

# Nutrient and population dynamics in a subglacial reservoir: a simulation case study of the Blood Falls ecosystem with implications for astrobiology

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**Abstract:** Subglacial ecosystems have recently become of interest within the astrobiological community, as they represent a potentially habitable location in otherwise uninhabitable environments. We used data from Blood Falls, particularly the periodic discharge from the subglacial reservoir beneath Taylor Glacier, Antarctica, to construct an ecosystem model of the putative subglacial microbial community residing there using system dynamics modelling. The model results were, for the most part, within an order of magnitude of the geochemical field data. Productivity was quite low, at  $6.4 \times 10^{-5}$  g carbon  $l^{-1}$  yr $^{-1}$ . Based on the results, we draw the following conjectures for the search for life on Mars: A similar ecosystem would require a continual supply of oxidized iron for energy and generate significant amounts of reduced iron as a waste product, be relatively resilient to temporary disturbances, and, thermodynamically, would require at least 0.003 kJ mol $^{-1}$  of energy to survive at that level of productivity. These results may help to better identify the constraints and boundaries of ecosystems in extreme environments, on Earth and other planetary bodies.

Received 10 March 2013, accepted 13 April 2013, first published online 29 May 2013

**Key words:** ecology, ecosystem modelling, subglacial, Mars, Psychrophiles.

## Introduction

Within the last decade, the study of subglacial ecosystems has advanced considerable (Hodson *et al.* 2008). While once thought to be relatively low in microbial activity, it is now known that much of the geochemical weathering that occurs at the glacier-bed interface is at least in part microbially mediated (Skidmore *et al.* 2000).

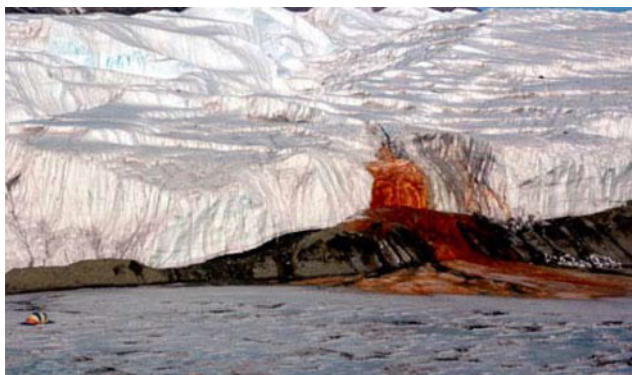
Compared with the supraglacial ‘surface’ component of the typical glacial ecosystem, the subglacial component is rather sparsely characterized (Hodson *et al.* 2008). It is thought that these ecosystems are supported primarily by a number of redox reactions as a source of energy (Tranter *et al.* 2005), suggesting a population with a significant majority of chemotrophs. Nonetheless, consumption of carbon, primarily in the form of organic debris, also plays a large role in glacial ecology and in the cycling of carbon on a global scale (Anesio *et al.* 2009).

Subglacial reservoirs or subglacial lakes are of particular interest within the realm of subglacial ecosystems. These are large bodies of liquid water or brine found deep within glacial features. They are most commonly found in Antarctica, though some geothermally warmed lakes have been found in Iceland (Gaidos *et al.* 2004). The Antarctic lakes in particular are of interest due to the fact that they have remained isolated from the rest of the biosphere for very long periods of time, ranging from thousands to tens of millions of years.

The extreme nature of the glacial environment, coupled with the fact that these ecosystems have apparently remained viable

and presumably relatively unchanged for extremely long periods of time, has made them of considerable interest to the astrobiological community. Due to the possibility of liquid water as an environment for extraterrestrial life on Mars (Skidmore *et al.* 2000) or the icy satellites of the outer planets (Irwin & Schulze-Makuch 2003), terrestrial subglacial ecosystems may subsequently provide an analogous guide for the possibilities and constraints of subglacial habitats. The Taylor Glacier reservoir in particular may be an especially relevant analogue for Mars, due to the fact that it formed from a pocket of seawater that was uplifted and isolated by the glacier at some point during the last 3–5 million years. For example, one possible explanation that has been hypothesized for the Martian hemisphere dichotomy is that Mars’ northern hemisphere may have once possessed an ocean (Carr & Head 2003), though this remains controversial. At the very least, it seems quite likely that Mars had a number of significant lakes early in its history (Fassett & Head 2008). As the planet cooled, much of this water is believed to have been incorporated into the ice caps, either by sublimation, or by direct freezing and glaciations. If a pocket of liquid water was trapped by a glacier in a manner similar to Blood Falls, then this reservoir could very well prove to be an ideal location for any relict life that may have arisen during Mars’ wetter and warmer epoch (Schulze-Makuch *et al.* 2013).

By modelling this unique subglacial reservoir ecosystem, we can develop a better understanding of the environmental and nutrient limits of cold-dwelling extremophiles, both here on



**Fig. 1.** The Blood Falls formation. Credit: Peter Rejcek, National Science Foundation.

Earth and possibly elsewhere in the Solar System, and in turn, allow better evaluation of what environments are actually potentially habitable by microbial life. On a more general level, this approach could also aid in determining the viability of an ecosystem in a given extreme environment, and what traits might be required to sustain it. A model makes it possible to estimate the maximum productivity and supported biomass of the ecosystem, determine its limiting nutrients and their impact on microbial growth, and gain a better understanding of what biosignatures and geosignatures might be generated by such an ecosystem.

### Blood Falls

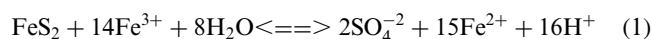
The primary reservoir used for the creation of this model was Blood Falls, a subglacial reservoir associated with Taylor Glacier in Antarctica. Blood Falls is periodically discharging water from a saline reservoir deep within Taylor Glacier. This reservoir is believed to be marine in origin, having been isolated by the glacier for the last 3–5 million years, when the expanding ice cut it off from the rest of the ocean (Mikucki 2005). The water that wells up from the reservoir is highly enriched in iron; the oxidation of this iron results in the bright, crimson colour that gives Blood Falls its name (Fig. 1). Geochemically, the discharge is anoxic and contains high levels of sulphur ( $50 \mu\text{M l}^{-1}$  on average), organic carbon ( $>400 \mu\text{M l}^{-1}$ ), inorganic carbon ( $50 \mu\text{M l}^{-1}$ ), dissolved inorganic nitrogen ( $94 \mu\text{M l}^{-1}$ ) and chloride ( $>1000 \mu\text{M l}^{-1}$ ). Soluble reactive phosphorus is relatively low, at  $>0.5 \mu\text{M l}^{-1}$  (Mikucki *et al.* 2009) (Table 1). Microbial assays have shown that the reservoir possesses a number of microbial species, including sulphur oxidizers, sulphur reducers, and heterotrophic organisms (Mikucki *et al.* 2009). Carbon fixation has been estimated at  $1.2 \text{ nM Carbon l}^{-1} \text{ day}^{-1}$  (Mikucki & Priscu 2007).

The ecosystem of Blood Falls is thought to rely on chemotrophic sulphur oxidizers as the primary producers, presumably using non-oxidized sulphur from the bedrock; the clone libraries are dominated by *Thiomicrospira arctica*, a psychrophilic autotroph capable of oxidizing a number of sulphur compounds (Mikucki 2005). While the reservoir is anoxic, studies of other subglacial ecosystems and isotopic

**Table 1.** Biogeochemical data from Blood Falls during ancient brine discharge event (from Mikucki *et al.* 2009)

Temperature	$-5.2^\circ\text{C}$
pH	6.2
$E_h$	90 mV
Dissolved oxygen	Not detectable
Dissolved inorganic carbon (DIC)	$55 \text{ mM l}^{-1}$
Dissolved organic carbon (DOC)	$450 \mu\text{M l}^{-1}$
Total iron	$3.45 \text{ mM l}^{-1}$ ( $>97\%$ as Fe(II))
Sulphate	50 mM
Chloride	1375 mM
Total cells	$6 \times 10^4 \text{ mL}^{-1}$
Thymidine (Tdr) incorporation rate	$1.9 \times 10^{-4} \text{ nM Tdr day}^{-1}$ ( $\pm 2 \times 10^{-5}$ )

analysis suggest that the sulphur compounds are oxidized by the sulphur oxidizers using the reduction of Fe(III) as an electron acceptor, such as seen in Haut Glacier d'Arolla in Switzerland:



(Bottrell & Tranter 2002). However, it is worth noting that the exact mechanisms by which Fe(III) reduction is mediated by sulphur cycling is not fully characterized; it appears that sulphur intermediaries are used as an electron 'shuttle' between the insoluble Fe(III) mineral and the organisms (Schink 2006). Nonetheless, as the basement complex underlying Taylor glacier is thought to be composed of metamorphic rock and granodioritic and granitic intruding plutons, rich in iron-bearing minerals such as pyrite, goethite, and various iron oxides and hydroxides, and the redox state of these rocks is reported to be minimally  $\text{Fe}^{2,4+}$  (Mikucki *et al.* 2009), these mechanisms would be plausible.

Sulphur reducers, autotrophic and organotrophic, are also known to be present, and appear to play a major role in cycling the organic carbon present in the system. Interestingly enough, however, sulphur reduction does not appear to proceed to hydrogen sulphide, as with most other known sulphur reducing communities. Instead, a number of sulphur intermediates (such as sulphite, elemental sulphur, thiosulphate and iron sulphide) are used (Mikucki *et al.* 2009). Chemoorganotrophic heterotrophs are also present (Mikucki 2005) and there is considerable overlap between the heterotroph and sulphur-reducing communities.

Thus, the overall Taylor Glacier system appears to rely heavily on microbial cycling of nutrients not surprising, given the isolation of the reservoir. Inorganic carbon is fixed by the autotrophic sulphur oxidizers; the subsequent organic carbon is then oxidized into carbon dioxide by the sulphur-reducing heterotrophs, which act as consumers and detritivores. The sulphate produced by the sulphur oxidizers is cycled back into intermediate forms by the heterotrophs. The entire ecosystem, then, is dependent on the availability of Fe(III), which functions as the terminal electron acceptor for the microbial community as a whole (Mikucki 2005).

Table 2. *Model organism characteristics*

Model organism	$K_s$ Carbon	$K_s$ Nitrogen	$K_s$ Phosphorus	$K_s$ Sulphur	$K_s$ Iron	$\mu_{\max}$ (per day)	Death rate (per day)	Maintenance energy (per day)
Sulphur oxidizer	0.66 <sup>a</sup>	0.09 <sup>b</sup>	0.005 <sup>c</sup>	0.63 <sup>d</sup>	2.1 <sup>e</sup>	1.8 <sup>f</sup>	0.001 <sup>g</sup>	0.0019 <sup>h</sup>
Heterotroph	1 <sup>i</sup>	0.1 <sup>j</sup>	0.01 <sup>k</sup>	0.3 <sup>l</sup>	2.1 <sup>m</sup>	0.002 <sup>n</sup>	0.001 <sup>o</sup>	0.000005 <sup>p</sup>

<sup>a</sup>In the form of DIC, based on the data for relative *T. crunogena* (Dobrinski *et al.* 2005).

<sup>b</sup>In the form of DIN, approximated from Redfield ratio; actual value unknown.

<sup>c</sup>In the form of SRP, approximated from Redfield ratio; actual value unknown.

<sup>d</sup>Based on data for relative *T. CVO* (Gadekar *et al.* 2006).

<sup>e</sup>Approximated stoichiometrically from  $K_s$  sulphur.

<sup>f</sup>Derived from the estimated doubling time of 37–54 days of bacteria in Blood Falls (Mikucki *et al.* 2004).

<sup>g</sup>Assumed arbitrarily; actual value unknown.

<sup>h</sup>Based on the energy requirement of *Thiomicrospira denitrificans* under anaerobic conditions (Brannan & Caldwell 1983).

<sup>i,j,k</sup>Values based on a model of heterotrophic bacteria by Thingstad (1987).

<sup>l</sup>Arbitrarily selected; actual value unknown.

<sup>m</sup>Same as sulphur oxidizer; actual value unknown.

<sup>n</sup>Based on estimated doubling time of 300 days for Blood Falls heterotrophs from Mikucki *et al.* (2009).

<sup>o</sup>Arbitrarily selected; actual value unknown.

<sup>p</sup>Model comes into equilibrium at this value; actual value unknown.

## Methodology

The model was constructed using Vensim PLE, a freely available system dynamics modelling software (Ventana Systems, 2007). Models based on system dynamics theory are composed of three main components: stocks, flows and converters. Stocks represent a quantity of material, and are mathematically expressed in the general form for stock  $x$  as  $dx/dt = (\text{inflow}_x - \text{outflow}_x)$ . Flows represent the transfer of material from one stock to another, or in and out of the system; in the example,  $\text{inflow}_x$  is a flow. Lastly, there are converters, which modify the stocks and flows. In schematic diagrams, stocks are represented by boxes, flows by 'conveyor belt' arrows and converters (omitted for clarity in the diagrams below) by small arrows.

Portions of the model are derived from a similar model originally developed for the study of eutrophication in lakes (Anderson, 1973). The model is driven by two interrelated cycles, one for nutrients, and the other for metabolism. The elements used in the nutrient flow are carbon, nitrogen and phosphorus, which were modelled to be in proportion to the Redfield ratio of 106:16:1; since Blood Falls is marine in origin, this is likely a close approximation of actual conditions. The metabolic cycle transforms sulphate into a number of undescribed sulphur intermediates (assumed to be primarily sulphite, thiosulphate and elemental sulphur in the actual reservoir (Mikucki *et al.* 2009)), which is catalysed by the reduction of Fe(III) into Fe(II). Both of these cycles are utilized by two model organisms, a chemoautotrophic primary producer and a heterotrophic consumer representing the putative biota of a subglacial reservoir in general and Blood Falls in particular.

The behaviour of these microbial organisms is simulated based on Monod kinetics, a form of Michaelis–Menten kinetics modified specifically for modelling microbial dynamics, where the rate of growth is described in Monod (1949) as

$$\mu = \mu_{\max} \left( \frac{S}{K_s + S} \right), \quad (2)$$

where  $\mu$  is the specific growth rate,  $\mu_{\max}$  is the maximum growth rate per hour,  $S$  is the amount of substrate (in this case, vital nutrients) and  $K_s$  is the half-saturation constant of the organism. The half saturation constant refers to the substrate concentration at which the growth rate is half of the maximum, and is usually an empirically determined value. This equation is used to determine the effect of nutrient availability on the growth of the organism, in the form of  $\mu/\mu_{\max}$ . These separate effects are then multiplied to produce the organism's actual growth rate.

The traits of the model organisms are based on bacteria found to be performing the corresponding ecological role (primary producer, detritivore, etc.) in Blood Falls. It should be noted that frequently, the reservoir's microbial population remains poorly characterized, and certain values (half-saturation constants, growth and death rates, etc.) have to be approximated or estimated when incorporated into the model (Table 2).

## Model organisms

**Primary producer:** the primary producer of the model is a sulphur oxidizing chemoautotroph, based on *Thiomicrospira arctica*. Based on clone library results, *T. arctica* is the most predominant organism in the Blood Falls reservoir (Mikucki & Priscu 2007). *T. arctica* is a psychrophilic marine aerobe, originally isolated from Antarctica sea sediment (Knittel *et al.* 2005). It forms the backbone of the ecosystem, and plays a vital role in the cycling of sulphur.

**Heterotroph:** The heterotroph performs the important function of breaking down reduced, organic matter into an oxidized, inorganic form that can then be used by the autotrophs; in essence, they behave as detritivores. The heterotroph is not based on any one particular species, but rather is an amalgam of isolated strains, though they are almost all in the *Bacteroidetes* superfamily. They are assumed to be primarily chemolithoheterotrophs, using sulphate or other oxidized sulphur species as an electron acceptor.

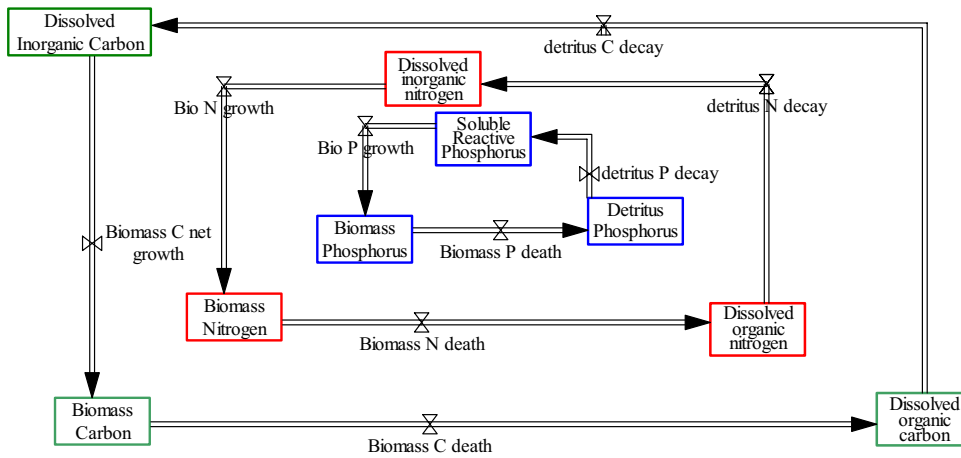


Fig. 2. A simplified schematic drawing of the nutrient cycle.

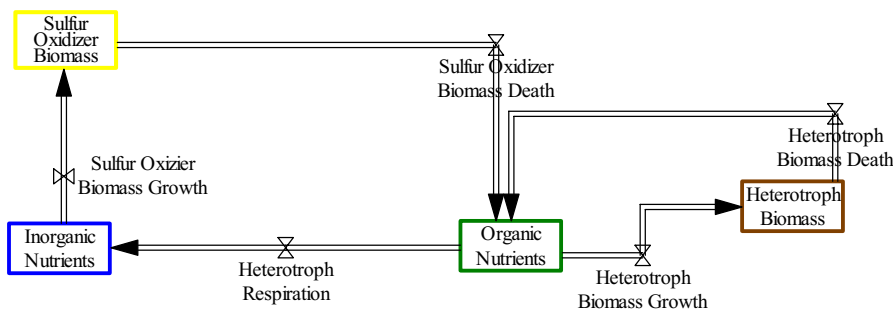


Fig. 3. A simplified schematic of the cycling of nutrients through the biomass of the three organisms.

## Nutrient cycle

In the nutrient cycle, a nutrient starts out in its inorganic form and is then assimilated into the biomass stock of the autotrophic sulphur oxidizers (Figs 2 and 3). The assimilation rate is proportional to the growth rate of the organisms, which in turn is governed by nutrient and metabolic resource availability. Nutrient assimilation of the organisms is then determined by simply multiplying the growth rate by the existing biomass to determine the net growth of the biomass. For example, the consumption of dissolved inorganic carbon (DIC) by the sulphur oxidizing microbes is represented as  $\mu_{\text{sulphox}} \times \text{sulphox biomass C}$ . Initial values of this cycle are based on field data from Blood Falls (Table 3).

As the biomass dies at a predetermined rate, the nutrient is passed into the stock of its organic form, where it is either assimilated into the heterotroph biomass, or ‘decays’ and is oxidized back into its dissolved inorganic form. The decay rate is the sum of an arbitrary constant representing abiotic decay (equal to  $3.27 \times 10^{-8} \text{ day}^{-1}$ ) and the respiration rate of the heterotrophs. The respiration rate is comprised of the maintenance energy required by the heterotrophs to continue living multiplied by the heterotroph biomass. While nitrogen and phosphorus are not ‘respired’ in any sense, it is assumed that they are excreted or otherwise lost by the heterotrophs and re-entered back into the available nutrient pool at a rate equal to the respiration.

Soluble reactive phosphorus (SRP) is modelled in a fundamentally different way than the other variables rather than represented by a stock, it is expressed through the use of a converter described by a complex equation

$$\frac{d\text{SRP}}{dt} = -\frac{KOD + HM}{(DO + HMO) - V} \quad (3)$$

where  $K$  is the half-saturation constant for phosphorus,  $O$  is the amount of dissolved organic carbon,  $H$  is the rate of heterotrophic respiration,  $D$  is the detritus decay rate,  $M$  is the sulphur oxidizer biomass, and  $V$  is equal to the sulphur oxidizer  $\mu/\mu_{\text{max}}$ . In this matter, the level SRP is calculated continuously, instead of discretely, which avoids the oscillation or ‘ringing’ generated by stocks with extremely fast turn-over.

## Metabolic cycle

As pointed out in Gaidos *et al.* (1999), for an ecosystem to be viable, it cannot be entirely based on a closed-loop cycle. According to the laws of thermodynamics, there must be energy from outside the system, or else the system will reach chemical equilibrium and biological activity will cease. In the case of Blood Falls, the ecosystem is driven by the redox cycling of sulphur with Fe(III) used as the terminal electron acceptor. As a result, Fe(III) acts as the primary source of external energy for the ecosystem, and its availability considerably influences the behaviour of the system (Fig. 4).

Table 3. Initial values for the nutrient cycle

Variable	DIC ( $\mu\text{M l}^{-1}$ )	DOC ( $\mu\text{M l}^{-1}$ )	DIN ( $\mu\text{M l}^{-1}$ )	SRP ( $\mu\text{M l}^{-1}$ )	Biomass carbon ( $\mu\text{M l}^{-1}$ )
Initial value	50000 <sup>a</sup>	450 <sup>a</sup>	94 <sup>a</sup>	0.009 <sup>b</sup>	0.0002 <sup>c</sup>

<sup>a</sup>Based on Blood Falls data from Mikucki *et al.* (2009).

<sup>b</sup>Based on Blood Falls data from Mikucki (2005), but may not be accurate due to the adsorption of SRP to precipitated iron oxide (Mikucki *et al.* 2004).

<sup>c</sup>Estimated from cell density values from Mikucki (2005) ( $6 \times 10^4 \text{ mL}^{-1}$ ), cross-referenced to the established cell density of 108 cells  $\text{ml}^{-1}$  being equal to 4.2  $\mu\text{g}$  established for *Thiomicrospira* L-12 by Ruby and Jannasch (1982), which is then converted into  $\mu\text{M}$  of carbon. It should be noted that this is a very crude estimate, as the biomass of subglacial microbial communities has proven difficult to measure accurately (Tranter *et al.* 2005).

Table 4. Initial values for the metabolic cycle of the model

Variable	Sulphur ( $\mu\text{M l}^{-1}$ )	Sulphate ( $\mu\text{M l}^{-1}$ )	Fe(III) ( $\mu\text{M l}^{-1}$ )	Fe(III) mobilization rate ( $\mu\text{M l}^{-1} \text{ Day}^{-1}$ )
Initial values	50000 <sup>a</sup>	50000 <sup>b</sup>	1000 <sup>b</sup>	10 <sup>b</sup>

<sup>a,b</sup>Assumed arbitrarily; actual value unknown.

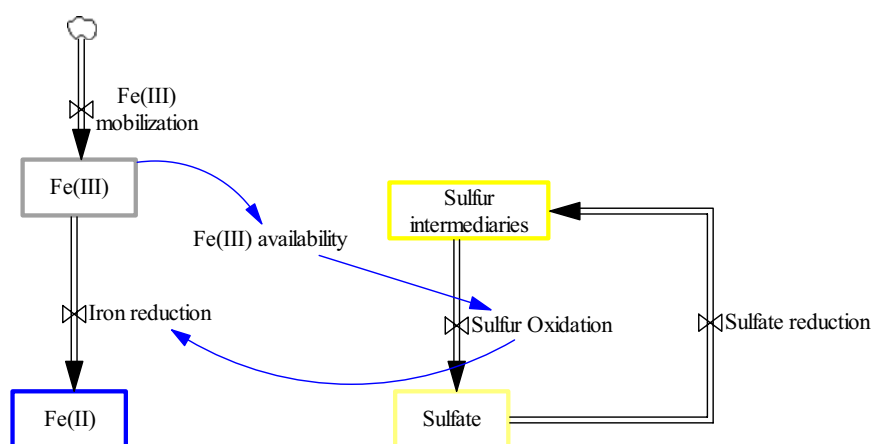
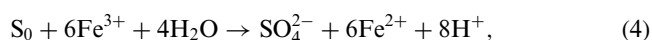


Fig. 4. Simplified schematic of the metabolism cycle.

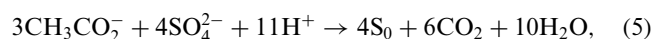
The sulphur oxidizers produce sulphate from a stock of 'sulphur' (representing sulphur intermediates), reducing Fe(III) to Fe(II) in the process, at a rate governed by the growth rate of sulphur oxidizers. The sulphate is then reduced back into its intermediate form by the sulphur reducers and heterotrophs at a rate proportional to those organisms' growth rate plus the maintenance energy required by the two organisms. Fe(III) is most likely made available for microbial mobilization by the exposure of iron-rich minerals at the bed-glacier interface by glacial movement. The exact rate of mobilization is not known. As with the nutrient cycle, initial values of the model are based on field data from Blood Falls where possible (Table 4).

In terms of redox reactions, the redox pair used for the sulphur oxidizers is



which provides  $-164.5 \text{ kJ mol}^{-1}$  per  $2e^-$  under *in situ* subglacial conditions (Mikucki *et al.* 2009, supporting material). This energy is then assumed to be available for the fixation of carbon, which, in terms of free energy, is represented by the reduction of inorganic carbon to acetate at *in situ* subglacial conditions, and has an

energy requirement of  $142.0 \text{ kJ mol}^{-1}$  (Mikucki *et al.* 2009, supporting material). The heterotrophs' redox pair is assumed to be



which yields  $-19.6 \text{ kJ mol}^{-1}$  per  $2e^-$  under *in situ* conditions (Mikucki *et al.* 2009, supporting material). This is obviously a highly idealized simplification of microbial metabolism, but has proven to be sufficient for the purposes of the model, and makes it possible to calculate the energy requirements for the ecosystem in  $\text{kJ mol}^{-1}$ .

Additionally, while it is suspected that some of the heterotrophs in Taylor Glacier are organotrophs, and therefore do not reduce sulphur, they appear to be a very small percentage of the population (<5%) (Mikucki & Priscu 2007), and therefore are not included for the purposes of keeping the model no more complicated than necessary.

Due to the presumed longevity of the Blood Falls ecosystem, and its isolation from the rest of the biosphere, it was assumed that the ecosystem achieved a state of stable equilibrium. Consequently, equilibrium was sought in the model results. For the purposes of calibration, the initial run of the model used parameters that attempted to mimic the actual data from



Table 5. Comparison of model results with field data

	Sulphate	DOC	DIC	DIN	SRP	Carbon fixation rate
Actual Blood Falls data	50000 $\mu\text{M l}^{-1}$	450 $\mu\text{M l}^{-1}$	55000 $\mu\text{M l}^{-1}$	94 $\mu\text{M l}^{-1}$	0.09 $\mu\text{M l}^{-1}$	1.2 $\text{nM C l}^{-1} \text{ day}^{-1}$ (est.)
Baseline model data	47000	450	55000	94	0.0004	0.015 $\text{nM C l}^{-1} \text{ day}^{-1}$
Discrepancy (theoretical/actual)	-6%	0	0	0	-99.5%	-98.75%

Table 6. Model sensitivity to Fe(III) mobilization. Significant impact was noted on the sulphate levels and biomass

Model Run	Fe(III) mobilization rate ( $\mu\text{M l}^{-1} \text{ day}^{-1}$ )	Sulphate ( $\mu\text{M l}^{-1}$ )	Biomass C ( $\mu\text{M l}^{-1}$ )	GPP ( $\text{g C l}^{-1} \text{ yr}^{-1}$ )	NEP ( $\text{g C l}^{-1} \text{ yr}^{-1}$ )
Baseline	10	47000	0.016	$6.4 \times 10^{-5}$	$6.4 \times 10^{-5}$
High Iron	100	30000	0.11	0.0004	0.0004
Low Iron	1	71000	0.01	$4.3 \times 10^{-5}$	$4.3 \times 10^{-5}$

Blood Falls as much as possible. From this, a baseline model was derived. In cases where field parameters were not known, e.g. microbial death rate and SRP, multiple different values were then used for sensitivity testing. The model was run at a time step ( $dt$ ) of 0.0625 for a period of 40 000 days, by which point the model had reached an equilibrium.

## Results and discussion

Compared with the field data, the model generally produced results within an order of magnitude or less; exceptions were soluble reactive phosphorus and carbon fixation, which were off by two orders of magnitude (Table 5). Further investigation revealed that the amount of SRP in the system was primarily an effect of the sulphur oxidizer phosphorus half-saturation constant, due to the unique way the quantity of SRP was calculated in the model.

In terms of biological activity, total biomass carbon peaked at  $0.016 \mu\text{M l}^{-1}$ , at which point the system reached equilibrium. This total was composed of  $0.014 \mu\text{M l}^{-1}$  biomass carbon from the sulphur oxidizers, and  $0.002 \mu\text{M l}^{-1}$  biomass carbon from the heterotrophs. Phosphorus was found to be the most limiting nutrient for both sulphur oxidizers, and, to a slightly lesser extent, the heterotrophs. This finding is supported by the high level of activity of phosphorus-scavenging enzymes in the Blood Falls derived microbial cultures (Mikucki 2005). Unsurprisingly, both were also limited by the level of available Fe(III), which lends support to the assertion that iron reduction is the ultimate energy source for this ecosystem.

Based on the amount of sulphur oxidized and reduced, the free energy requirements to maintain the ecosystem at equilibrium come out to be about  $0.003 \text{ kJ mol}^{-1}$ .

General and net ecosystem productivity were calculated as the production and consumption of carbon by the biomass in grams per litre per day. Both start at around  $0.0001 \text{ g carbon (C) l}^{-1} \text{ yr}^{-1}$ , and then sharply by several orders of magnitude before reaching a steady state of  $6.4 \times 10^{-5} \text{ g C per year}$  for gross primary productivity, and net ecosystem primary productivity being almost undetectably lower. Given how marginal this ecosystem is, and that heterotroph respiration is extremely low, this result is not surprising.

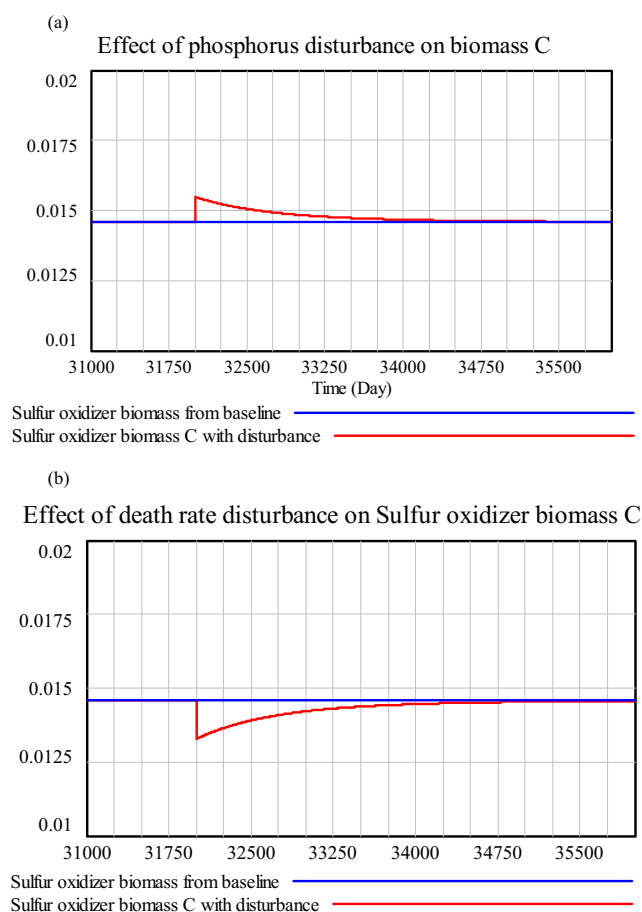
## Sensitivity testing

Several parameters, including soluble reactive phosphorus, death rates, Fe(III) mobilization, and the rate of nutrient cycling and respiration, were subject to sensitivity testing to determine the model's response to variation and disturbance.

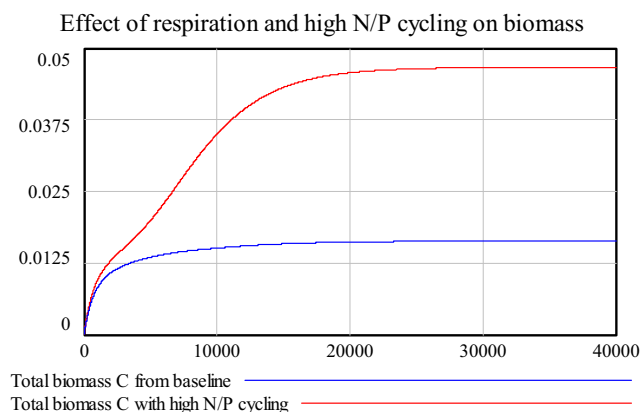
Generally speaking, variations in the level of available SRP at the beginning of the model did not noticeably affect the model results compared with the baseline; this may be a reflection of the fast cycling of phosphorus, and the limitations of other nutrients. Changing the rate of Fe(III) mobilization, however, did affect the amount of biomass and the level of sulphate substantially (see Table 6), and can be considered to be a key parameter in determining the dynamics of the model. Significantly, changing the intrinsic death rate tended to destabilize the model, either leading to a complete population collapse when it was increased or an overshoot and gradual decline when decreased. Temporarily introducing an order of magnitude larger influx of phosphorus at day 32000 did produce a noticeable change in the amount of sulphur oxidizer biomass, but this proved to be essentially temporary (see Fig. 5(a)). Similarly, introducing a pulse disturbance that raised the death rate for the sulphur oxidizers to 0.1 (meaning a mortality rate of 10% of the population) also had an observable, but ultimately temporary effect (see Fig. 5(b)). Raising the rate of nutrient cycling to  $0.0001 \mu\text{M l}^{-1} \text{ day per } \mu\text{M l}^{-1}$  of heterotroph biomass, so that nutrients were cycled faster and in greater quantity, resulted in higher levels of biomass, as well (see Fig. 6). These results suggest that the subglacial ecosystems may be more resilient than expected in the face of temporary disturbances, and may help explain how this ecosystem has been able to survive in an isolated fashion for so long.

## Implications for astrobiology

This model suggests that an ecosystem such as beneath Taylor Glacier could be stable for long periods of time. Several factors contribute to this longevity. The resilience in the system suggests it would be able to cope with significant disturbances, as long as they were of relatively short duration. If the ecosystem is primarily driven by chemosynthesis, then a large and continuous supply of redox pairs is necessary, and this supply ultimately determines the viability and behaviour



**Fig. 5.** (a) Biomass reaction to a temporary increase in phosphorus. (b) Biomass reaction to temporary increase in death rate.



**Fig. 6.** Total biomass C with and without a higher rate of nutrient cycling.

of the ecosystem. In the case of Blood Falls, iron and sulphur made up the backbone of the metabolism of the ecosystem, and fortunately, Mars is quite rich in these two elements. However, Blood Falls relies on the glacial mobilization of Fe(III) to keep it supplied, and it remains to be seen if glaciers on Mars perform similar scouring, and whether other mechanisms, such as volcanic activity or solar-driven photochemistry, can supply potential sources of chemical energy.

This information can then be used to inform strategies for searching for evidence of life on present day Mars. First and foremost, the production or presence of large amounts of reduced iron, crucial to this ecosystem, would also be highly indicative of possible life, and would stand out in stark relief against the oxidized iron that makes up most of the visible iron on the Martian surface. While the hydrological controls that lead to the periodic discharge of Blood Falls are not well-characterized, and therefore the likelihood of a similar event occurring on Mars are unknown, it may be worth investigating remote sensing data of the polar regions of Mars for similar surface deposits.

Lastly, it is important to note the discrepancy of scale in terms of primary productivity of icy ecosystems versus more temperate ones. Terrestrial productivity has been estimated as being as high as  $3500 \text{ g carbon m}^{-2} \text{ yr}^{-1}$  (Polis & Hurd 1996), many orders of magnitude greater than even the maximum productivity of the hypothetical Martian subglacial ecosystem, if Blood Falls in any indication. Consequently, even a thriving Martian ecosystem may be very hard to detect indeed.

## Conclusion

The Blood Falls formation at Taylor Glacier allows tantalizing insights at what type of organisms might make their living miles beneath the ice. Even with limited information, it is possible to construct a working ecosystem model that generates results that can greatly shape expectations of the actual ecology. The limiting nutrients can be determined in this case, phosphorus and Fe(III), and an upper limit for productivity and biomass can be determined, at  $6.4 \times 10^{-5} \text{ g C l}^{-1} \text{ yr}^{-1}$  and  $0.016 \mu\text{M C l}^{-1}$ , respectively. This ecosystem model can then be used to determine a possible lower and upper bound for what a Martian ecosystem in similar conditions might be limited by, the amount of biomass and secondary consumers that can be supported and in turn, how such an ecosystem might be detected.

As the search for life in the universe goes on, and the list of potentially habitable environments grows, this strategy of ecosystem modelling will become increasingly critical to furthering our understanding of what really is needed to support a viable living microbial community.

## Acknowledgements

The authors would like to acknowledge Dr Andrew Ford for his invaluable modelling insight and advice, and Dr. Jill Mikucki for her helpful correspondence.

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