anoxic (Wharton et al. 1989, Hawes & Schwarz 1999). These microbial mats are dominated by filamentous cyanobacteria, pennate diatoms, and heterotrophic bacteria, and vary in composition with depth (Wharton et al. 1983, 1989, Squyres et al. 1991, Doran et al. 1994, Hawes & Schwarz 1999). Cyanobacteria have a higher density in mats from 3.5 to 10 m, whereas diatom relative abundance increases below 10 m (Hawes & Schwarz 1999). A clear distinction exists between mats growing under perennial ice and those in the marginal areas of lakes where seasonal melt provides open water. The latter are termed “moat mats”.

Rates of photosynthesis and respiration are low and vary with location, photosynthetically available radiation (PAR) flux and species composition (Howard-Williams et al. 1989, Vincent & Howard-Williams 1989, Hawes 1993, Hawes & Schwarz 1995, Vincent et al. 1993a, 1993b, Moorhead et al. 1997b). According to Hawes & Schwarz (1999) moat mats are acclimated to high levels of PAR but use it inefficiently. Mats beneath the permanent ice cover are more efficient, maintaining photosynthesis at 50% of their maximum rates even at < 5% ambient PAR (Hawes & Schwarz 1999, 2000). Hawes & Schwarz (1999) estimated that moat mats fix 140 mg C m⁻² d⁻¹ in Lake Hoare, and that deeper mats may fix as much as 100 mg C m⁻² d⁻¹ despite much lower PAR.

Hawes & Schwarz (1999) attribute differences in production efficiency of mats at different depths to shade acclimation, suggested by increasing ratios of phycoerythrín:phycoeryxin with increasing depth and decreasing PAR irradiance, as well as high concentrations of light shielding carotenoid pigments in moat communities. Although under-ice mats are adapted to extremely low levels of PAR and have very low irradiance-saturating photosynthesis, PAR at the mat surface is often less than saturating (Hawes & Schwarz 1999, 2000). For these reasons environmental conditions affecting incident PAR are likely to also affect mat production.

Respiration rates of microbial mats in Lake Hoare also vary with water depth. Moat mats had respiration rates approaching 2 µg C cm⁻³ h⁻¹ (c. 480 mg C m⁻² d⁻¹) whereas rates of mats under the permanent ice cover (3.5 to 19 m depth) were < 1 µg C cm⁻² h⁻¹ (Hawes & Schwarz 1999). Moreover, Hawes & Schwarz (1995) observed that respiration rates slowed as periods of darkness increased. Thus the respiratory process also varies temporally, probably as carbohydrate reserves are exhausted (Hawes et al. 2001).

**Radiant energy regime**

Radiant energy regime is a primary control on the
productivity of benthic mats (Hawes & Schwarz 1995, 1999, 2000). At the latitude of Lake Hoare, PAR regimes include 24 hours of light during three summer months, 24 hours of darkness during three winter months, and rapidly changing diel patterns during seasonal transitions (Dana et al. 1998). Incident PAR is strongly affected by ice cover and both clarity and depth of the water column (Howard-Williams et al. 1998). Permanent ice covers generally transmit less than 5% ambient solar radiation, although the actual value varies with thickness, albedo, and sediment content (McKay et al. 1994, Howard-Williams et al. 1998). The water column further attenuates PAR resulting in extremely low irradiance at the mat surface (McKay et al. 1994, Hawes & Schwarz 1999, 2000).

Ice covers on McMurdo Dry Valley lakes have been changing over the past two decades. For example, the ice on Lake Hoare measured 3.5 m thick in 1983 (Wharton et al. 1993, Spaulding et al. 1997), but has increased to c. 5 m since that time (Doran et al. 2002). Clearly, lake ice thickness is dynamic and has a major impact on transmittance of PAR to the underlying water that, in turn, likely affects production of benthic mats.

Modelling parameters

This modelling study has three objectives. The first is to explore the sensitivity of carbon dynamics in these models of mat communities to uncertainty in parameter estimates, including changing light (PAR) regime that might realistically accompany observed changes in ice cover. The second is to compare benthic production to phytoplankton production in the overlying water column, and to simulate potential whole lake production of benthic microbial mats. The final objective is to simulate year-round whole lake benthic production.

Table I. List of parameters for equations used in model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Initial value</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{max}}$</td>
<td>$\mu g O_2 cm^{-2} h^{-1}$</td>
<td>Table II</td>
<td>1</td>
</tr>
<tr>
<td>$a$</td>
<td>$\mu g O_2 cm^{-2} h^{-1}(\mu mol photons m^{-2} s^{-1})^{-1}$</td>
<td>Table II</td>
<td>1</td>
</tr>
<tr>
<td>$R_{\text{max}}$</td>
<td>$\mu g O_2 cm^{-2} h^{-1}$</td>
<td>Table II</td>
<td>2</td>
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<tr>
<td>$D$</td>
<td>hours</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>$c$</td>
<td>dimensionless</td>
<td>12</td>
<td>2</td>
</tr>
<tr>
<td>$M$</td>
<td>days</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>$\phi$</td>
<td>day</td>
<td>-1</td>
<td>3</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>$\mu mol photons m^{-2} s^{-1}$</td>
<td>554.591</td>
<td>3</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>$\mu mol photons m^{-2} s^{-1}$</td>
<td>843.387</td>
<td>3</td>
</tr>
<tr>
<td>$\alpha_3$</td>
<td>hours</td>
<td>1 to 24</td>
<td>3</td>
</tr>
<tr>
<td>$J$</td>
<td>day</td>
<td>1 to 365</td>
<td>4</td>
</tr>
<tr>
<td>$\theta$</td>
<td>day</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>$\alpha_4$</td>
<td>$\mu mol photons m^{-2} s^{-1}$</td>
<td>1100</td>
<td>4</td>
</tr>
<tr>
<td>$\alpha_5$</td>
<td>hours</td>
<td>450</td>
<td>4</td>
</tr>
<tr>
<td>$S_{\text{max}}$</td>
<td>$\mu mol photons m^{-2} s^{-1}$</td>
<td>1500</td>
<td>4</td>
</tr>
<tr>
<td>$t$</td>
<td>percent</td>
<td>1 to 15</td>
<td>5</td>
</tr>
<tr>
<td>$Y$</td>
<td>decimal year</td>
<td>1996.0 to 2000.0</td>
<td>6</td>
</tr>
<tr>
<td>$z$</td>
<td>metres</td>
<td>5,7,10,13,19</td>
<td>8</td>
</tr>
<tr>
<td>$k$</td>
<td>$m^{-1}$</td>
<td>0.14</td>
<td>7,8,9</td>
</tr>
</tbody>
</table>

Table II. Values of photosynthetic and respiration parameters used in simulations (Hawes & Schwarz 1999, Hawes et al. 2001); mean values ± standard deviations.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>$P_{\text{max}}$</th>
<th>$a$</th>
<th>$R_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>1.40 ± 0.24</td>
<td>0.11 ± 0.04</td>
<td>0.41 ± 0.16</td>
</tr>
<tr>
<td>7</td>
<td>2.32 ± 0.12</td>
<td>0.52 ± 0.07</td>
<td>0.58 ± 0.10</td>
</tr>
<tr>
<td>10</td>
<td>2.06 ± 0.29</td>
<td>0.70 ± 0.20</td>
<td>0.34 ± 0.06</td>
</tr>
<tr>
<td>13</td>
<td>1.45 ± 0.09</td>
<td>0.44 ± 0.06</td>
<td>0.25 ± 0.08</td>
</tr>
<tr>
<td>19</td>
<td>0.70 ± 0.11</td>
<td>0.04 ± 0.03</td>
<td>0.33 ± 0.16</td>
</tr>
</tbody>
</table>

These objectives illustrate some of the greatest practical benefits offered by mathematical models. First, simulations can be viewed as surrogates for experiments in systems that are difficult to study. Indeed relatively few observations can be made of benthic mats in situ because SCUBA diving in freezing water beneath the permanent ice on Lake Hoare is both logistically limiting and dangerous. A rigorous modelling assessment of both the responses of mats to changing environmental conditions and the importance of uncertainty in parameter estimates to those responses, can help focus subsequent field studies on the most relevant aspects of this system, ensuring maximum insight from limited data collection. Second, the model can readily be used to interpolate between depths and extrapolate across areas to estimate mat production for the entire lake. Lakes are among the most productive ecosystems and maintain the greatest densities of organic matter in the McMurdo Dry Valleys. Hence, knowledge of the relative contributions of benthic and planktonic communities would also provide insight to the larger patterns of carbon dynamics in the valleys. Finally, these simulations can provide insight to likely impacts on benthic mat productivity resulting from environmental changes that alter incident PAR.

Biomass dynamics

Our model was constructed using the computer program STELLA® Research 6.0 (High Performance Systems Inc. 2000). It was a modified version of a benthic mat production model first developed by Moorhead et al. (1997a, 1997b) and later improved by Hawes et al. (2001). The conceptual basis of this model is that PAR drives photosynthesis, which provides the only input of carbon to the mat. Respiration is assumed to be the only loss of carbon. Therefore, biomass accumulation is calculated as the difference between photosynthesis and respiration. Photosynthesis ($P$) was estimated using the hyperbolic tangent equation from Jassby & Platt (1976):

$$P = P_{\text{max}} \cdot \tanh(\alpha \cdot \frac{E_z}{P_{\text{max}}}) \quad (1)$$
where \( P_{\text{max}} \) is the maximum rate of photosynthesis, \( \alpha \) is the initial slope of the photosynthetic response curve and \( E_z \) is level of PAR at depth \( z \). Parameter values are listed in Tables I & II.

Respiration rates of benthic mats of Lake Hoare have been shown to decline during periods of darkness (Hawes et al. 2001), verifying speculations based on earlier modelling studies in Lake Hoare (Moorhead et al. 1997b).

Hawes et al. (2001) derived a best-fit model from laboratory studies in which respiration rate declined as a sigmoid function of cumulative period of darkness:

\[
R = (1 - 0.7 \cdot \left( \frac{D}{D + M} \right))^c \cdot R_{\text{max}}
\]  

(2)

where \( R_{\text{max}} \) is the maximum rate of respiration, \( D \) is the number of hours of darkness, \( c \) is an exponent, and \( M \) is the mid-point of the curve (Tables I & II).

\textbf{Ambient PAR regime}

Field observations used to calculate ambient PAR were obtained from the McMurdo Dry Valleys Long-Term Ecological Research program (McMurdo LTER; huey.colorado.edu/LTER/). A cosine equation was used to simulate hourly, ambient PAR irradiance:

\[
E_o = A_i \cdot \left( \cos \left( \frac{h + \sigma_j}{24} \right) \cdot 2\pi \right) + b_i + S
\]  

(3)

where \( E_o \) is ambient PAR, \( A_i \) is the amplitude, \( h \) is the hour of the day, \( \sigma_j \) is a phase shift, \( b_i \) is a constant, and \( S \) is a seasonal shift in maximum daily energy flux (Fig. 1; \( n = 144, r^2 = 0.993 \)). A cosine equation also was used to simulate the seasonal change in maximum daily PAR:

\[
S = S_{\text{max}} - A_s \cdot \left( \cos \left( \frac{J + \sigma_s}{24} \cdot 2\pi \right) \right) + b_s
\]  

(4)

where \( S_{\text{max}} \) is the maximum possible PAR irradiance during the year, \( A_s \) is the amplitude, \( J \) is the day of the year, \( \sigma_s \) is the phase shift, and \( b_s \) is a constant (Fig. 2; \( n = 366, r^2 = 0.948 \)).

The permanent ice cover on Lake Hoare transmits \( \leq 5\% \) of ambient PAR, but transmittance varies through space (Howard-Williams et al. 1998). Physical characteristics of the ice that affect transmittance include ice thickness,

\textbf{Fig. 1.} Match between simulated (line) and observed (filled circles) ambient PAR irradiance at Lake Fryxell meteorological station in Taylor Valley on 15 December 1993; \( n = 144, r^2 = 0.993 \) (McMurdo LTER; huey.Colorado.edu/LTER/).

\textbf{Fig. 2.} Match between simulated (line) and observed (filled circles) maximum daily PAR irradiance at Lake Fryxell meteorological station in Taylor Valley on 1993–99; \( n = 366, r^2 = 0.948 \) (McMurdo LTER; huey.Colorado.edu/LTER/).

\textbf{Fig. 3.} Observed (filled circles) and estimated (line) increase in ice thickness on Lake Hoare from 1995–2000; \( n = 58, r^2 = 0.402 \) (McMurdo LTER; huey.Colorado.edu/LTER/).
bubbles and sediment content (McKay et al. 1994). Although the sensitivity of mats to changing PAR is the central focus of this study, the underlying mechanisms that control transmittance are beyond the scope of this study. Hence we calculated transmitted PAR as a constant fraction of ambient radiation (but see Eq. (7)):

\[ E_t = E_o \cdot t \]  

(5)

where \( E_t \) is PAR transmitted through the ice cover and \( t \) is the fraction transmitted. This simple function allows modification of underwater PAR regimes to meet model objectives (see above), i.e. exploring shifts that may result from changing climate (Doran et al. 2002).

Ice thickness has a substantial impact on the transmittance of PAR to the underlying water column (McKay et al. 1994), and has increased on Lake Hoare over the past decade (Doran et al. 2002). The thickness of ice on Lake Hoare was available for several locations and dates in each of five years from 1995 to 2000 (Fig. 3). Regression analysis showed a significant, linear increase in ice thickness over this time period, and was used to estimate the ice thickness for model simulations (\( n = 58, \text{ mode} r^2 = 0.402 \)):

\[ T = 0.177 \cdot Y - 348.63 \]  

(6)

where \( T \) is ice thickness (metres) and \( Y \) is decimal year.

Transmittance of PAR through the ice cover was estimated by comparing diurnal regimes of ambient PAR and intensities at 10 m depth below the permanent ice cover on Lake Hoare. Observations were available between November 1996 and December 1999 (McMurdo LTER). Transmittance through the permanent ice cover (\( t \)) was calculated by rearranging the following equation:

\[ E_{10} = (E_o \cdot t) \cdot e^{-(k \cdot (10-T))} \]  

(7)

where \( E_{10} \) is PAR at 10 m depth, \( (10-T) \) is the thickness of the water column between the 10 m sensor and the underside of the ice, \( E_o \) is ambient PAR and \( k \) is the extinction coefficient (estimated with Eq. (9) below). These calculations showed an increase in transmittance of PAR through surface ice from the latter part of 1996 through 1999 (Table III). This pattern, in turn, suggests a positive relationship between transmittance and ice thickness, which is contrary to expectations. Of course, many other factors also influence transmittance, such as sediment loading and water content of ice (MacKay et al. 1994, Howard-Williams et al. 1998), which were not reported during this period.

The water column further attenuates PAR transmitted through the permanent ice cover, and was calculated with an exponential equation:

\[ E_z = E_{10} \cdot e^{(k \cdot (z-T))} \]  

(8)

where \( E_z \) is the PAR at depth \( z \), \( k \) is the attenuation coefficient of the water column and \( (z-T) \) adjusts water depth for the thickness of the overlying ice (Table I).

Profiles of PAR irradiance with depth below the perennial ice cover on Lake Hoare were reported for 23 dates between November 1993 and December 1999 (McMurdo LTER; huey.Colorado.edu/LTER/). Values of PAR were too low in September 1995 for analysis, but the extinction coefficients \( (k) \) on 17 other dates were estimated as the negative exponent of the decline in PAR with depth. Regression analysis showed that extinction coefficients did not vary between years, but did have a significant decline over the summer within years (Fig. 4). This linear relationship was used to estimate the coefficient of extinction for model simulations (\( n = 17, \text{ model } r^2 = 0.434 \)):

\[ k = 0.2251 - 0.0011 \cdot J \]  

(9)

where \( J \) is day of year (values of \( J \) exceeded 365 for days within the austral summer season that extended beyond 31 December of the calendar year).

Photosynthetically usable radiation (PUR)

Not only is PAR attenuated by the ice cover and water...
column of Dry Valley lakes, but the spectral composition of transmitted radiation is also modified. In particular, intensities of longer wavelengths (> 600 nm) are reduced in proportion to shorter wavelengths (McKay et al. 1994, Hawes & Schwarz 2000). Microbial mats in Lake Hoare show high absorbance at wavelengths < 600 nm, but little absorbance at longer wavelengths, with the exception of a chlorophyll a peak at 675 nm (Hawes & Schwarz 2000). For this reason, measures of photosynthetic response to full spectrum PAR probably underestimate photosynthesis in mat communities (e.g. Hawes & Schwarz 2000, Hawes et al. 2001). In fact, Hawes & Schwarz (2000) showed that the proportional transmittance of radiation at wavelengths useable for photosynthesis (PUR) was approximately 50% higher than the overall transmittance of PAR, due to the relative enrichment of shorter wavelengths that are more effectively absorbed by the pigment arrays found in microbial mats.

The relationship between PAR and PUR becomes problematic as photosynthetic parameters (Hawes & Schwarz 1999, 2000) were based on light passed through optical filters to mimic the under-ice spectrum, yet our measures of under-ice irradiance are based on broad-spectrum instruments. For this reason, estimating the transmittance of ice from measurements of incident and under-ice PAR will underestimate the true transmittance of PUR, as it will be biased by low transmittance of long wavelengths. We corrected for the impact of this higher apparent transmittance by moderating our estimate of ice transparency upwards by a factor of 1.5 (see below).

Simulations

Simulations I: Impacts of changing PAR
This model was used to simulate net organic carbon production by microbial mats of Lake Hoare over a one-year period beginning 1 January and ending 31 December. Simulations included mats at five water depths (5, 7, 10, 13, 19 m) using photosynthesis and respiration parameters listed in Tables I & II. The effects of incident PAR were assessed at each depth, by repeating each simulation 15 times, and by varying PAR transmittance through lake ice from 1 to 15%. This range of transmittances includes values much higher than observed for lakes in Taylor Valley (Howard-Williams et al. 1998), hence there was no need to specifically include the impacts of a spectral shift in under-ice irradiance in this set of simulations.

An uncertainty analysis was then conducted to examine the sensitivity of model behaviour to variation in key parameter estimates. Three model parameters were chosen for this analysis ($P_{\text{max}}$, $\alpha$ and $R_{\text{max}}$) which earlier studies have shown to be important determinants of model behaviour (Moorhead et al. 1997a, 1997b), and for which measures of natural variation have been reported (Hawes et al. 2001). These are also the physiological parameters most likely to be varied by photosynthetic organisms in response to fluctuating irradiance (MacIntyre et al. 2002). The reported values were expressed as coefficients of variation for each parameter (Hawes et al. 2001), and were converted to standard deviations for use in this analysis (Table II) by multiplying each mean by the corresponding coefficient of variation (Motulsky 1995).

For simulations, 50 values were selected randomly for each model parameter from within one standard deviation of each parameter mean, using the Monte Carlo function in STELLA. Thus each simulation used a unique set of random values for the three parameters. Each set of parameters was used to estimate production at each of 1–15% values for PAR transmittance (see above). A Pearson’s Product-Moment correlation test was performed to verify that selected parameter values were not correlated ($P > 0.05$; SPSS Inc., Chicago: Version 9.0, 1999). The results of these simulations were used in an analysis of variance to evaluate variability in model behaviour due to the uncertainty associated with each parameter (Moorhead et al. 1997a, 1997b). In this analysis, the dependent variable was total organic carbon accumulated in one year, and the model parameters $P_{\text{max}}$, $\alpha$ and $R_{\text{max}}$ were treated as independent variables. The uncertainty in model result (net annual production) attributable to each parameter was quantified as the partial sums of squares (Type II) associated with each parameter, given depth in the water column and percent transmittance of PAR (SPSS Inc., Chicago: Version 9.0, 1999). Again, we did not include the impacts of a spectral shift in PAR for this set of simulations.

Simulations II: Comparison of daily benthic to planktonic primary production
The intention of this series of comparisons was to compare observed measurements of planktonic photosynthesis (McMurdo LTER) with same-day simulations of benthic photosynthesis. For each of 10 dates between 8 November 1996 and 12 December 1999 on which planktonic production data were available, we calculated the coefficient of extinction ($k$) according to Eq. (9). Depth of the water column was adjusted for ice thickness (Eq. 6). Transmittance ($t$) through the ice cover was set equal to the mean of calculated values (Eq. 7) for each season (Table III), based on extinction coefficient ($k$). Large variation in these parameter values produced considerable uncertainty in incident PAR regimes and subsequent estimates of mat production. This uncertainty was incorporated in simulations by randomly selecting 50 independent estimates of $k$ within a range of ± 20% of the calculated value for that day (Eq. 9). Similarly, values of PAR transmittance were selected randomly within 1 SD of the calculated mean for that season (Table III). The impact of an altered spectral composition for transmitted radiation was simulated by setting transmittance of photosynthetically useable radiation (PUR) as 150% of that of PAR (discussed above),
and then driving photosynthesis with PUR (Eq. 1). These conditions were used to generate daily net primary production for mats at each of the five depths (5, 7, 10, 13 and 19 m).

Daily mat production was expressed as mean ± standard deviation from the 50 simulations at each depth (Table IV) and used to make comparisons with production of phytoplankton on the same dates. These comparisons were made on a whole-lake basis, based on a detailed analysis of the bathymetry of Lake Hoare (Fig. 5). The production of phytoplankton communities at 1 m depth increments within the water column of Lake Hoare was estimated by linear interpolation between the depths at which net primary production was reported (Table V). Plankton production at 1 m depth intervals was multiplied by the volume of water and used to make comparisons with production of mats at each of the five depths (5, 7, 10, 13 and 19 m).

Table IV. Simulated values of net primary production for benthic communities in Lake Hoare (µg C cm⁻² d⁻¹; mean ± standard deviation). Negative values indicate estimated rates of respiration exceeded photosynthesis.

<table>
<thead>
<tr>
<th>Date</th>
<th>Depth (m)</th>
<th>5</th>
<th>7</th>
<th>10</th>
<th>13</th>
<th>19</th>
</tr>
</thead>
<tbody>
<tr>
<td>08 Nov 96</td>
<td>0.13 ± 0.02</td>
<td>1.64 ± 0.45</td>
<td>2.21 ± 0.85</td>
<td>0.02 ± 0.56</td>
<td>-2.41 ± 0.03</td>
<td></td>
</tr>
<tr>
<td>02 Dec 96</td>
<td>0.64 ± 0.01</td>
<td>6.04 ± 0.43</td>
<td>6.88 ± 0.92</td>
<td>3.22 ± 1.05</td>
<td>-2.15 ± 0.17</td>
<td></td>
</tr>
<tr>
<td>12 Jan 97</td>
<td>4.75 ± 0.04</td>
<td>11.66 ± 0.18</td>
<td>11.72 ± 0.44</td>
<td>7.15 ± 0.81</td>
<td>-1.36 ± 0.50</td>
<td></td>
</tr>
<tr>
<td>15 Nov 97</td>
<td>-0.37 ± 0.02</td>
<td>3.69 ± 0.34</td>
<td>4.94 ± 0.78</td>
<td>2.20 ± 0.85</td>
<td>-2.20 ± 0.14</td>
<td></td>
</tr>
<tr>
<td>26 Dec 97</td>
<td>-0.21 ± 0.02</td>
<td>4.24 ± 0.44</td>
<td>5.38 ± 0.90</td>
<td>2.37 ± 0.96</td>
<td>-2.21 ± 0.14</td>
<td></td>
</tr>
<tr>
<td>03 Nov 98</td>
<td>1.46 ± 0.03</td>
<td>7.74 ± 0.42</td>
<td>8.14 ± 0.98</td>
<td>3.73 ± 1.16</td>
<td>-2.16 ± 0.16</td>
<td></td>
</tr>
<tr>
<td>01 Dec 98</td>
<td>3.92 ± 0.06</td>
<td>11.16 ± 0.26</td>
<td>11.03 ± 0.70</td>
<td>5.86 ± 1.18</td>
<td>-2.00 ± 0.24</td>
<td></td>
</tr>
<tr>
<td>26 Dec 98</td>
<td>-0.41 ± 0.02</td>
<td>3.98 ± 0.53</td>
<td>4.84 ± 1.08</td>
<td>1.61 ± 0.94</td>
<td>-2.31 ± 0.09</td>
<td></td>
</tr>
<tr>
<td>17 Nov 99</td>
<td>3.26 ± 0.01</td>
<td>9.29 ± 0.29</td>
<td>9.26 ± 0.70</td>
<td>4.69 ± 1.07</td>
<td>-2.11 ± 0.19</td>
<td></td>
</tr>
<tr>
<td>12 Dec 99</td>
<td>1.56 ± 0.03</td>
<td>7.67 ± 0.43</td>
<td>7.66 ± 1.03</td>
<td>3.04 ± 1.13</td>
<td>-2.26 ± 0.11</td>
<td></td>
</tr>
</tbody>
</table>

Simulations III. Annual whole-lake mat production

The net annual production of plankton communities in Lake Hoare has not been calculated and is beyond the scope of this study. However, we simulated net annual production of mats for the years 1996–99, given simulated ambient PAR (Eqs 3 & 4), extinction coefficient (Eq. 9), ice thickness (Eq. 6), mean transmittance through the ice cover (Table III) and spectral shift (PUR = 150% PAR). We estimated net annual production for benthic mats in a manner similar to daily production (see above), by linearly interpolating between the mean annual simulated values at 5, 7, 10, 13 and 19 m. Production estimates were multiplied by the benthic surface area at each 1 m depth increment (Fig. 5), to calculate total annual production of benthic mats of the entire lake. Total annual production of benthic mats was estimated to a depth of 19 m. Although Lake Hoare has a maximum depth of 34 m, water below 23 m is anoxic and primary production is nearly undetectable below 19 m. Hence, our calculations exclude a small proportion of the phytobenthos.

Results

Seasonal patterns of photosynthesis and annual patterns of carbon fixation were similar for mats at all five depths
although absolute values differed (Fig. 6). All mats reached greatest production during the summer when PAR was highest (December and January). Photosynthesis did not occur during the winter (July–August), thus simulated carbon accrual increased rapidly during the summer months and then declined slowly during the winter as respiration reduced carbon pools (Fig. 6).

Although all mats showed an increase in productivity with an increase in transmittance through lake ice, this response tended to saturate at high transmittance (Fig. 7). This response also varied with depth. For example, annual carbon accumulation showed little increase for transmittance greater than 5% ambient PAR, except for mats at 19 m depth. The greatest values of estimated annual production were c. 15–16 g C m⁻² y⁻¹ for mats at 10 m depth, when transmittance ≥ 5% ambient PAR. Only mats at 19 m failed to show a positive net annual productivity regardless of transmittance value (Fig. 7).
Table VI. Production estimates for planktonic and benthic communities (mg C m$^{-2}$ d$^{-1}$). Estimates based on mean daily, simulated values of benthic communities and recorded values for plankton (McMurdo LTER). Cumulative daily PAR (mol photons m$^{-2}$ d$^{-1}$) calculated from meteorological records of Lake Hoare meteorological station (McMurdo LTER).

<table>
<thead>
<tr>
<th>Date</th>
<th>Benthos</th>
<th>Plankton</th>
<th>Ratio*</th>
<th>Transmitted PAR</th>
<th>Ambient PAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>08 Nov 96</td>
<td>11.63</td>
<td>1.80</td>
<td>15.5%</td>
<td>0.22</td>
<td>41.05</td>
</tr>
<tr>
<td>02 Dec 96</td>
<td>9.38</td>
<td>0.98</td>
<td>10.5%</td>
<td>0.20</td>
<td>37.03</td>
</tr>
<tr>
<td>12 Jan 97</td>
<td>0.98</td>
<td>0.47</td>
<td>48.0%</td>
<td>0.14</td>
<td>26.49</td>
</tr>
<tr>
<td>15 Nov 97</td>
<td>17.10</td>
<td>1.55</td>
<td>11.2%</td>
<td>0.29</td>
<td>25.89</td>
</tr>
<tr>
<td>26 Dec 97</td>
<td>27.17</td>
<td>7.38</td>
<td>37.2%</td>
<td>0.01</td>
<td>55.59</td>
</tr>
<tr>
<td>03 Nov 98</td>
<td>10.20</td>
<td>0.23</td>
<td>4.2%</td>
<td>0.20</td>
<td>34.98</td>
</tr>
<tr>
<td>01 Dec 98</td>
<td>21.58</td>
<td>0.79</td>
<td>3.7%</td>
<td>0.35</td>
<td>60.85</td>
</tr>
<tr>
<td>26 Dec 98</td>
<td>19.93</td>
<td>1.39</td>
<td>7.0%</td>
<td>0.36</td>
<td>61.68</td>
</tr>
<tr>
<td>17 Nov 99</td>
<td>37.83</td>
<td>11.27</td>
<td>29.8%</td>
<td>1.10</td>
<td>41.58</td>
</tr>
<tr>
<td>12 Dec 99</td>
<td>33.42</td>
<td>0.35</td>
<td>1.1%</td>
<td>0.63</td>
<td>23.88</td>
</tr>
</tbody>
</table>

*aRatio = (Plankton/Benthic Production) *100

Impacts of the spectral shift in PAR resulting from transmittance through lake ice were not incorporated into these simulations, but can be evaluated by reinterpreting the results. Because transmittance of PUR is about 150% of PAR (Hawes & Schwarz 2000), the carbon accrual calculated for transmittance of 15% ambient PAR more accurately corresponds to that expected for transmittance of 10% of PAR. Thus the spectral effect generates a photosynthetic response as much as 50% greater than the transmittance of PAR alone would suggest.

Uncertainty analysis

No significant correlation was found among parameter estimates used in the uncertainty analysis ($P > 0.05$). Thus we assumed that variation in model output resulted from independent variations in each model parameter. Variations in $P_{\text{max}}$, $\alpha$, and $R_{\text{max}}$, together explained 72–99% of variation in model behaviour, although their relative contributions varied with depth and transmittance (Fig. 8). Overall, the largest amount of variation in model outcome was attributed to $R_{\text{max}}$. This parameter explained ≥ 50% of the total variation in model output, with the exception of mats at 10 m depth (Fig. 8). Contributions of $\alpha$ usually accounted for < 25% of the total variation and decreased with increasing transmittance of PAR at all depths. Contributions of $P_{\text{max}}$ increased with transmittance for mats at all depths, although the relative importance of $P_{\text{max}}$ greatly varied with depth. For example, over 70% of model variation was associated with $P_{\text{max}}$ for the 10 m mats, at > 3% transmittance, but $P_{\text{max}}$ was seldom responsible for more than 35% of model variation at other depths.

Production of plankton and benthic communities

Our estimates of whole-lake, daily production for plankton and benthic communities showed considerable variation between dates (Table VI). Production of plankton communities ranged between 0.23–11.27 mg C m$^{-2}$ d$^{-1}$, whereas benthic mats produced 0.98–37.83 mg C m$^{-2}$ d$^{-1}$. Plankton production averaged only 15% of mat production values (range = 1.1–48.0%), suggesting a relatively large, albeit variable, contribution by benthic communities to whole lake production.

Pearson Product-Moment Correlations indicated that daily production estimates of plankton and mats were positively correlated to each other ($n = 10$, $r = 0.647$, $P = 0.043$). Moreover, both benthic and plankton production values were significantly related to transmitted PAR ($n = 10$, $r = 0.927$, $P < 0.001$; $n = 10$, $r = 0.793$, $P = 0.006$, respectively) although neither production value was related to surface incident PAR irradiance. This pattern of relationships seems counter-intuitive, but a decoupling of above- and below-ice radiant energy regimes resulted from changes in ice transmittance over years (Table III) and changes in attenuation coefficient over season (Eq. 9).

Whole-lake, annual mat production

The simulated, net annual production (1 January–31 December) of mat communities in Lake Hoare (to a depth of 19 m) totalled 0.90, 4.79, 1.62 and 7.98 10$^6$ g C for the austral years 1996–2000, respectively (Table VII). The total surface area of Lake Hoare is about 1.94 10$^6$ m$^2$, so these estimates represent about 0.47, 2.47, 0.83 and 4.11 g C m$^{-2}$ yr$^{-1}$, respectively. Of course a significant fraction of Lake Hoare is < 5 m in depth, where benthic production tends to be low and highly variable (Table IV). Also, simulated production of mats at 19 m was never positive despite the presence of mats at 20 m.

Discussion

This modelling analysis suggests that benthic microbial mats have the capacity to fix quantities of carbon that rival or exceed carbon fixation by planktonic communities in Dry Valley lakes. On average, simulated benthic mat production represented over 85% of the combined benthic + planktonic carbon fixation. In comparison, Fogg (1977) estimated that 27–67% of the annual production in Skua Lake and > 95% of the production in Algal Lake (Ross Island) was contributed by benthic mats. More recently, Sabbe et al. (2004) reported the widespread distribution of benthic mats in 56 lakes of the Larsemann Hills region of east Antarctica.
Organic matter accumulations ≤ 35 cm thick, despite low planktonic chlorophyll concentrations (Sabbe et al. 2004), argue for substantial production by benthic communities. Other studies also have demonstrated both wide distribution and potential for high rates of carbon fixation by benthic mats (Heath 1988, Vincent et al. 1993a, Hawes & Howard-Williams 1998, Hawes & Schwarz 1999, 2000, Sabbe et al. 2004), but few studies have examined production by mat communities under circumstances approximating field conditions in McMurdo Dry Valley lakes (Moorhead et al. 1997b, Hawes et al. 2001).

The long-term role of benthic microbial mats may extend beyond the Dry Valley lakes. A recent analysis showed that lake sediments represent the largest concentration of organic matter in the McMurdo Dry Valleys (Burkins et al. 2000). Moreover, Burkins et al. (2000) found a strong lacustrine influence on the isotopic signature of soil organic matter at elevations < 300 m a.s.l. These organic materials may have accumulated in benthic sediments of ancient glacial lakes that once inundated the valleys to c. 300 m a.s.l. (Moorhead et al. 1999). However, the importance of these potential contributions of benthic microbial communities to the carbon dynamics of the McMurdo Dry Valleys must be evaluated within the context of uncertainties in model structure and behaviour, as well as the limited number of empirical observations.

**Errors**

This modelling study had three primary objectives:

1) to determine how varying parameters within realistic ranges of uncertainty would affect predicted carbon yields, and thus guide future experimental research,

2) to compare model estimates of whole-lake benthic production to that of phytoplankton in the overlying water column, and

3) to place benthic production within a larger ecosystem context by simulating whole-lake, year-round benthic productivity.

The reliability of our estimates of depth-specific production determines the confidence that can be attached to extrapolations of whole-lake processes. Indeed, three distinct sources of errors occur in this study; first, the error attached to measurement of physiological parameters, second, the error attached to extrapolation from one site and one time to many sites at many times, and third, the error induced from derivation of driving variables (specifically the complex and variable PAR at depth).

**Physiological errors**

As part of our uncertainty analysis we estimated the impact of variance in key model parameters. Figure 8 clearly indicates that respiration rate and light-saturated photosynthetic rate had a strong influence on model yields, the later being most important at shallow depths and the former being important at all depths. The pervasive impact of respiration rate on model results encourages a closer examination of respiratory metabolism. In a previous modelling study, Moorhead et al. (1997b) achieved a positive net annual production in benthic mats of Lake Hoare only by assuming that respiration rate declined during prolonged darkness. This hypothesis was confirmed by experimental observations (Hawes et al. 2001) and is consistent with similar responses reported for algae in other systems (e.g. Grande et al. 1991, Heraud & Beardall 2002). We also assumed that the relationship between respiration and period of darkness reported by Hawes et al. (2001) was constant throughout the long Antarctic winter, although no observations are available to confirm this assumption. Finally, other studies report differences in respiration rates of algae at different levels of post-illumination irradiation (Falkowski & Raven 1997, Bulychevtsva et al. 2003, Ursi et al. 2003), but no data were available to evaluate this relationship for benthic communities in Lake Hoare.

It is significant that the parameters used to drive the model are community values, not those of a homogenous culture or suspension of individuals. Because α is already close to maximum sustainable values in the under-ice mats (Hawes & Schwarz 2000), there is little scope for this parameter to affect model yield. However, it seems unreasonable to conclude that algae and cyanobacteria would not adjust their photosynthetic and respiratory characteristics to match ambient conditions on seasonal and inter-annual time scales. Indeed, P<sub>max</sub> and R<sub>max</sub> in particular are flexible in algae and cyanobacteria (e.g. Campbell et al. 1998, Tang & Vincent 2000, MacIntyre et al. 2002) and would change as the active biomass within the mat fluctuates. Observations of photosynthetic parameters were made with mat collected during 1998–99, a period of unusually low transmittance of PAR (Table III). Microbial mats should have been acclimated to very low irradiance, and the failure of simulations at high transmittance to yield high production (Fig. 7) may simply reflect the consequences of extreme low light acclimation. Alternatively, acclimation to increased irradiance, for example through increasing P<sub>max</sub>, would result in a much greater increase in carbon accrual at high transmittance (Fig. 8). Our simulations indicate that an understanding of the seasonal and inter-annual variation in biomass, P<sub>max</sub> and R<sub>max</sub>, in response to growth cycles and fluctuating irradiance transmittance, are critical to understanding patterns in productivity of benthic photosynthetic mats in these systems.

**Extrapolation errors**

Potential errors are introduced through extrapolation of both...
physiological and physical parameters from limited times and locations to whole-lake, whole-year estimates. Dana et al. (1998) illustrate how the incident irradiance regime varies spatially within the Taylor Valley and specifically across the surface of Lake Hoare. Ice transmittance is strongly affected by inclusions within the ice (McKay et al. 1994) and this, too, is likely to vary spatially. We have unpublished data on spatial variability of ice transmittance, which show that transmittance may vary by an order of magnitude (from 0.1 to 2%) within a 50 m radius. While scattering of light within the ice and water will tend to reduce small-scale variability with increasing depth, the probability is high that there will be spatial heterogeneity within a given ice-covered lake in irradiance reaching the lake floor. Because small changes in irradiance can generate large changes in production (Fig. 7), an improved understanding of spatial variability in ice and microbial mat characteristics would increase the reliability of whole-lake estimates.

**Benthic vs planktonic production**

Errors associated with extrapolating temporally and spatially restricted physiological and physical data to estimate *in situ* benthic production also apply to comparisons with planktonic carbon fixation. However, most errors associated with benthic production, particularly the use of physiological parameters that were obtained during a period of low light transmittance, will tend to under-estimate carbon accrual. This further supports our general conclusion that benthic production is at least as great as planktonic production, and often greater.

Despite its perennial ice cover, Lake Hoare has a relatively large littoral zone, defined here as that part of the lake where benthic production exceeds zero (< 20 m depth), comprising c. 80% of lake area. Productivity of temperate oligotrophic lakes with large littoral areas also is often dominated by benthic production (Hecky & Hesslein 1995). The reasons underlying this dominance in temperate systems are likely to be the same in Lake Hoare; benthic phototrophs are fixed in favourable light regimes and have access to nutrients accumulating in lake sediments (Loeb et al. 1982). In weakly or non-mixing Antarctic lakes, this differential nutrient supply is likely to be particularly important, as planktonic phototrophs may be dependent on diffusive flux of nutrients from the sediment or anoxic parts of the water column (Priscu 1995). Our simulations suggesting that benthic production exceeds planktonic production in this oligotrophic lake with a high littoral:pelagic ratio are, therefore, consistent with current limnological understanding.

**Conclusions**

To date, the role of benthic microbial mats in the carbon budget of McMurdo Dry Valley lakes has been largely unknown. Most studies of primary production in these lakes have focused on plankton communities (Priscu et al. 1999), with little attention to benthic microbial mats. Moreover, Priscu et al. (1999) noted that considerable organic matter enters these lakes through surface lake ice, either from aeolian deposition to the ice surface or from production of communities entrained within the ice column. Sediment cores taken from these lakes, including Lake Hoare, suggest annual patterns of organic matter accumulation (Squyres et al. 1991, Doran et al. 1994), which could result from either benthic production or deposition from the overlying water column. An earlier modelling study estimated net annual production of benthic mats as high as 58 and 2.8 g C m⁻² at 8 and 23 m depths, respectively (Moorhead et al. 1997b), suggesting significant input to benthic organic matter from microbial mat communities. However, these estimates were based on the untested assumption of reduced respiration rates during periods of darkness, preliminary estimates of photosynthetic parameters, and crude estimates of PAR transmittance through surface ice. The current model incorporated additional experimental observations and generated more modest estimates of annual production at 15–16 g C m⁻² at 10m depth. Hawes et al. (2001) were able to equate these rates of production to both organic mass and number of annual bands in benthic mats of known age. These results have considerable implication to interpreting both short and long-term responses of McMurdo Dry Valley ecosystems to climate change, as well as the importance of benthic mats to overall carbon dynamics of the valleys.

In the short term, Doran et al. (2002) reported that climate in the McMurdo Dry Valleys has become cooler and drier over the past decade. This trend was accompanied by changes in hydrological budget, including lower stream flow, falling lake levels and increased lake ice thickness. These changes were coincident with reduced PAR transmittance through lake ice and falling primary productivity of plankton communities. Impacts on benthic communities were not monitored, but our model suggests that mat production may also have declined during this time.

In the long term, cycles of greater inundation and desiccation of the McMurdo Dry Valleys have occurred in the past, with the last major inundation concurrent with the last glacial maximum (Lyons et al. 1997). Burkins et al. (2000) noted that the isotopic signature of organic matter in McMurdo Dry Valley soils < 300 m a.s.l. suggest a strong lacustrine influence. Moreover, Doran et al. (1998) reported organic materials in ancient river deltas and soils far above current lake levels. Our conceptual model of the McMurdo Dry Valley ecosystem is that lacustrine organic matter was deposited in sediments of deeper glacial lakes that were subsequently exposed when these lakes receded (Moorhead et al. 1999). Results of this modelling study suggest that benthic communities may have made a substantial
contribution to this pool of organic matter during times and in places where the lake was shallow enough for sufficient sunlight to reach the benthic surface.

Acknowledgements

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References


