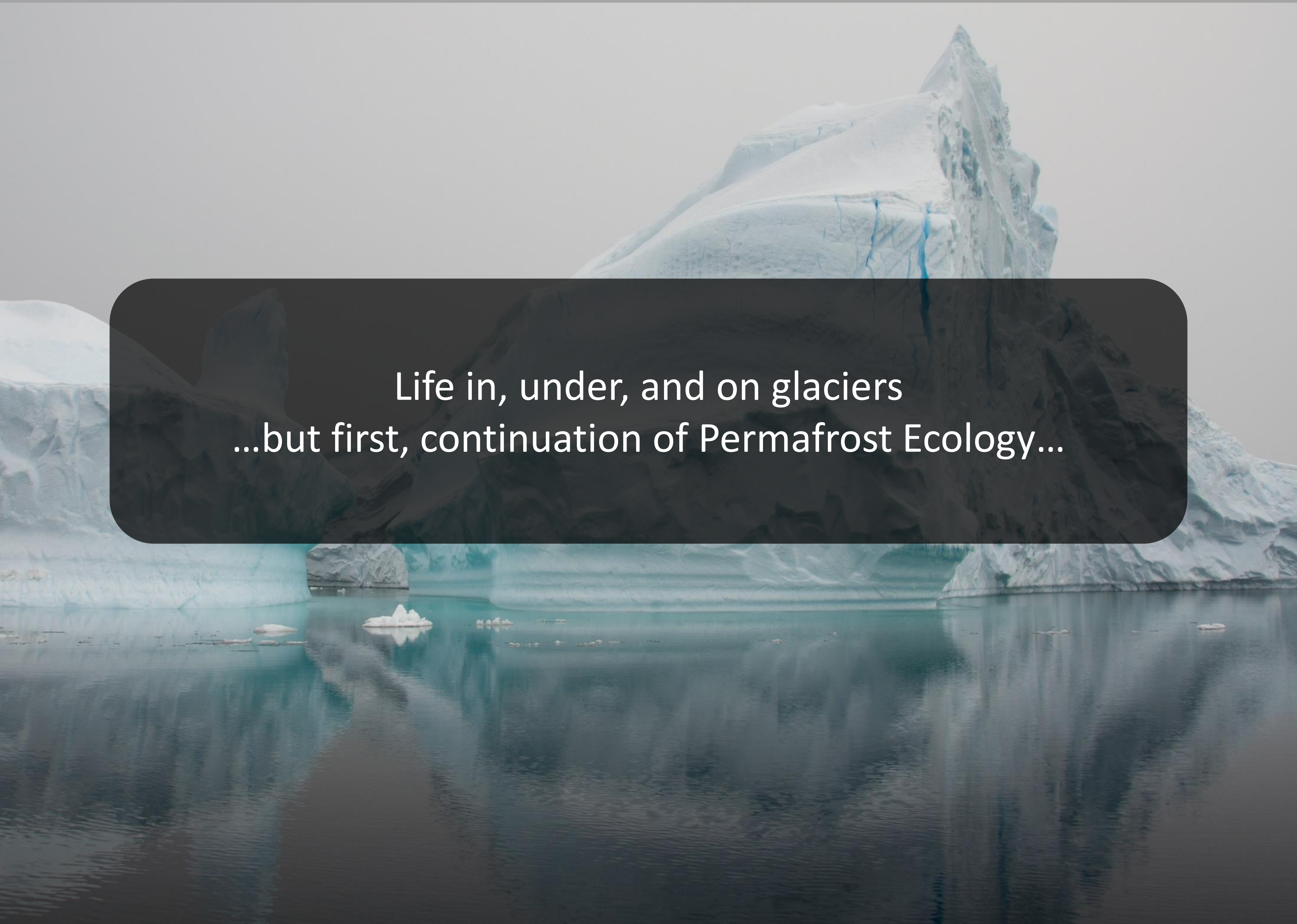


Life in, under, and on glaciers
…but first, continuation of Permafrost Ecology…

Announcements

- Questions on annotated bibliography, presentations…
  - Annotated bibliographies will be graded for:
    1. Minimum number of unique refs
    2. Refs appropriate
    3. Formatted correctly
    4. Reasonable effort to summarize

1. From where does the *Chlamydomonas* bloom originate each year?

The soil

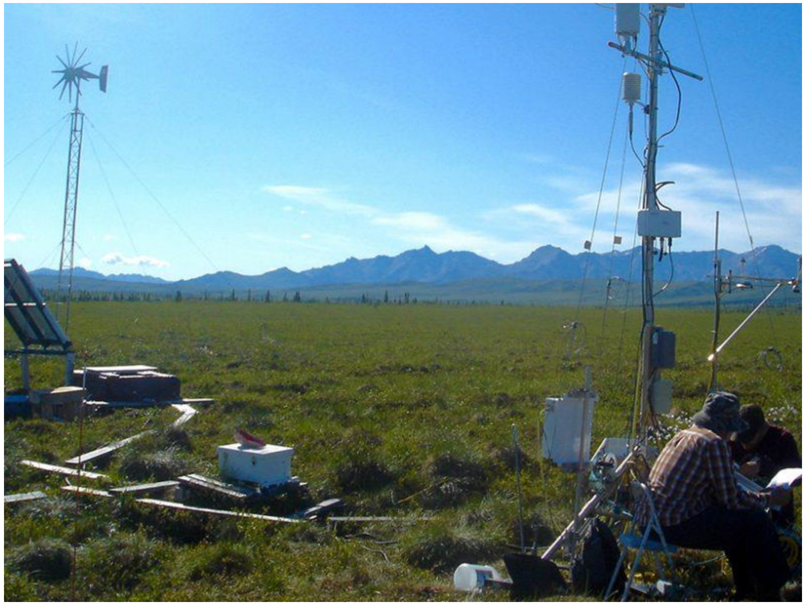
2. List three reasons the snow surface is a more harsh environment than the ice-water interface.

Radiation, low temperature, temperature fluctuations, nutrients, water activity…

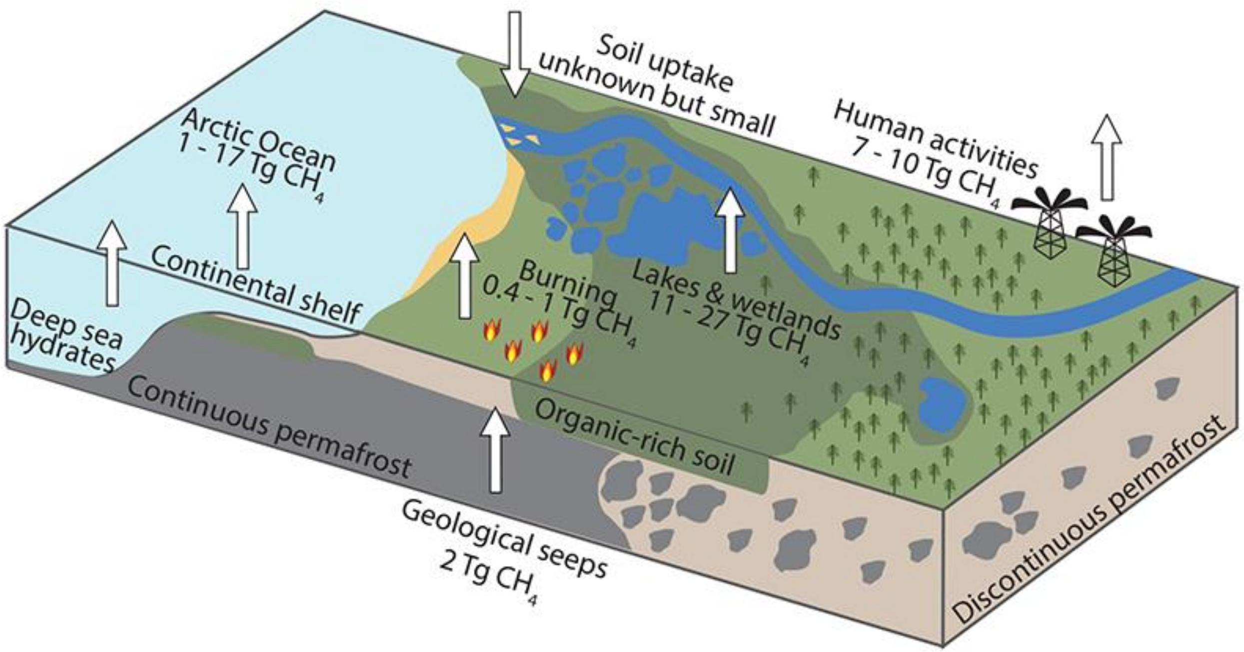
3. Why might snow algae blooms be enhanced near penguin rookeries?

Nutrients from penguin feces

1. Permafrost is a significant source of what volatile organic compound?
2. List two ways that mummified seals improve habitat for Antarctic permafrost microbes.
3. What macromolecule derived from plants is the base material for permafrost methanogenesis?



- ~6 Pg (6000 Tg) methane in atmosphere
- But we are NOT in steady state!
- Sources exceed sinks by ~25 Tg yr^{-1}



- Methanogenesis is significant wherever (wet) permafrost is found…
- Hypothesis: as permafrost melts tundra drains, reducing methane emissions
  - Evidence does not support this!

Environmental Science & Technology Article

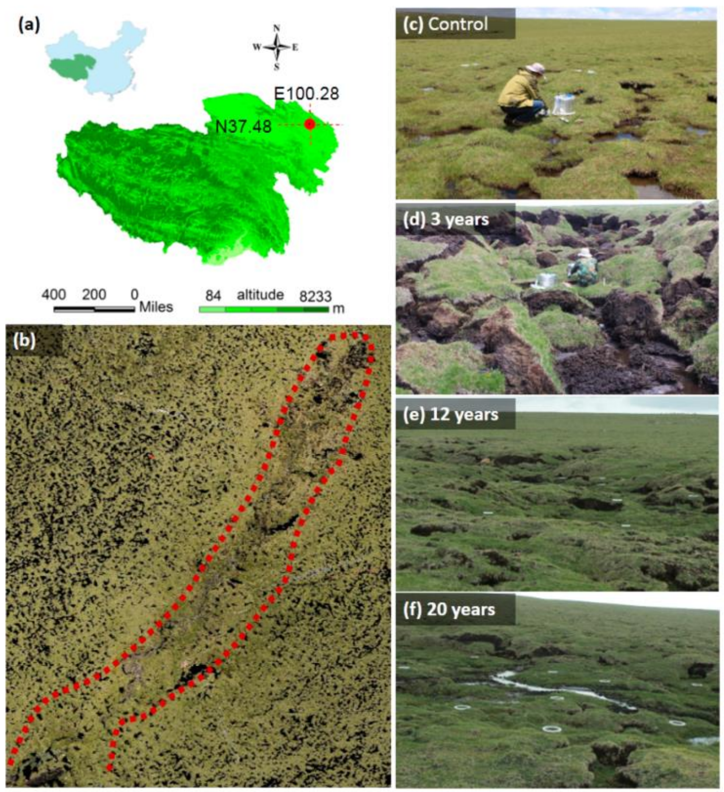
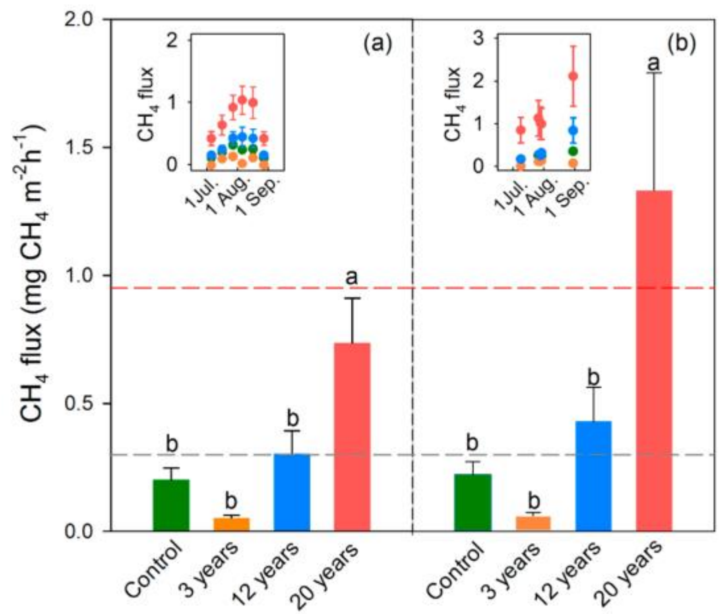
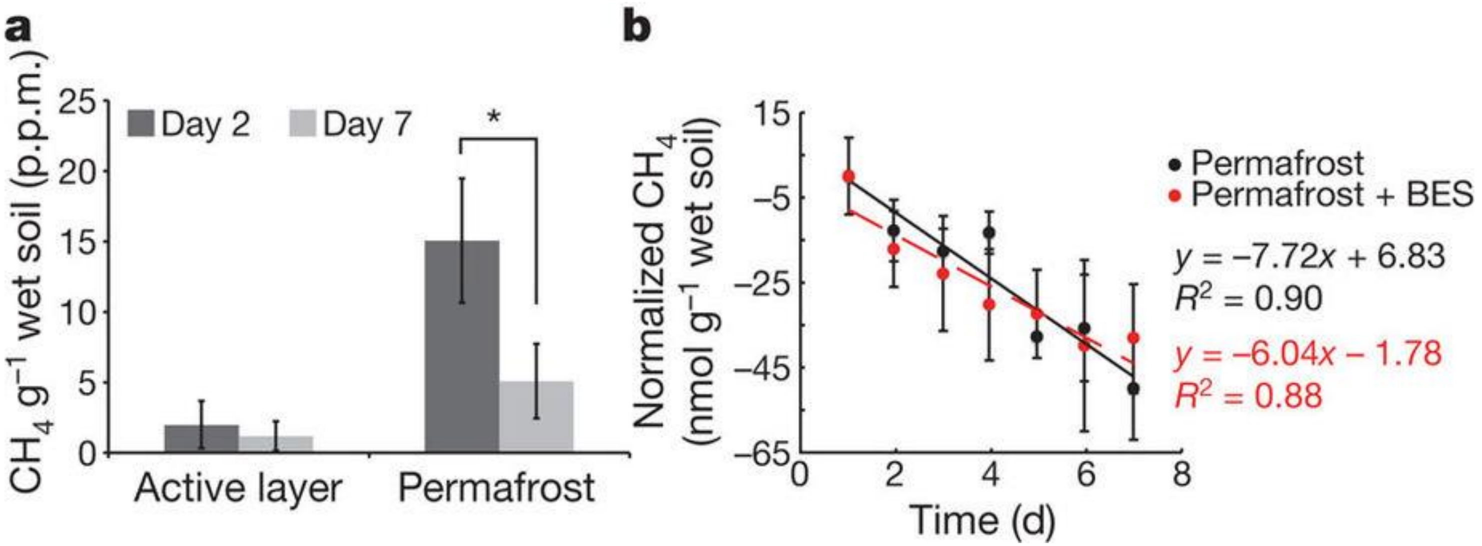


Figure 1. Location map of the study area (a), image of the thermo-erosion gully (b), and photographs of the different thaw stages (c–f). The red dot indicates our study site, and the image of the thermo-erosion gully was obtained by a high-resolution topographic model with LiDAR (VZ-400, Riegl, Horn, Austria, analyzed with Riscan pro 2.0 software).



Yang et al., 2018

- What about the soil biological sink term?
- Very poorly constrained!



Mackelprang et al., 2011

- Back to the sunlit surface… concurrent with permafrost decay the Arctic is undergoing "Arctic Greening", also known as borealization

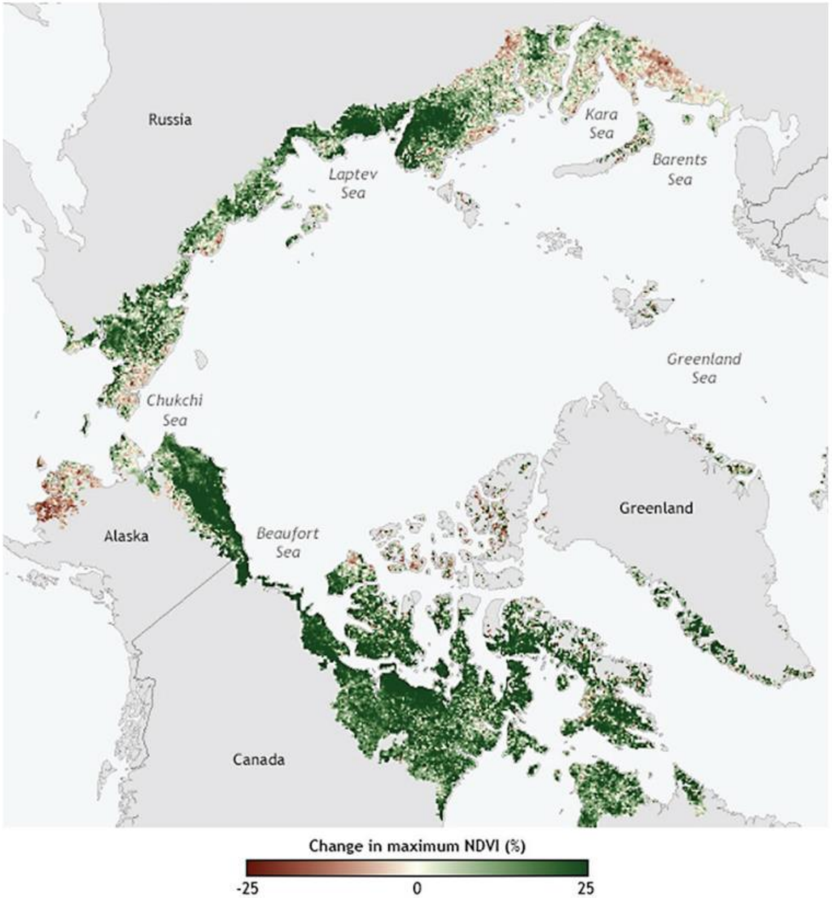
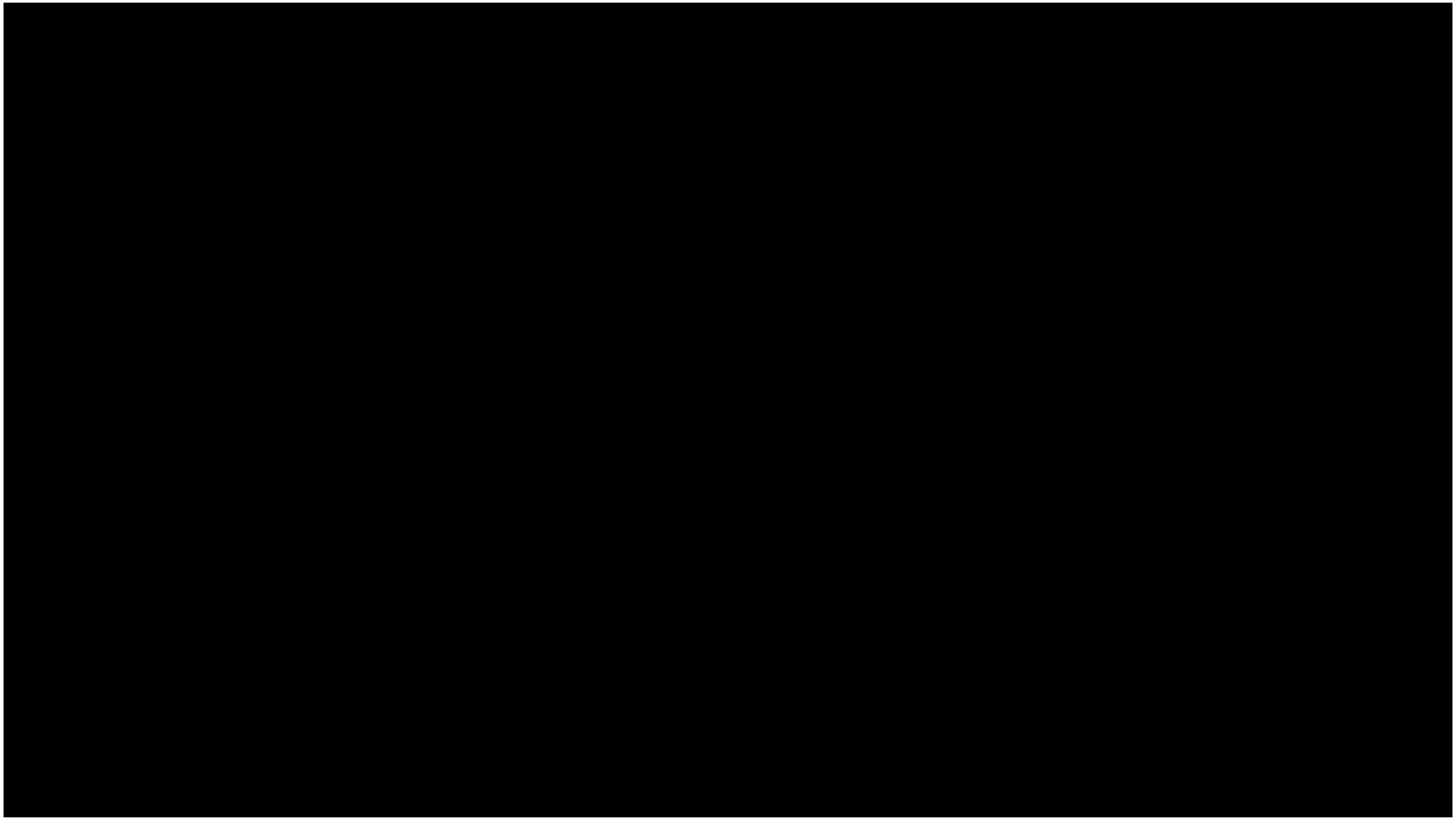
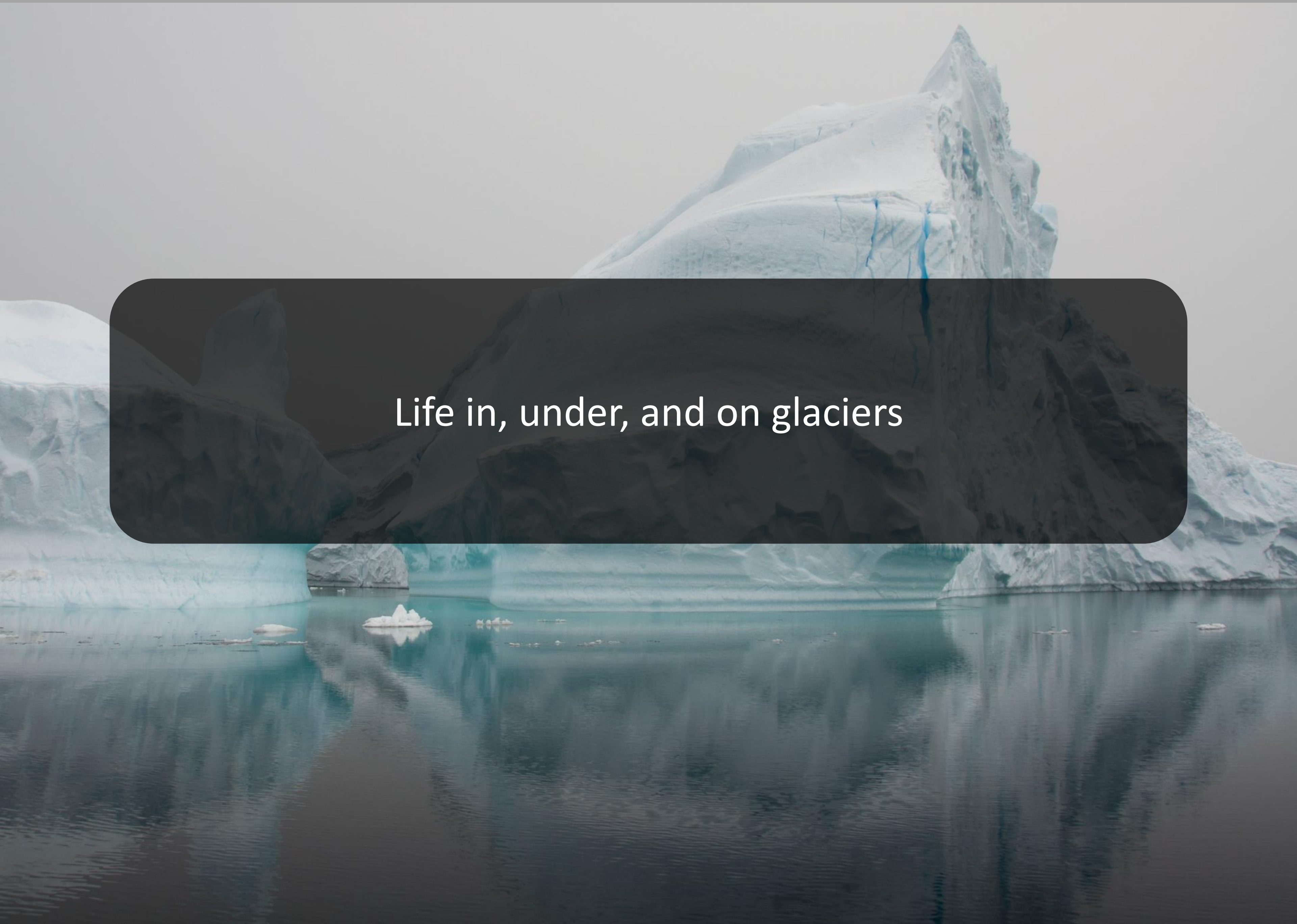
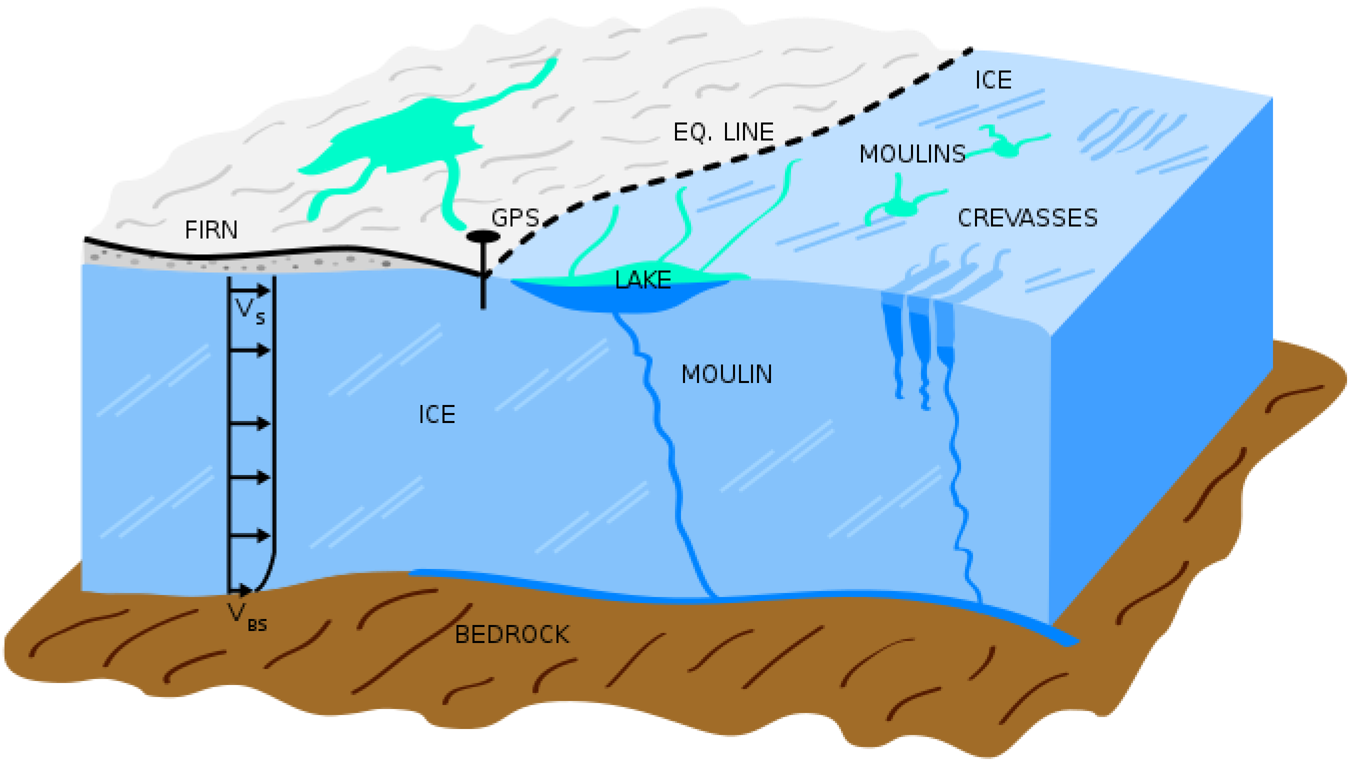


FIGURE 3.6 Land areas adjacent to newly opened water in the Arctic are becoming "greener." Since observations began in 1982, Arctic-wide tundra vegetation productivity has increased. In the North American Arctic, the rate of greening has accelerated since 2005. SOURCE: NOAA.





Life in, under, and on glaciers



- Supraglacial ice (cryoconite holes, cryolakes, etc.)
- Interior ice (*englacial*; brine veins and triple junctions)
- Subglacial environment (basal ice, subglacial lakes)

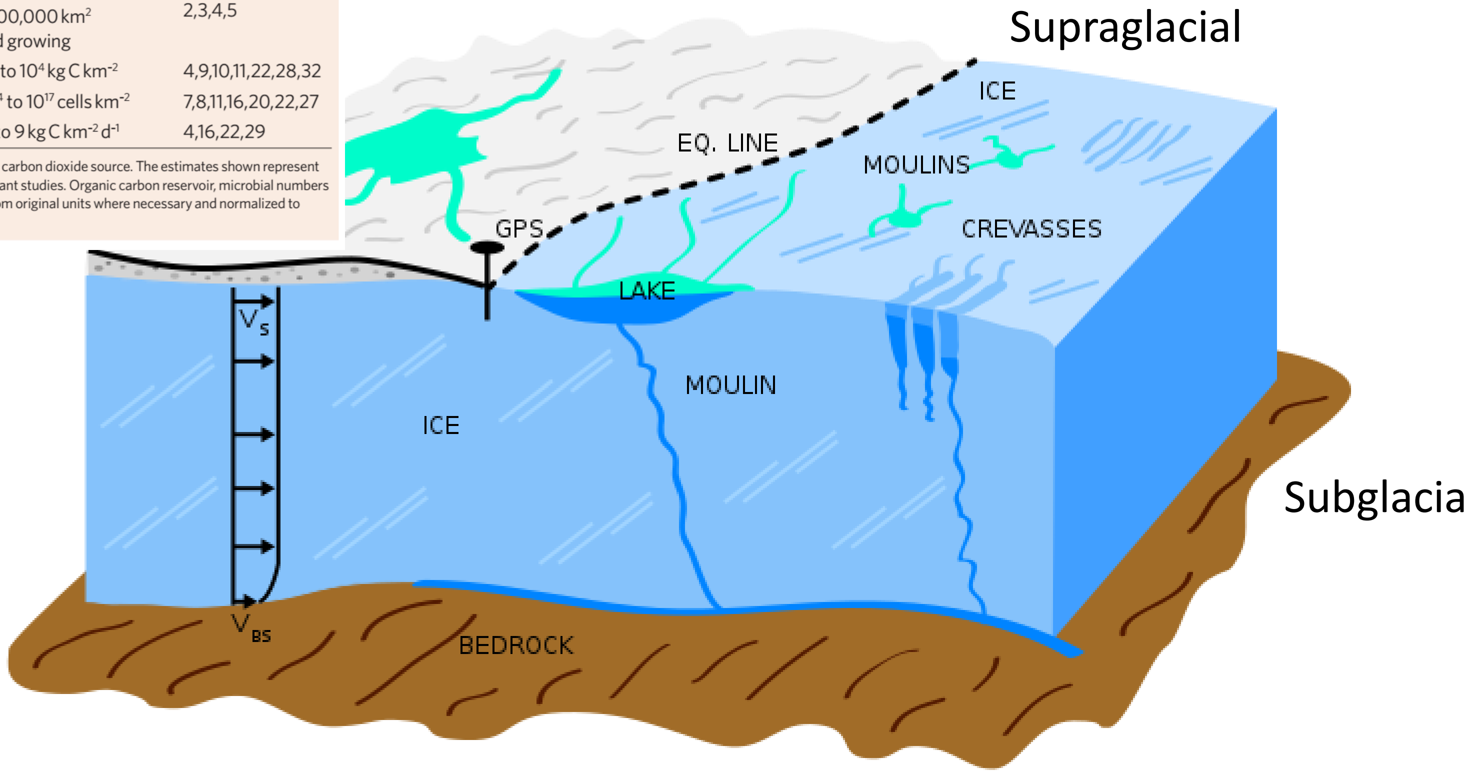
SIO 121, Lecture 9: Life in, under, and on glacial ice

Table 1 | Supraglacial environments in numbers.

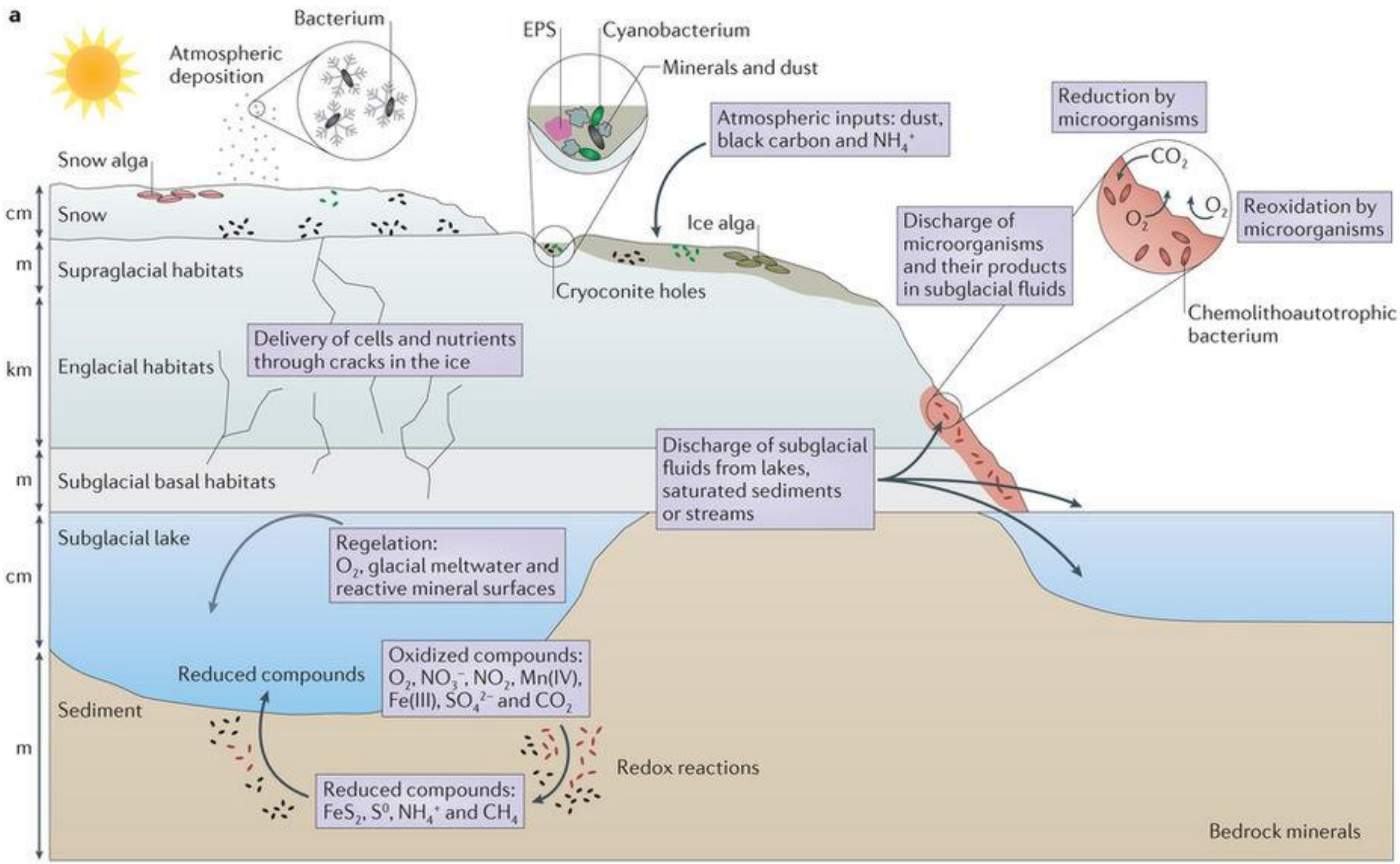
		Reference
Surface area of glaciers and ice sheets	~16,000,000 km^2 and shrinking	1
Biologically active area	~800,000 km^2 and growing	2,3,4,5
Organic carbon reservoir	10^1 to 10^4 kg C km^{-2}	4,9,10,11,22,28,32
Microbial abundance	10^{14} to 10^{17} cells km^{-2}	7,8,11,16,20,22,27
Net ecosystem production*	-3 to 9 kg C km^{-2} d^{-1}	4,16,22,29

*Negative values denote net heterotrophy, or carbon dioxide source. The estimates shown represent combined values and/or ranges from all relevant studies. Organic carbon reservoir, microbial numbers and net production values were converted from original units where necessary and normalized to glacier surface area.

Stibel et al., 2012



Q: What are the challenges and opportunities for life at the glacier surface?



Boetius et al., 2015

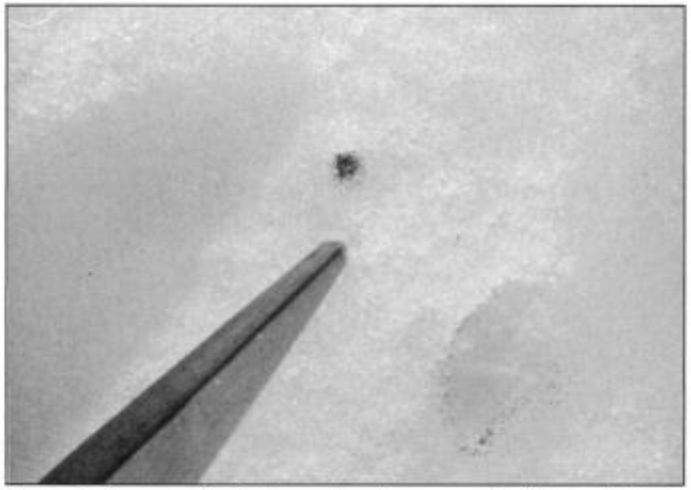
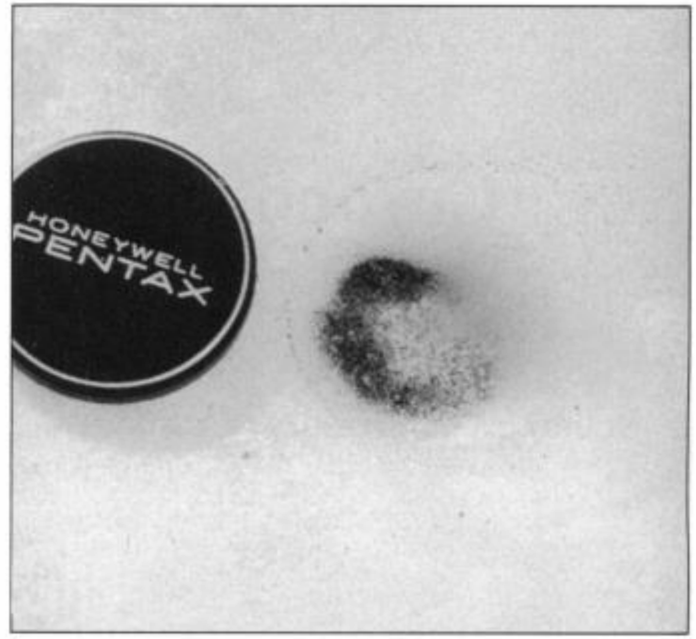
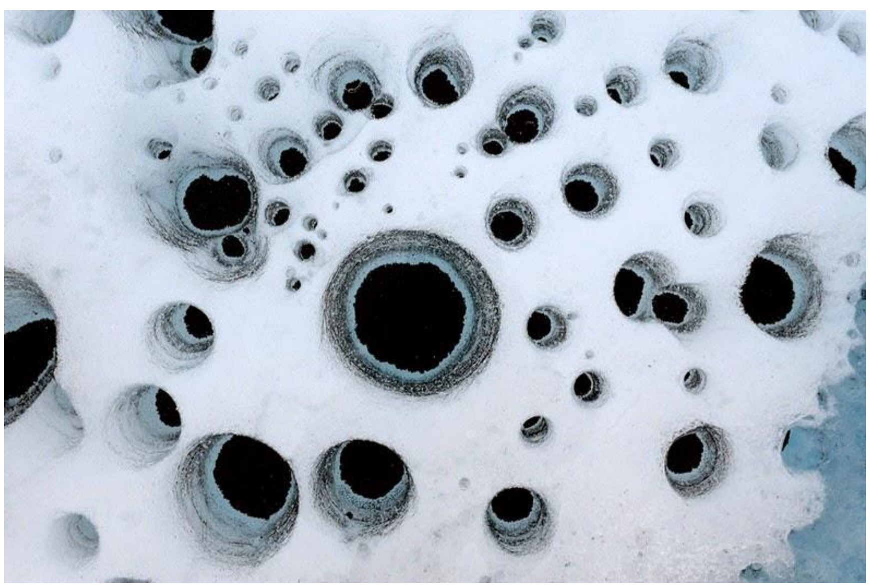
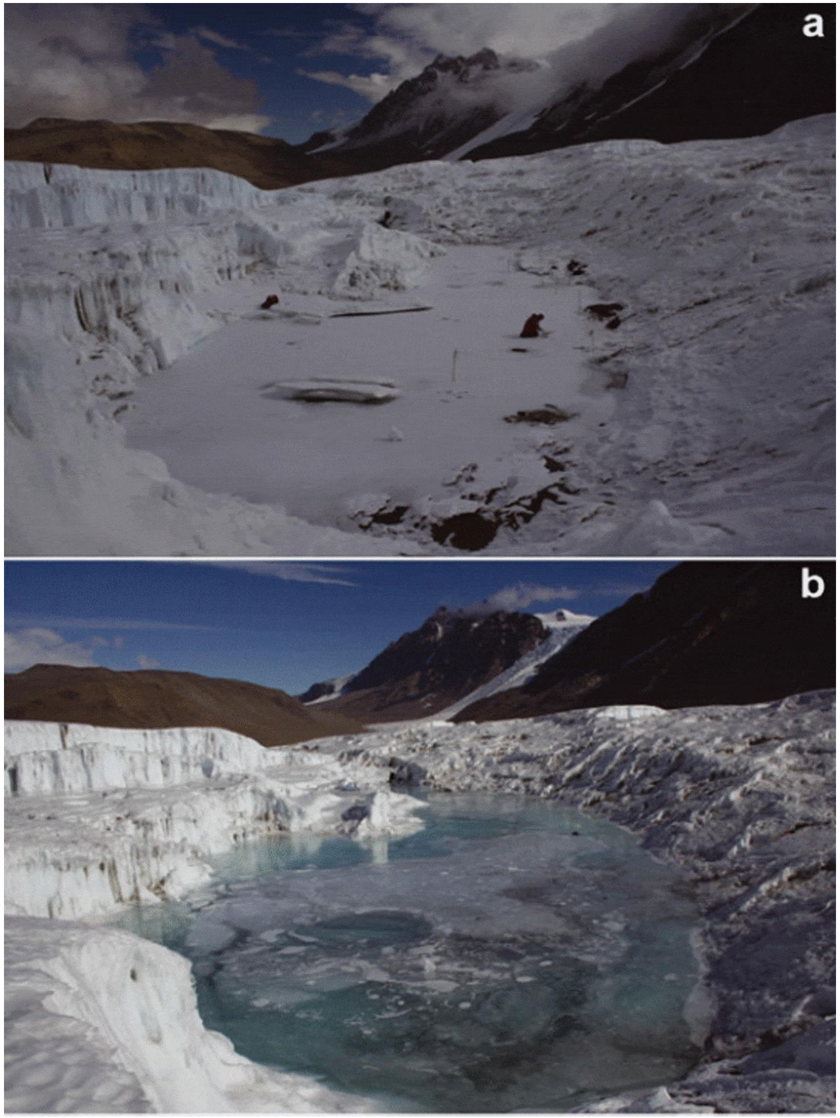


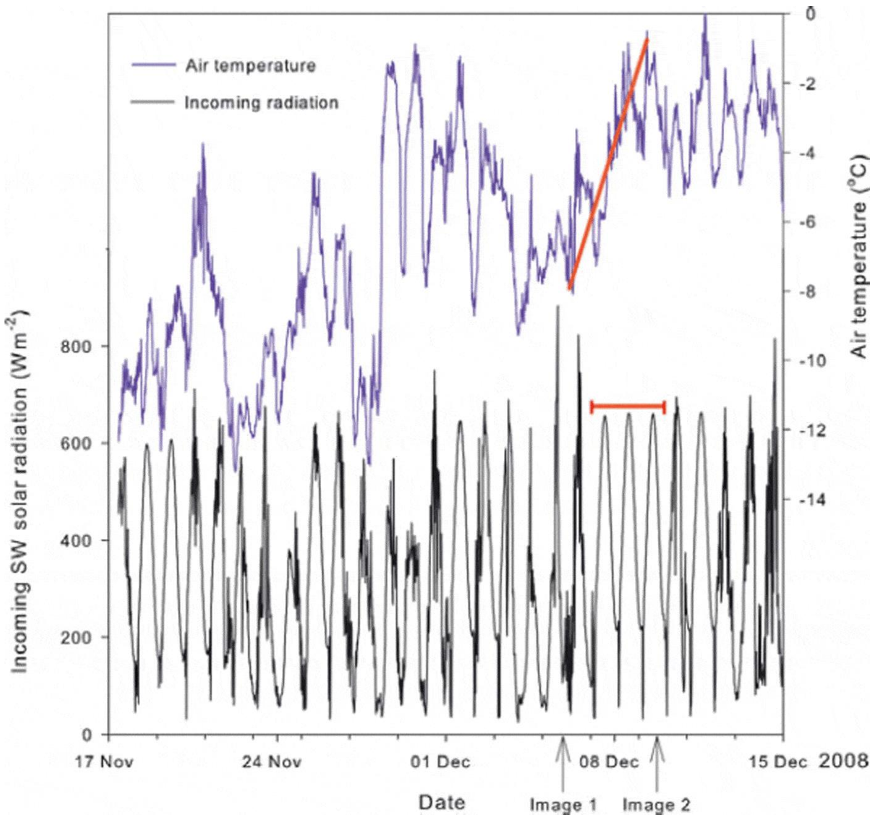
Figure 2. Sequence in the formation of a cryoconite hole on Canada Glacier, Southern Victoria Land, Antarctica. Accumulated dust and sand-sized particles start a hole several millimeters in diameter; more sediment enlarges the hole. Continued enlargement combined with melting and other erosional processes may produce a pond. Photos: Dale Andersen and G. M. Simmons, Virginia Polytechnic Institute.





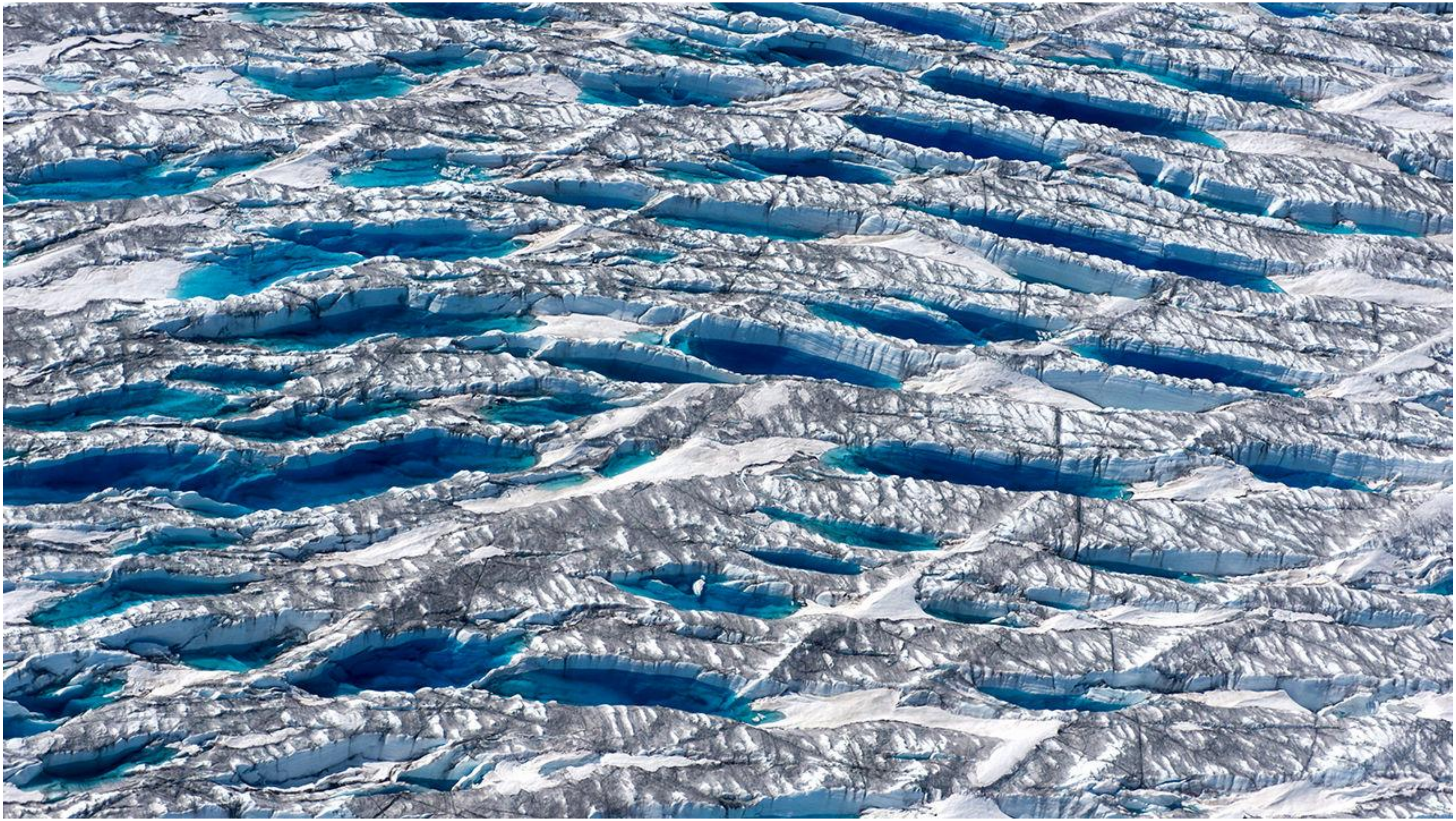
Wharton et al., 1985





Fountain et al., 2010

- Cryoconite holes can grow to become cryolakes
- The glacier surface is highly dynamic, remember the impact of positive feedbacks!



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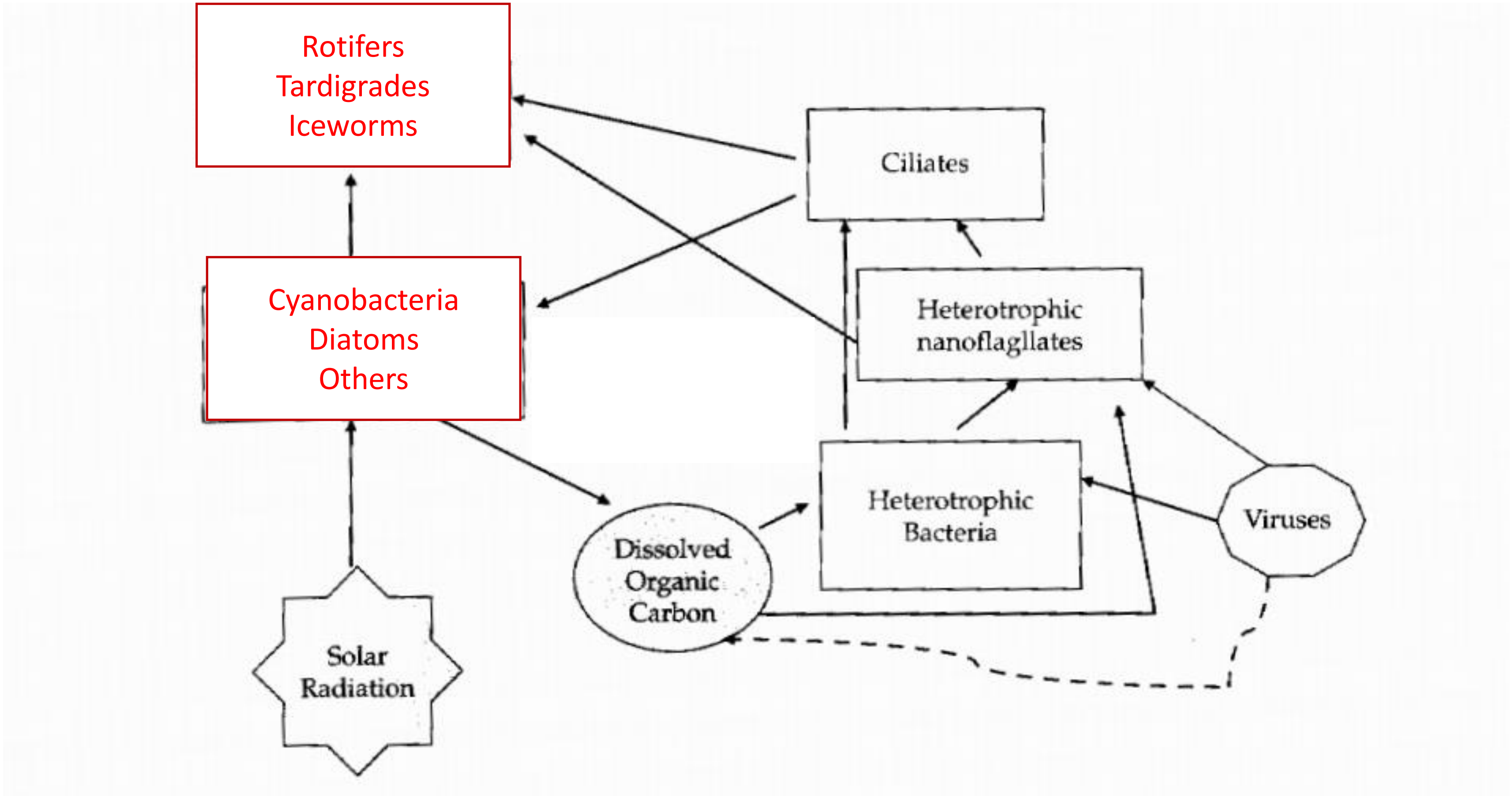
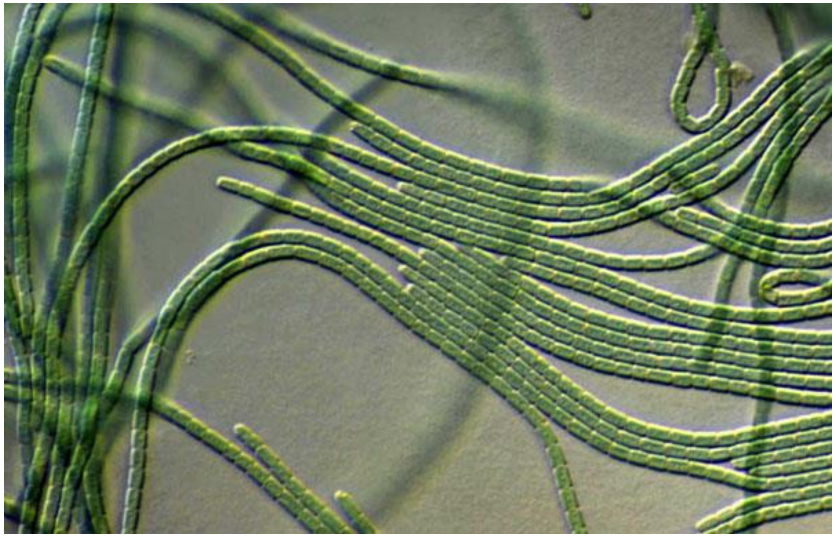

Rotifers
Tardigrades
Iceworms
Ciliates
Cyanobacteria
Diatoms
Others
Heterotrophic nanoflagllates
Heterotrophic Bacteria
Viruses
Dissolved Organic Carbon
Solar Radiation

SIO 121, Lecture 9: Life in, under, and on glacial ice: Supraglacial



- Very few estimates of primary production, but some measurements >> 1000 gC m^3 day^{-1}
- This carbon can subsidize ecosystems throughout the watershed
- Can subsidize the marine ecosystem for tidewater glaciers

Sorrell et al., 2013

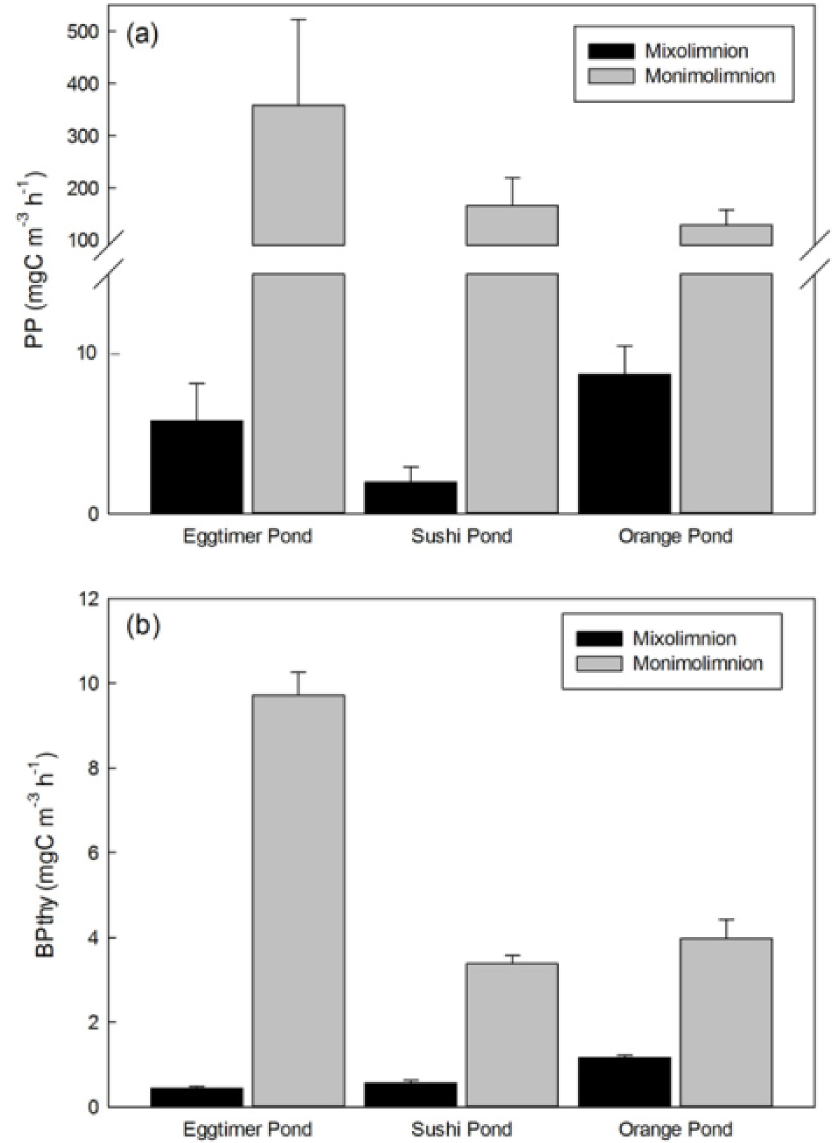
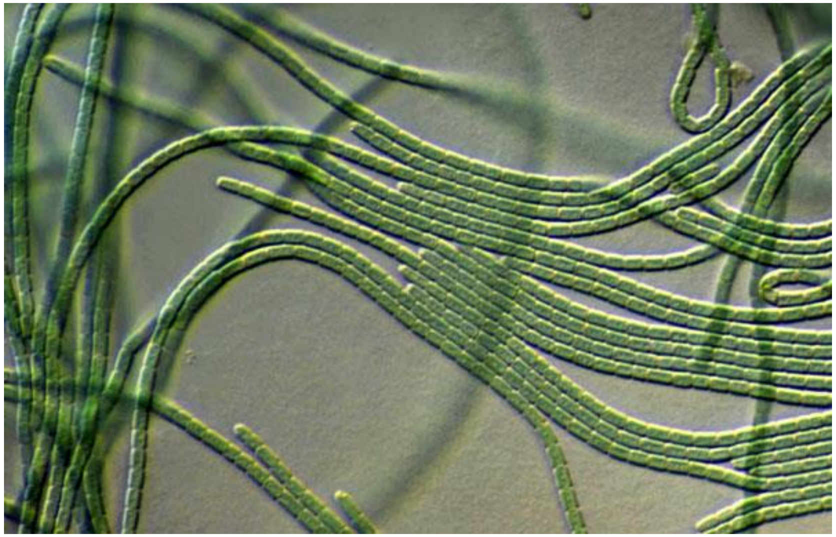
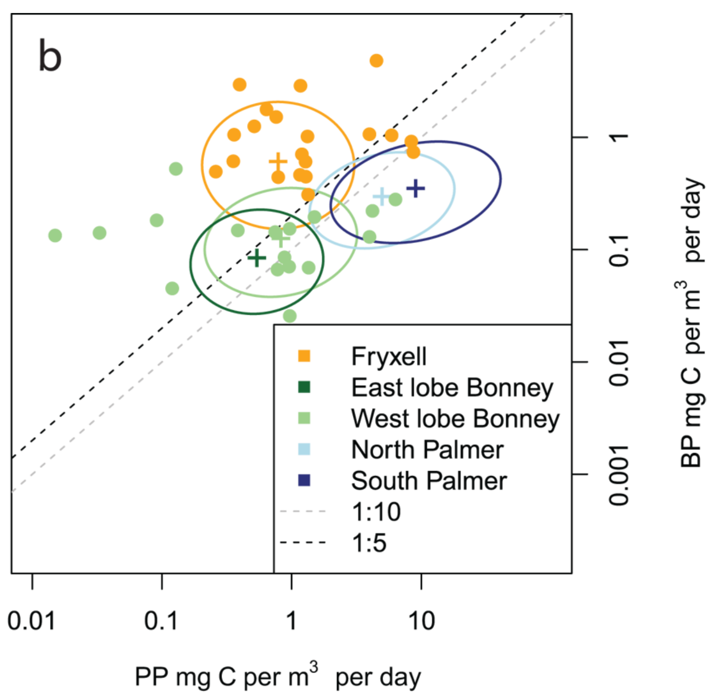


Figure 1. Comparison of (a) primary production and (b) secondary production (measured as BPthy) between layers of meromictically stratified ponds. Mean values with standard deviations ($n = 4$).

SIO 121, Lecture 9: Life in, under, and on glacial ice: Supraglacial





Sorrell et al., 2013

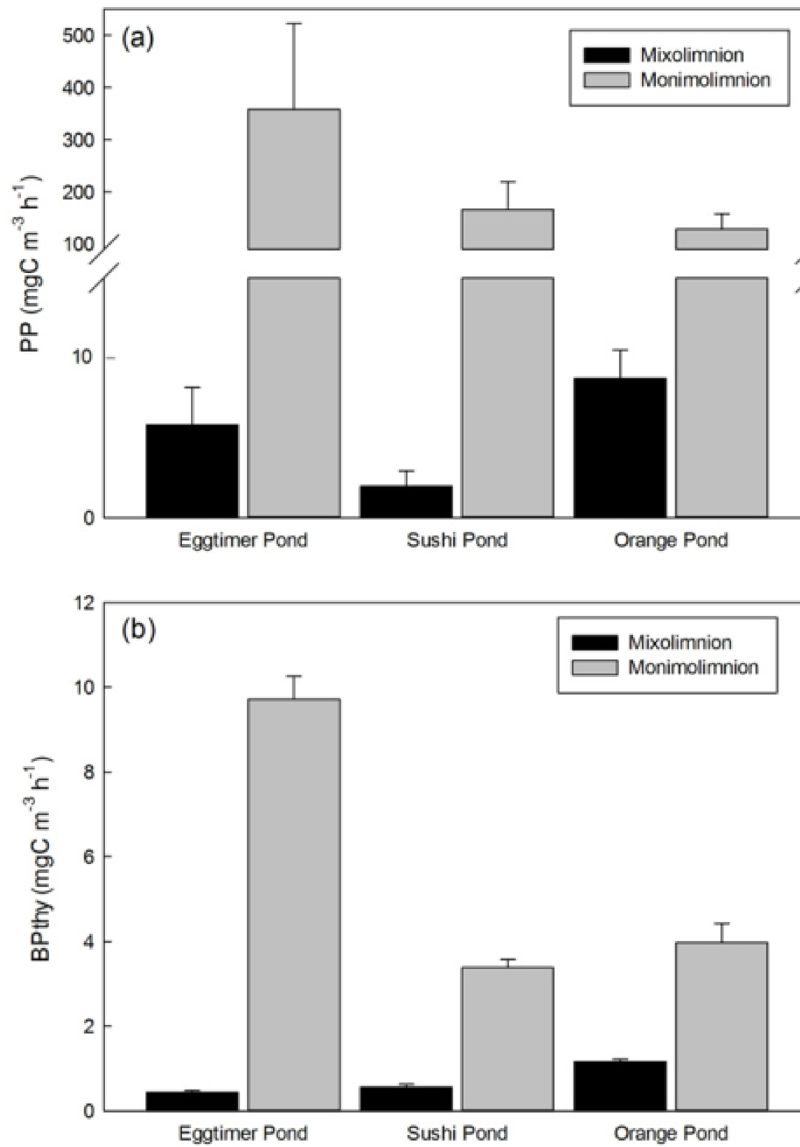
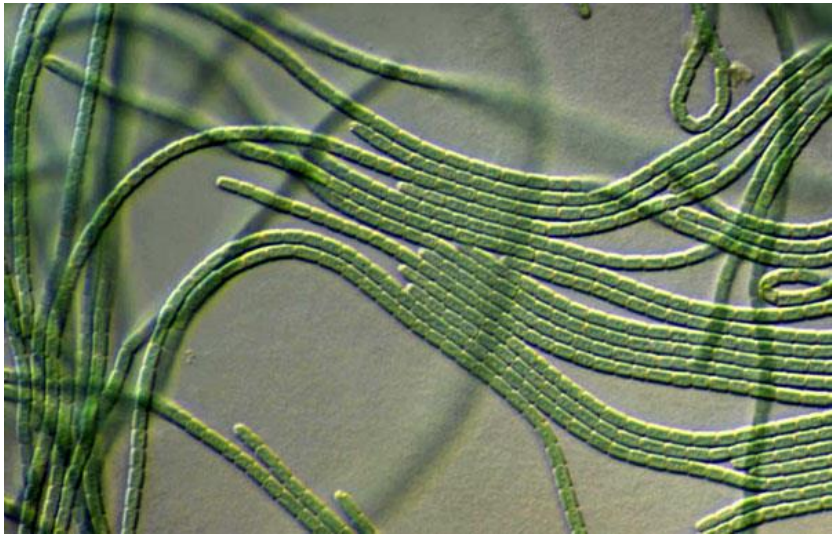
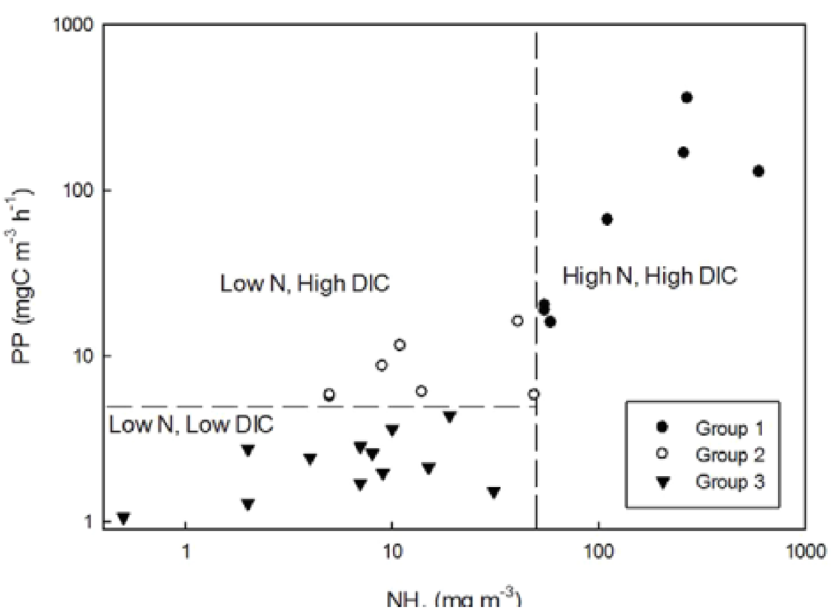
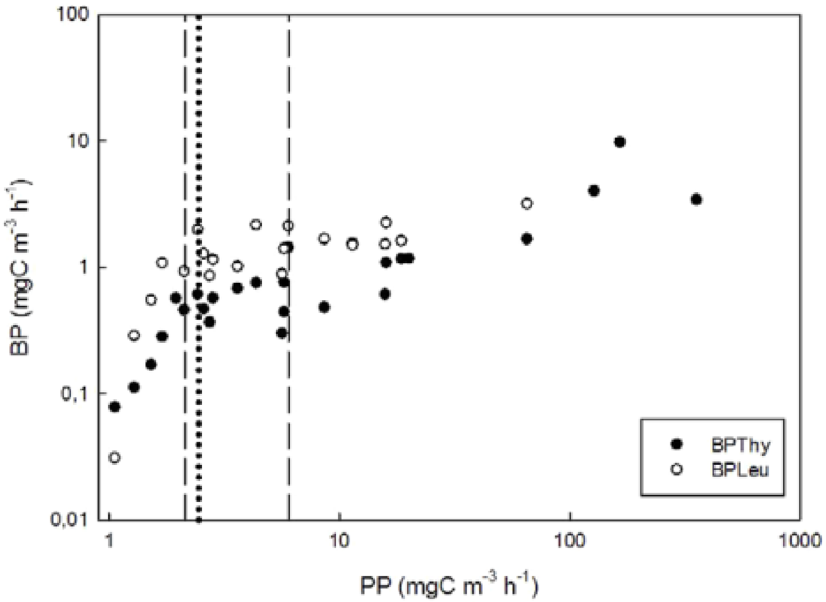


Figure 1. Comparison of (a) primary production and (b) secondary production (measured as BPthy) between layers of meromictically stratified ponds. Mean values with standard deviations ($n = 4$).

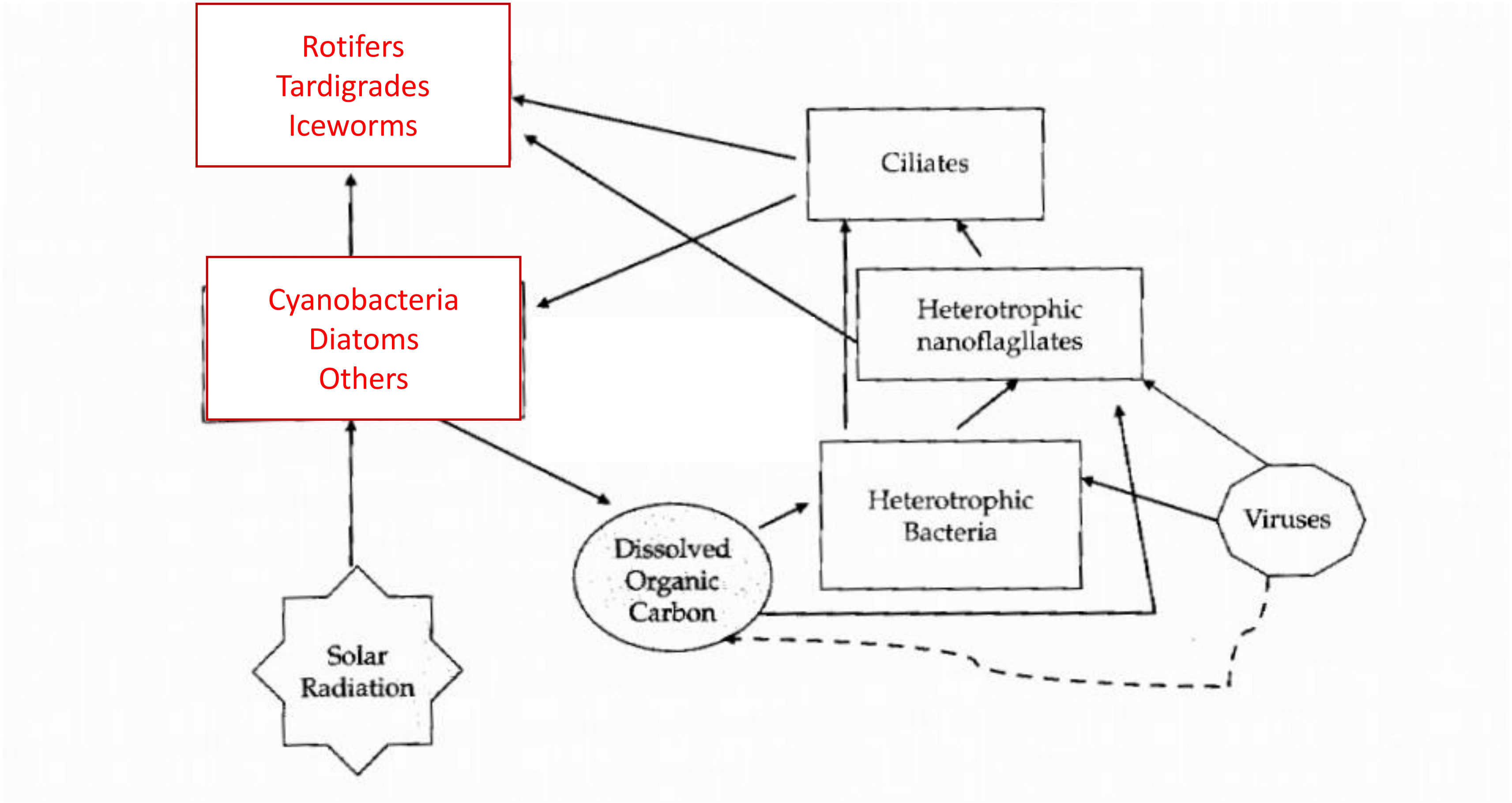


- PP appears tightly correlated to nutrient concentrations, suggesting nutrient limitation exerts strong control
- BP tightly correlated to PP, suggesting the bacteria are dependent on new DOC



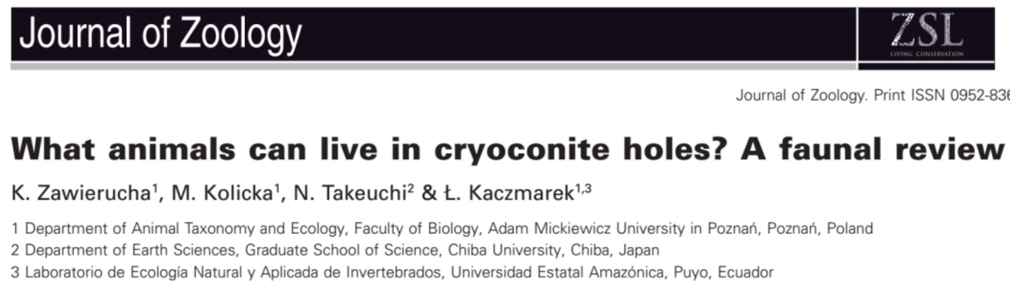


Sorrell et al., 2013


Rotifers
Tardigrades
Iceworms
Ciliates
Cyanobacteria
Diatoms
Others
Heterotrophic nanoflagllates
Heterotrophic Bacteria
Viruses
Dissolved Organic Carbon
Solar Radiation

SIO 121, Lecture 9: Life in, under, and on glacial ice: Supraglacial

- Glacier PP is feeding:
  - Heterotrophic bacteria
  - Downstream ecosystems
  - Metazoans, fewer than 30 publications on metazoans at the glacier surface!
    - Tardigrades
    - Ice worms
    - Rotifers
    - Nematodes, copepods, etc.


Journal of Zoology ZSL
Journal of Zoology. Print ISSN 0952-8369

What animals can live in cryoconite holes? A faunal review

K. Zawierucha[1], M. Kolicka[1], N. Takeuchi[2] & Ł. Kaczmarek[1,3]

1 Department of Animal Taxonomy and Ecology, Faculty of Biology, Adam Mickiewicz University in Poznań, Poznań, Poland
2 Department of Earth Sciences, Graduate School of Science, Chiba University, Chiba, Japan
3 Laboratorio de Ecología Natural y Aplicada de Invertebrados, Universidad Estatal Amazónica, Puyo, Ecuador

50 µm – 1.5 mm

- Tardigrades, “water bears”
- Feed on bacteria and algae
- Especially well adapted to glaciers and other extreme environments
- Exemplify common strategy of “inactive”, protected state (tun state, also *cryptobiosis*)
- Virtually indestructible in this state

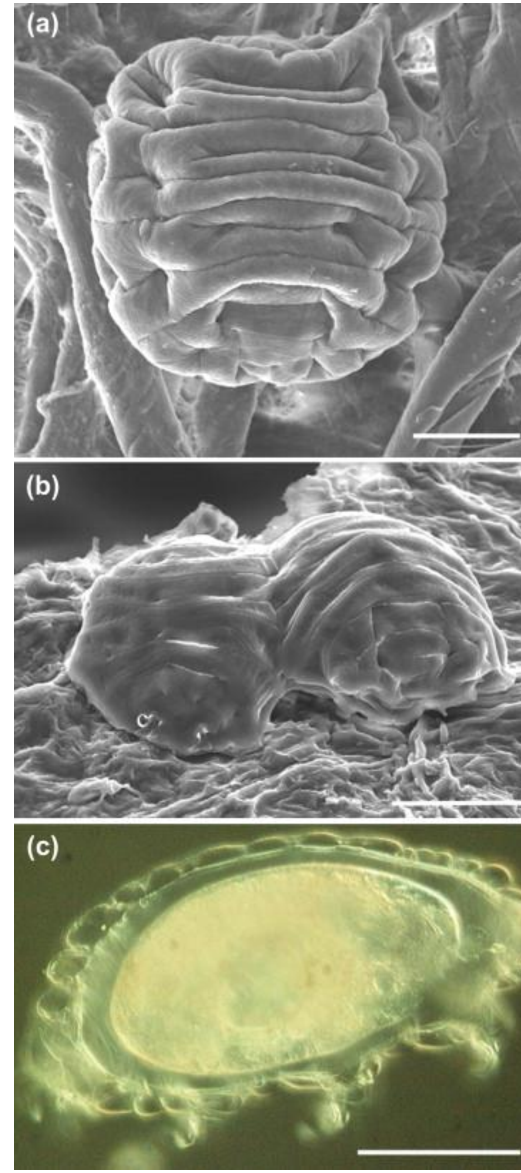
See Chapter 17 in Thorp and Covich’s Freshwater Invertebrates (4^{th} edition)

Tardigrade cryptobiosis

- Triggered by low water activity or low temperature, change must be gradual enough to allow tun formation
- Body contracts, synthesis of trehalose, glycerol, heat shock proteins, DNA supercoiling
- Voluntary loss of virtually all water (essentially freeze-dries)

50 µm – 1.5 mm

See Chapter 17 in Thorp and Covich's Freshwater Invertebrates (4th edition)

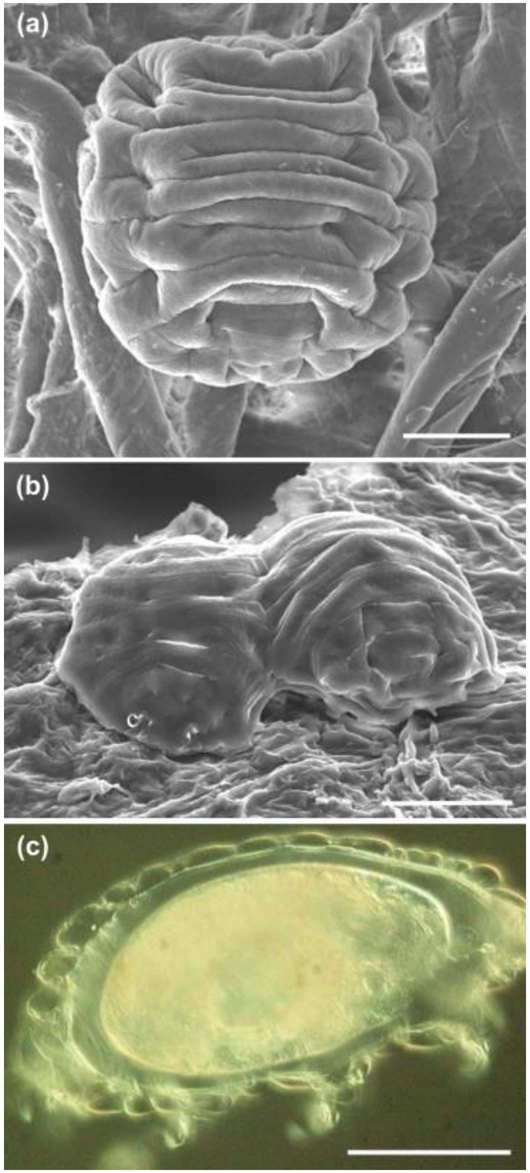


Tardigrade cryptobiosis

- In tun state can survive:
  - Temperatures from nearly 0 K to 151 C
  - 600 MPa pressure (and vacuum)
  - Extreme radiation
  - Solvents and acid exposure

50 µm – 1.5 mm

See Chapter 17 in Thorp and Covich's Freshwater Invertebrates (4th edition)

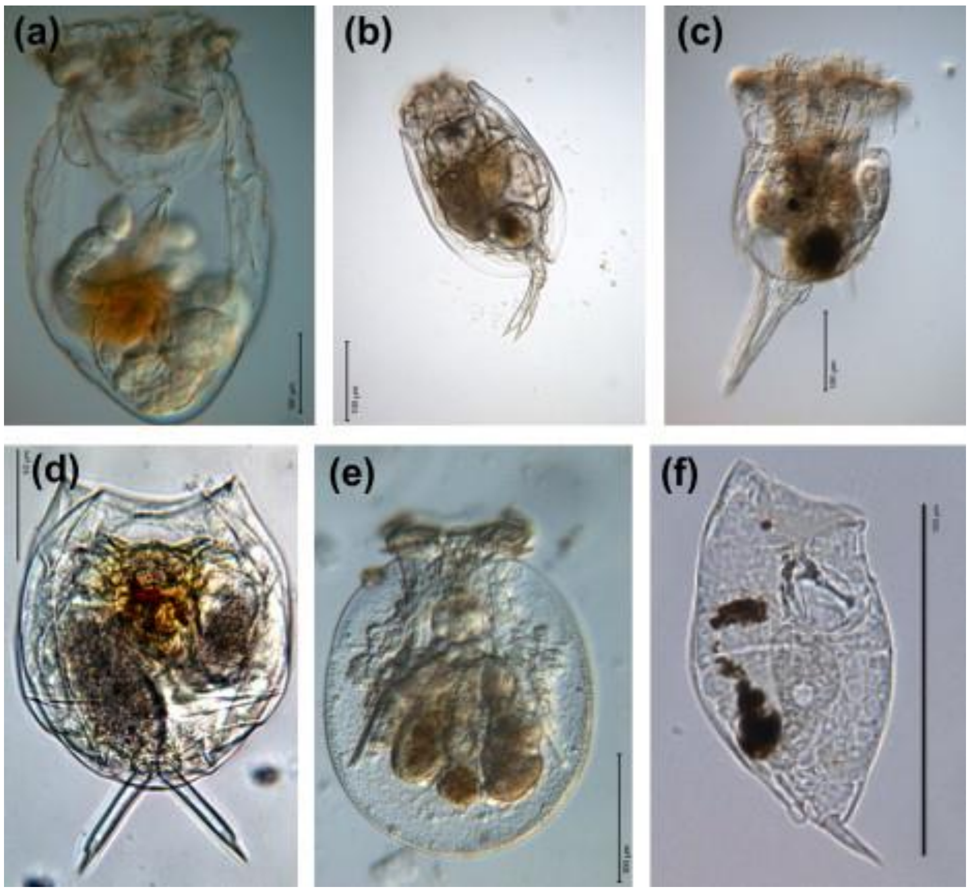


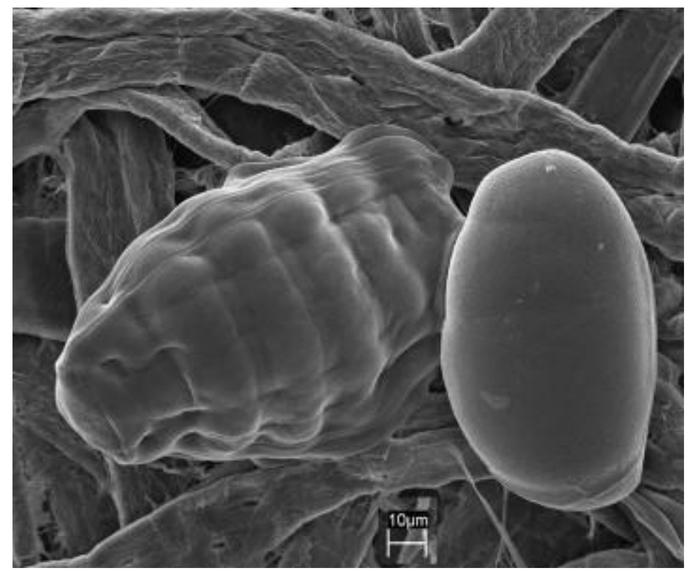
Ice worms

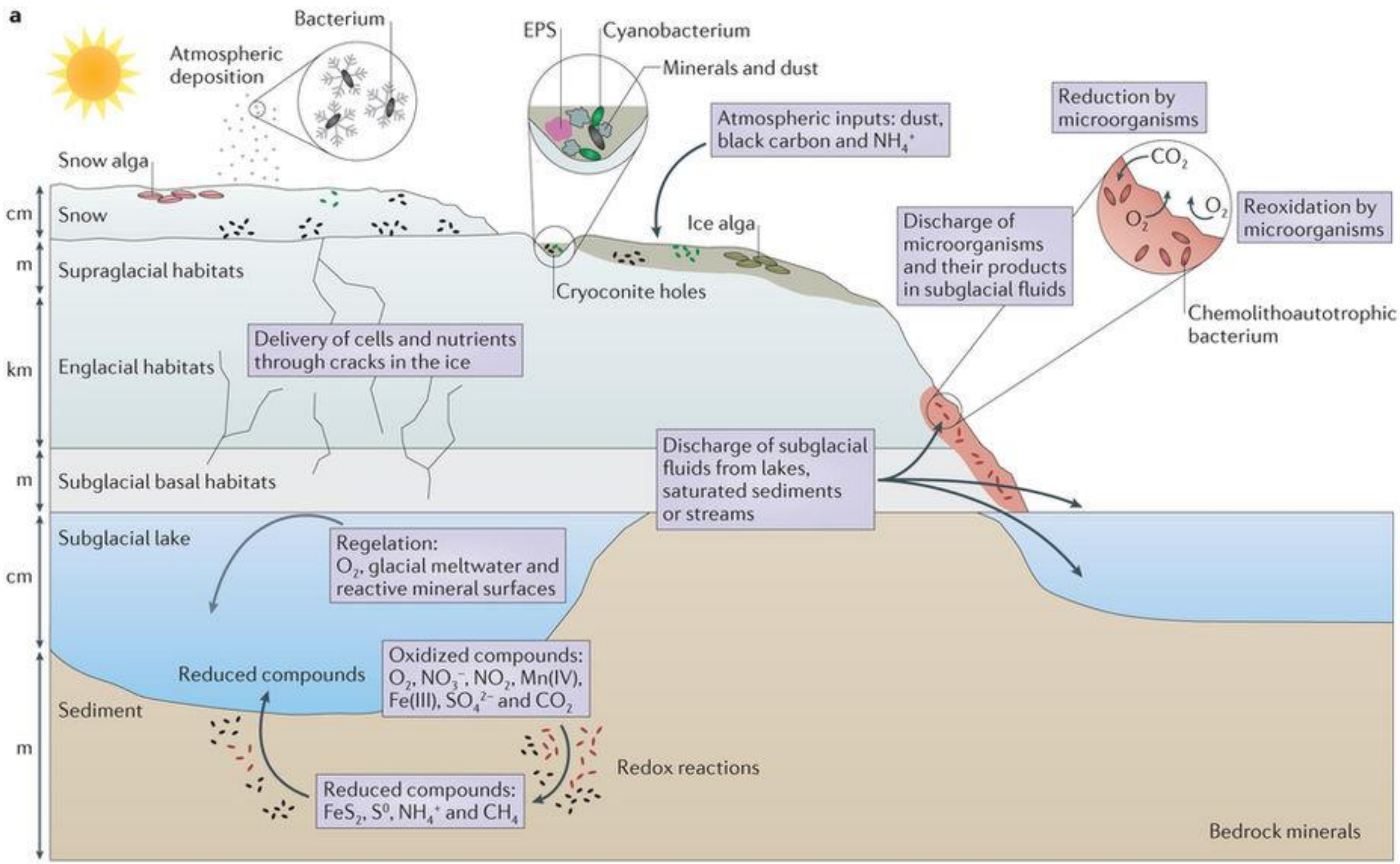
- Species *Mesenchytraeus solifugus* within the annelids
- Feed on algae at the snow surface and in cryoconite holes, retreat into the glacier during day

Rotifers

- Common in aquatic and marine habitats
- Major grazers of phytoplankton and bacteria
- Undergo anhydrobiosis similar to tardigrades, but not nearly as durable in that state







Q: In comparison with the supraglacial environment, what are the challenges and opportunities for life in the glacier interior?

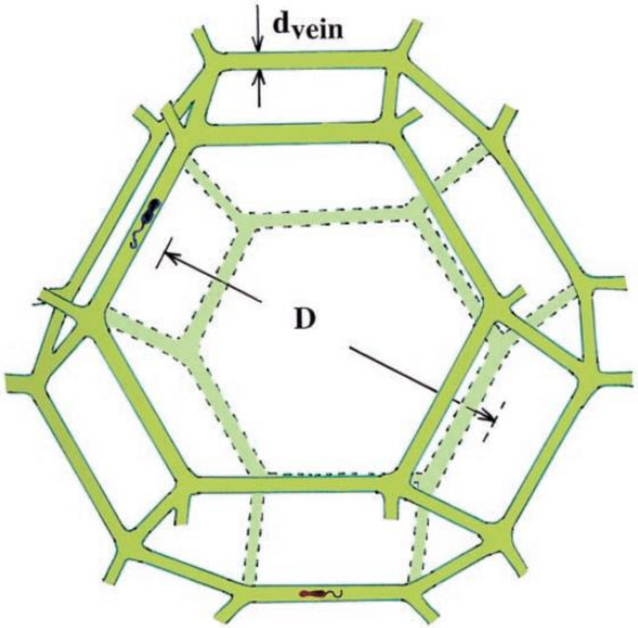


Fig. 1. Microbial habitat consisting of solid ice grains (approximated by truncated semiregular octahedra) bounded by liquid veins (not to scale). Two microbes are depicted as living in the vein of diameter d_{vein} surrounding a single grain of diameter D.

Table 1. Major ions in Vostok glacial ice at a depth of 3,300 m and in accretion ice at ≈3,600 m

	Glacial ice (4×10^5 years)		Accretion ice (filtered)	
Ion or compound	ng/g	Bulk molarity, μM	ng/g	Bulk molarity, μM
SO_4^{2-}	122	1.24	38	0.39
NaCl in solid grains	58.2	1	—	—
NO_3^-	18.6	0.3	10	0.164
Na^+	—	—	29	1.26
Cl^-	5	0.14	37.6	1.06
$CH_3SO_3^-$	7.99	0.084	—	—
$HCOO^-$	0.95	0.02	—	—
CH_3COO^-	0.77	0.013	—	—
Mg^{2+}	—	—	7.6	0.32
Ca^{2+}	—	—	9.7	0.24
Acidity in bulk	—	≈2	—	≈0
DOC (ref. 15)	?	?	?	≈7
DOC (ref. 14)	—	—	~500	?

DOC, dissolved organic carbon of unknown composition.

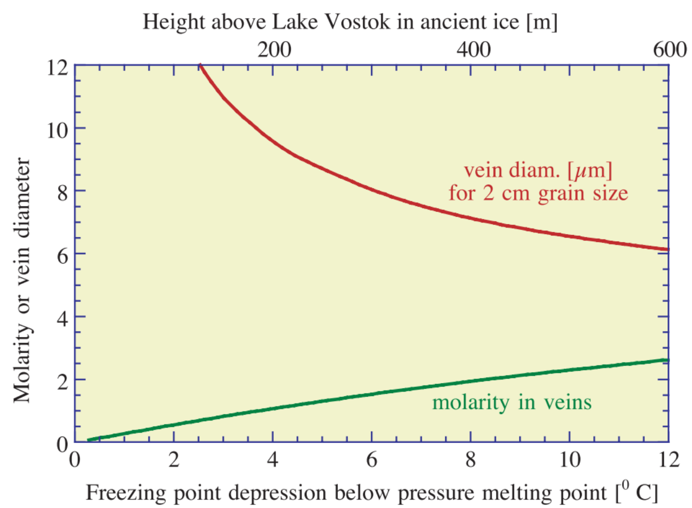


Fig. 2. Relationships among molarity of impurities in aqueous solution, vein diameter, and depression of freezing point below pressure melting point for the composition of impurities in glacial ice. Also shown is approximate height above Lake Vostok. For arbitrary grain size, vein diameter scales as grain size.

Price et al., 1999

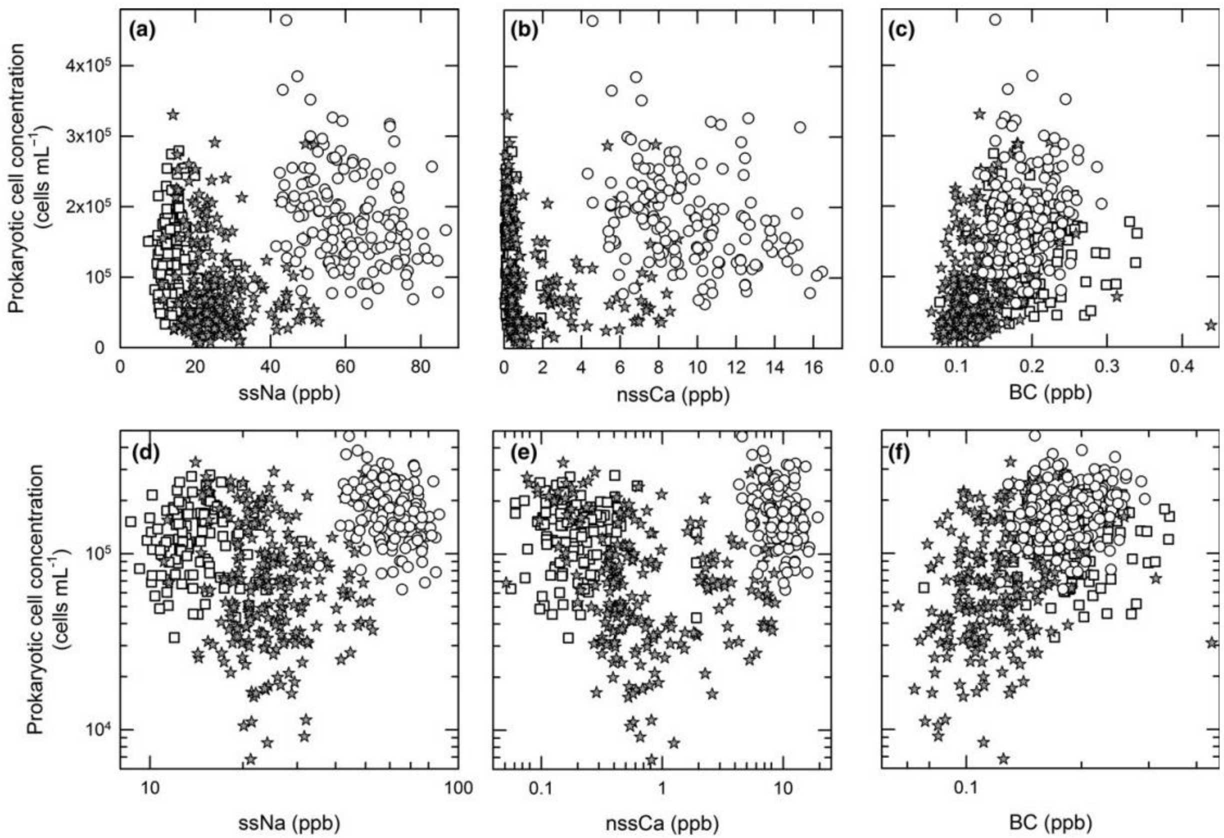
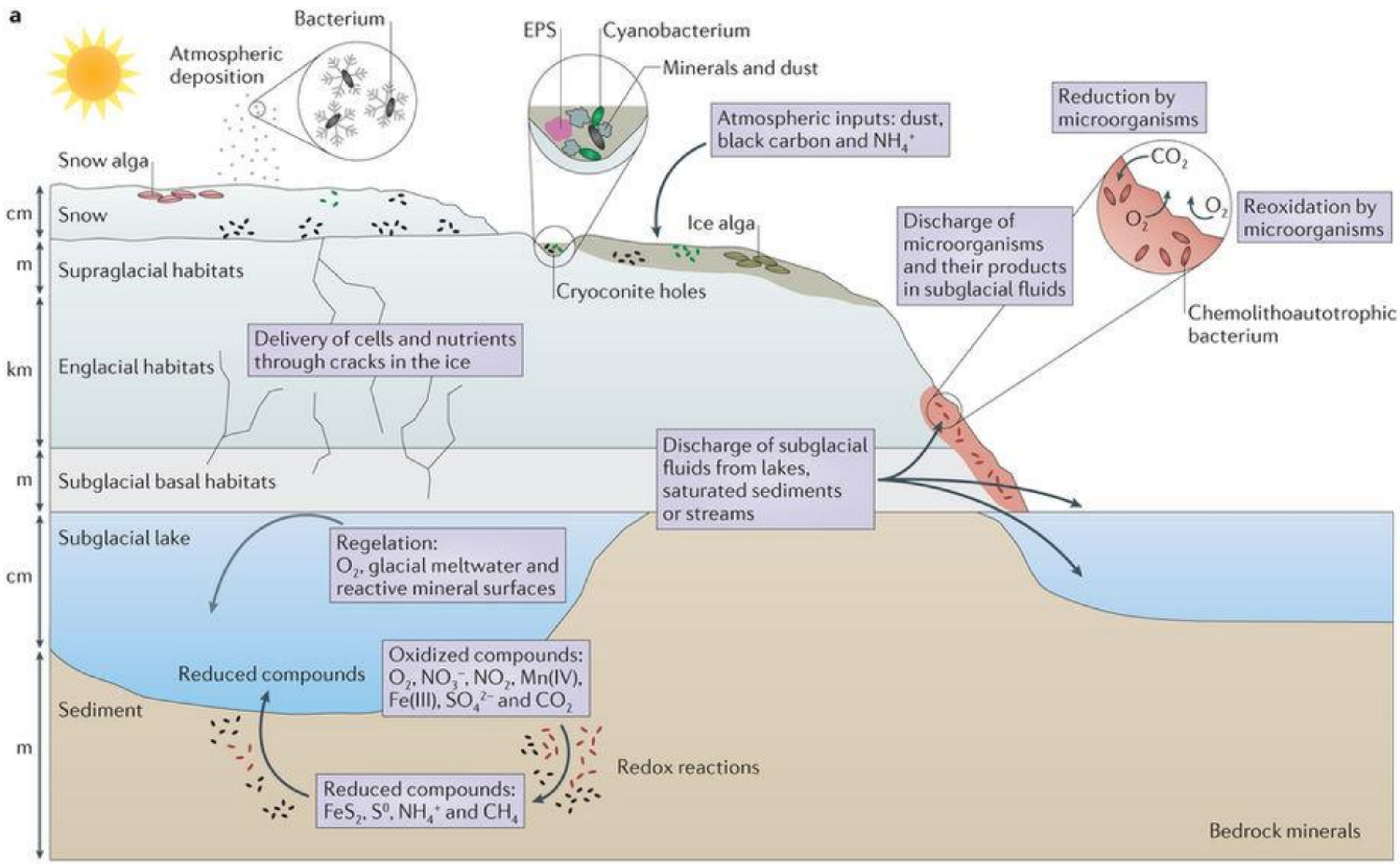


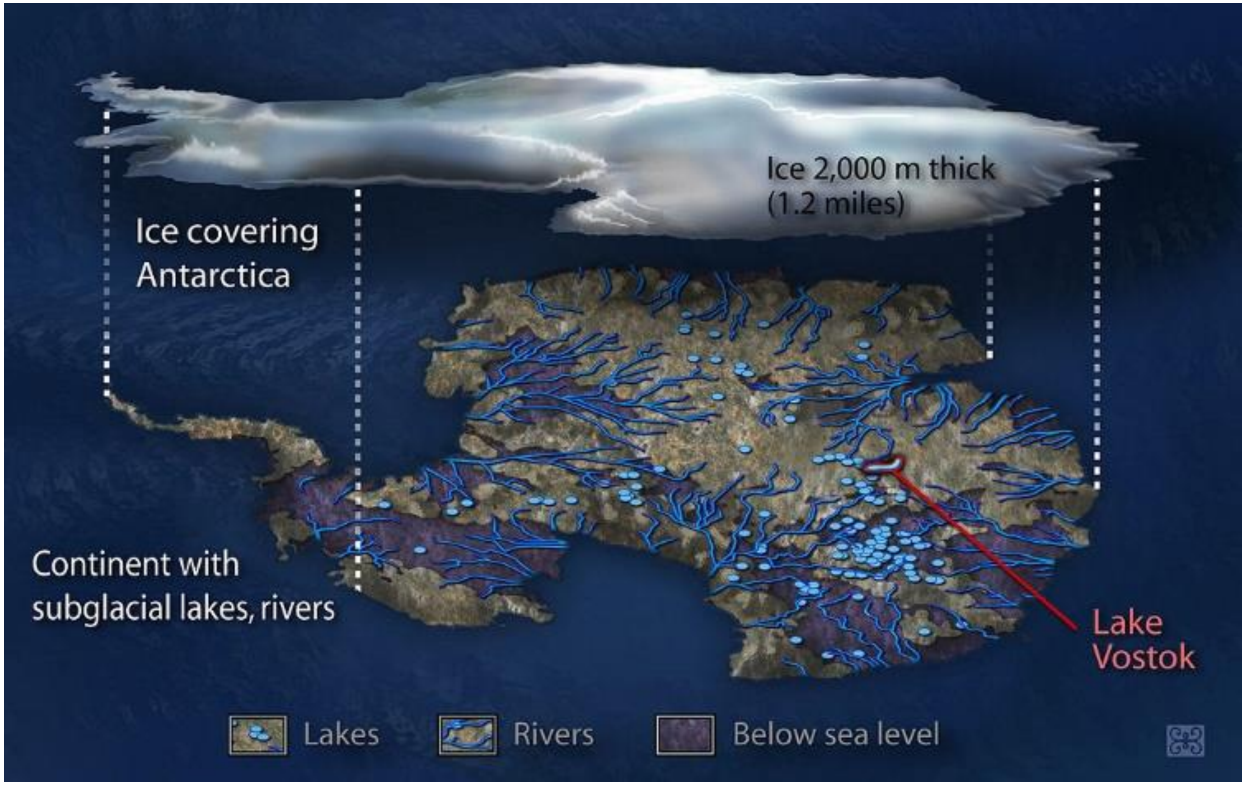
FIGURE 4 Scatterplots of prokaryotic cell concentration vs. ssNa, nssCa, and BC concentrations. Prokaryotic cell concentration vs. (a, d) ssNa (ppb), (b, e) nssCa (ppb), and (c, f) BC (ppb). Note the linear scale (concentration) on *y*- and *x*-axes for scatterplot (a) through (c), and the logarithmic scale (logarithmic concentration) on the *y*- and *x*- axes for scatterplots (d) to (f). Symbols indicate climatic intervals: circle = Last Glacial Maximum (LGM), star = Deglaciation (LDG), and square = early Holocene (EH)

- Trace levels of microbial activity are certainly present in glacial ice
- An active, specialized glacier ice community is considered unrealistic
- But there is an excess of speculation!

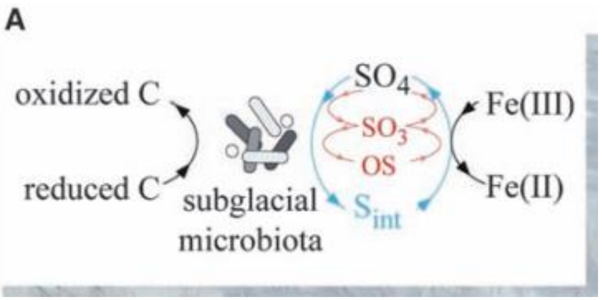
Santibanez et al., 2017



Q: In comparison with the supraglacial and englacial environments, what are the challenges and opportunities for life in the subglacial environment?



- In contrast to the englacial environment, the subglacial environment is expansive and known to be active
- Few observations however!
- Most observations have focused on chemolithotrophic bacteria and archaea, virtually nothing known about protists and metazoans

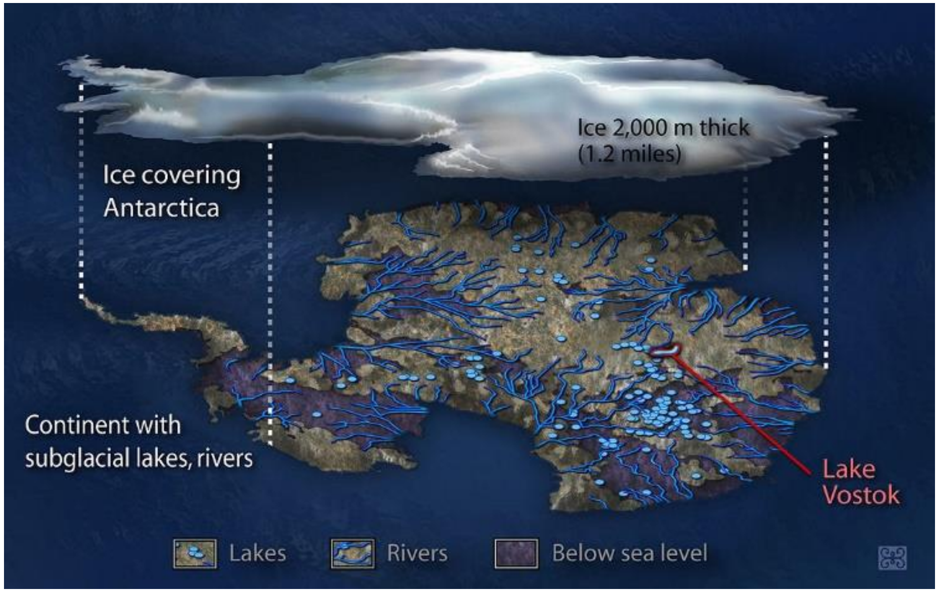


Mikuchi et al., 2009

- Blood falls at the base of Taylor Glacier
- Color of the outflow implies what metabolism?
  - Fe reduction, Fe(III) is being used as a terminal electron acceptor
  - Lots of sulfate, suggesting that organic sulfur is oxidized

What about other sites?

- Very few observations despite huge extent of the subglacial ecosystem
- Most have come from Lake Whillans, WAIS
- Other efforts underway, but huge challenges



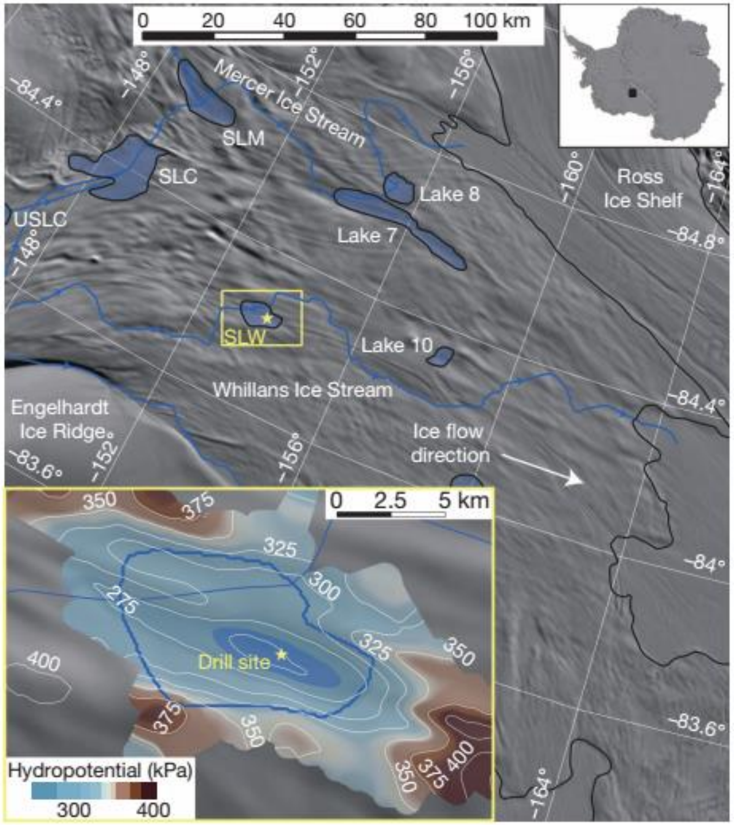


Figure 1 | Locator map of the WIS and SLW. The yellow box and star indicate the general location of the lake and the drill site; maximum extent of SLW and other lakes[28] under the ice stream are shaded in blue; predicted subglacial water flowpaths through SLW and other subglacial lakes are represented by blue lines with arrows; the black line denotes the ice-sheet grounding line at the edge of the Ross Ice Shelf[29]. Inset (expanded from area in yellow box) shows details of SLW with both maximum (solid blue line) and minimum lake extent (shaded blue area), hydropotential contours (white isolines; 25 kPa interval), and drill site (yellow star; 84.240° S 153.694° W). Background imagery is MODIS MOA[30].

Christner et al., 2014

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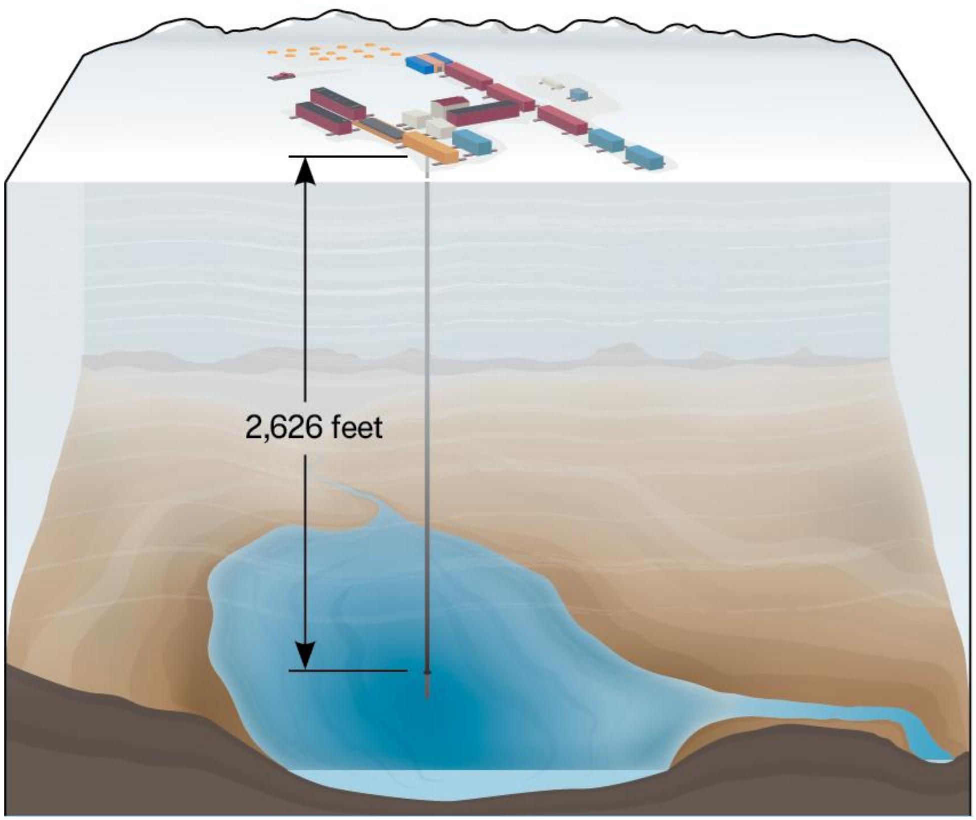

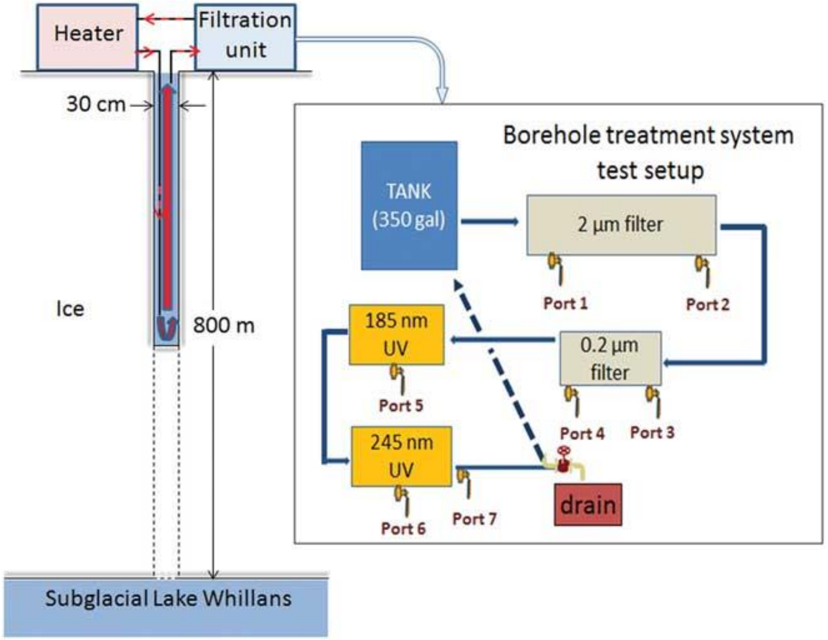

Table 1 | Biogeochemical data from the SLW borehole, water column, and surficial sediments

Parameter	Borehole*	Water column†	Sediments‡
Physical			
Temperature (°C)§	−0.17 (0.25)	−0.49 (0.03)	n.d.
Conductivity (μS cm^{-1} @ 25 °C)‖	5.3	720 (10)	860
pH‖	5.4	8.1 (0.1)	7.3
Redox (mV (SHE))‖	n.d.	382	n.d.
Microbiological			
Cell density (cells ml^{-1})	6.9×10^2 (51.0)	1.3×10^5 (0.4×10^5)	n.d.
Cellular ATP (pmol l^{-1})	0.04 (0.002)	3.70 (1.00)	n.d.
[^{3}H]thymidine¶	n.d.	13.7 (1.3)	46.6 (5.6)
[^{3}H]leucine¶	n.d.	2.9 (0.4)	0.9 (0.04)
^{14}C-bicarbonate (ng C l^{-1} d^{-1})	n.d.	32.9 (4.2)	n.d.
Carbon and nutrients			
Dissolved oxygen (μmol l^{-1})	n.d.	71.9 (12.5)	n.d.
DIC (mmol l^{-1})	n.d.	2.11 (0.03)	n.d.
DOC (μmol l^{-1})	n.d.	221 (55)	n.d.
Acetate (μmol l^{-1})	n.d	1.3 (0.2)	n.d.
Formate (μmol l^{-1})	n.d	1.2 (0.3)	n.d.
PC#	n.d.	78.5 (7.4)	384.2 (37.0)
PN#	n.d.	1.2 (0.4)	21.5 (1.7)
PC:PN (molar)	n.d.	65.4 (0.3)	17.9 (0.4)
NH_4^+ (μmol l^{-1})	n.d.	2.4 (0.6)	n.d.
NO_2^- (μmol l^{-1})	n.d.	0.1 (0.1)	n.d.
NO_3^- (μmol l^{-1})	n.d.	0.8 (0.5)	9.1
PO_4^{3-} (μmol l^{-1})	n.d.	3.1 (0.7)	7.3
DIN:SRP (molar)	n.d.	1.1 (0.4)	n.d.
Major ions (μeq l^{-1})			
Na^+	n.d.	5,276 (18)	6,977
K^+	n.d.	186 (4.2)	293 (1.0)★
Mg^{2+}	n.d.	507 (12)	596 (101)★
Ca^{2+}	n.d	859 (29)	860 (104)★
F^-	n.d.	31.5 (0.4)	34.0
Cl^-	n.d.	3,537 (3.4)	4,943
Br^-	n.d.	6 (0.01)	7 (0.4)★
SO_4^{2-}	n.d.	1,111 (0.4)	1,230
HCO_3^-	n.d	2,111 (35)	2,238**
Stable isotopes††			
$\delta^{18}O$ of H_2O	n.d.	−38.0‰	−37.5‰
$\Delta^{17}O$ of NO_3^-	n.d.	−0.1 to 0.2‰	n.d.

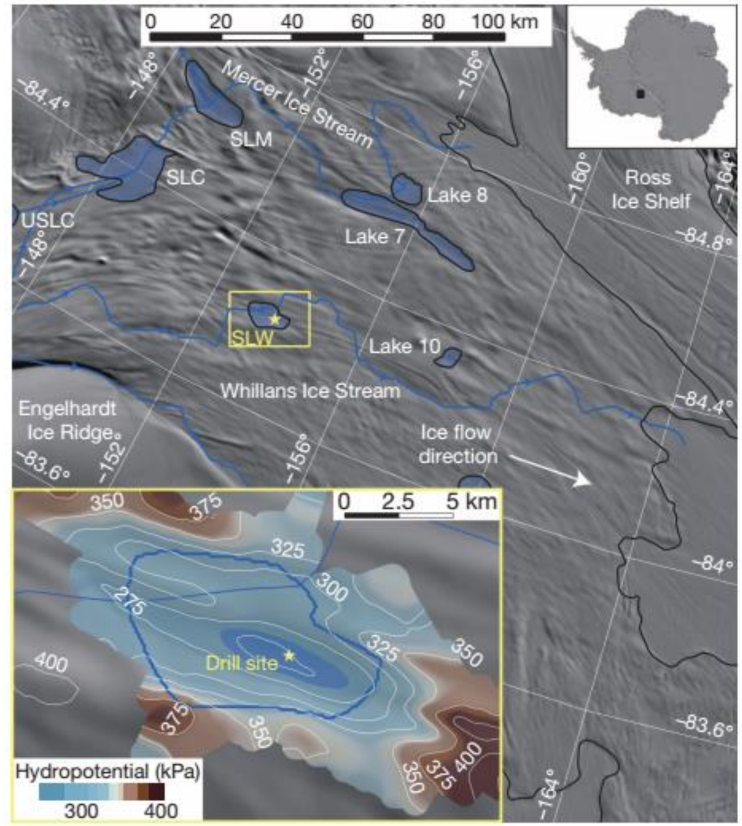

Figure 1 | Locator map of the WIS and SLW. The yellow box and star indicate the general location of the lake and the drill site; maximum extent of SLW and other lakes[28] under the ice stream are shaded in blue; predicted subglacial water flowpaths through SLW and other subglacial lakes are represented by blue lines with arrows; the black line denotes the ice-sheet grounding line at the edge of the Ross Ice Shelf[29]. Inset (expanded from area in yellow box) shows details of SLW with both maximum (solid blue line) and minimum lake extent (shaded blue area), hydropotential contours (white isolines; 25 kPa interval), and drill site (yellow star; 84.240° S 153.694° W). Background imagery is MODIS MOA[30].

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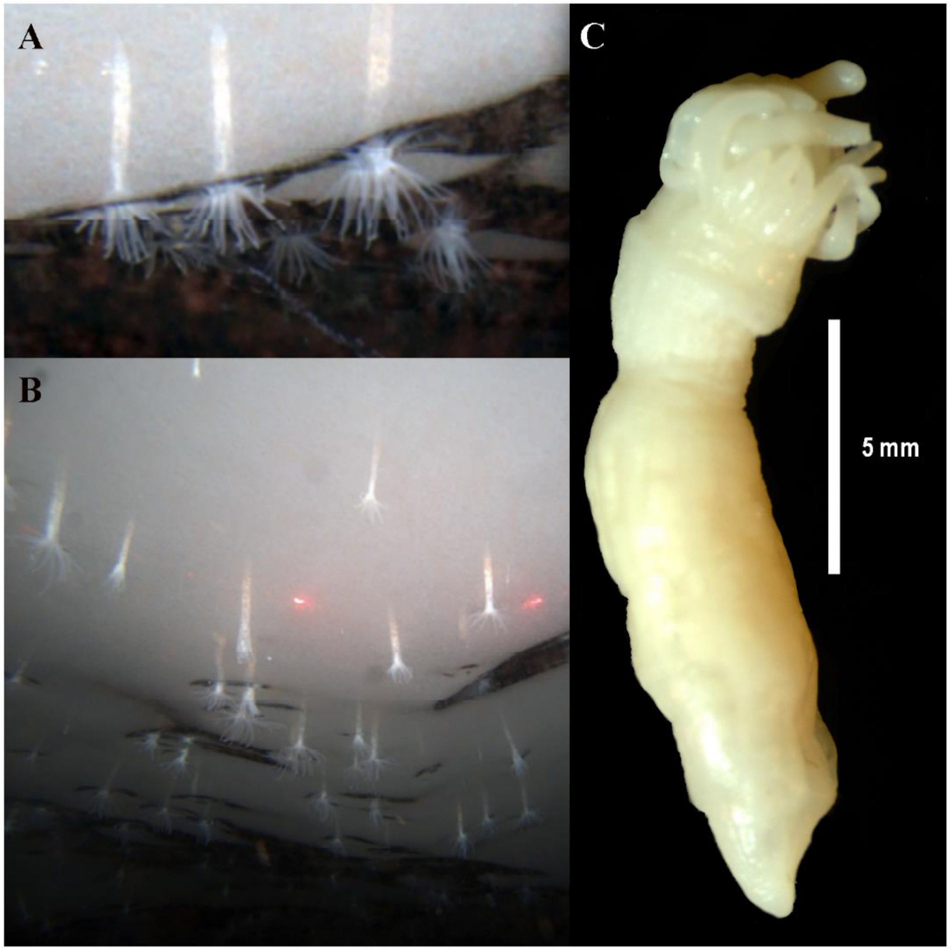

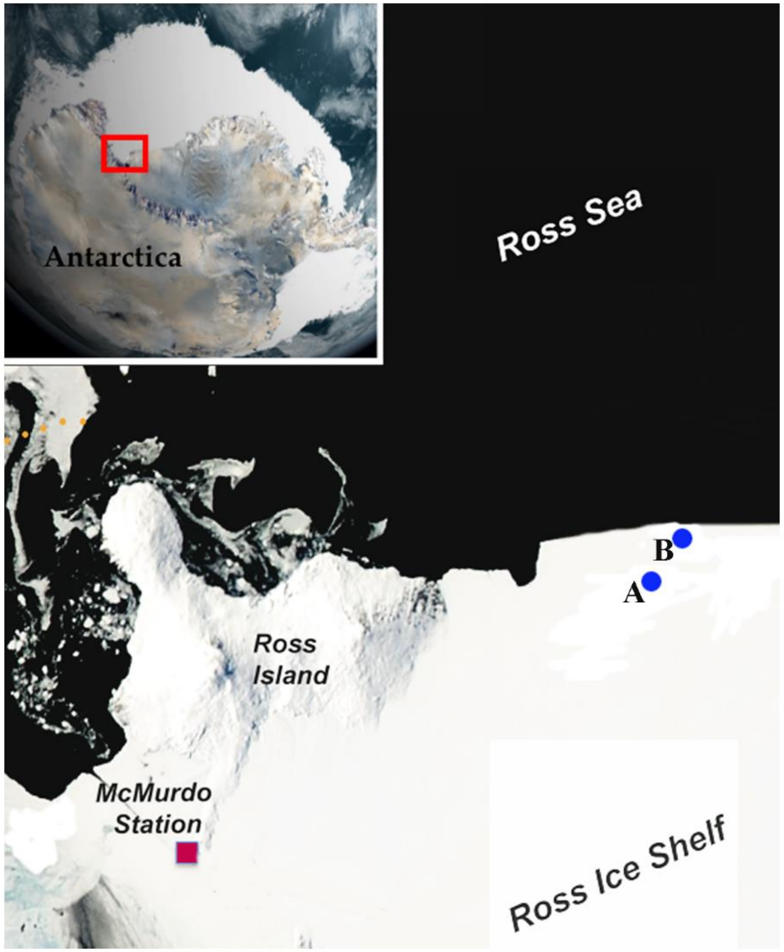

Daly et al., 2013

- Metazoans have turned up in some surprising places below ice
- These *Edwardsiella andrillae* actually embed within the bottom of the marine ice shelf
- Many similarities with extreme deep sea organisms