Abstract: The Arctic is rapidly warming. Responses to warming involve acceleration of processes common to all ecosystems (e.g., plant community changes) and changes to processes unique to the Arctic (e.g., loss of permafrost). Our objectives are to use the concepts of biogeochemical and community "openness" and "connectivity" to understand the responses of arctic ecosystems to climate change and disturbance. "Biogeochemical openness" relates to ecosystems dependence on external sources of nutrients and organic carbon versus nutrients recycled internally and organic carbon fixed locally by photosynthesis. "Community openness" relates to the effect of organism movement in and out of the ecosystem on community and trophic structure. "Landscape connectivity" describes the nature and strength of interactions among ecosystem components and the resultant propagation of ecological signals across the landscape. Components of the arctic landscape differ widely in biogeochemical and community openness. We will compare key ecosystems of the Arctic to determine how their degree of openness governs their responses to climate change and acute disturbance such as fire and surface slumping associated with permafrost thaw. We will also determine how the responses to climate change and disturbance are mediated by landscape connectivity and the movement of nutrients, carbon, and organisms across arctic landscapes, and how that movement is facilitated or impeded by the degree of openness of the ecosystems.

Arctic LTER: The Role of Biogeochemical and Community Openness in Governing Response to Climate Change and Disturbance

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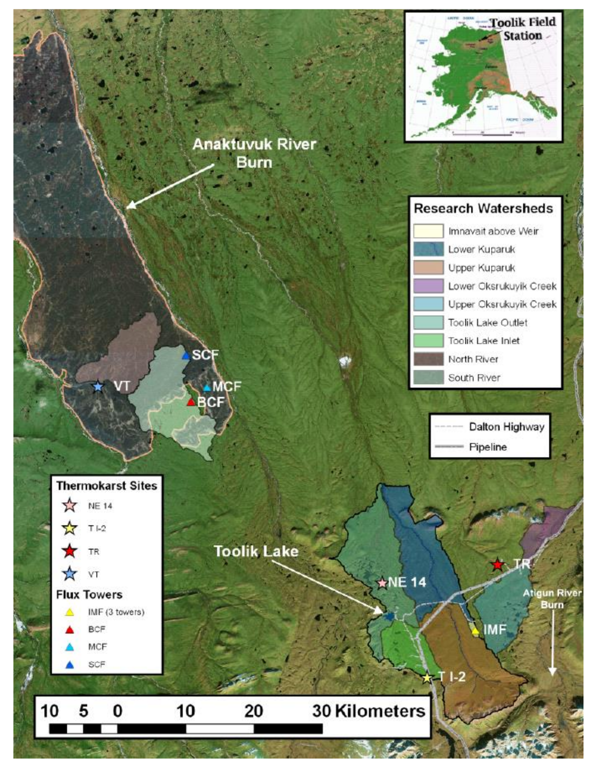
http://ecosystems.mbl.edu/arc

NSF 1637459



LOCATION

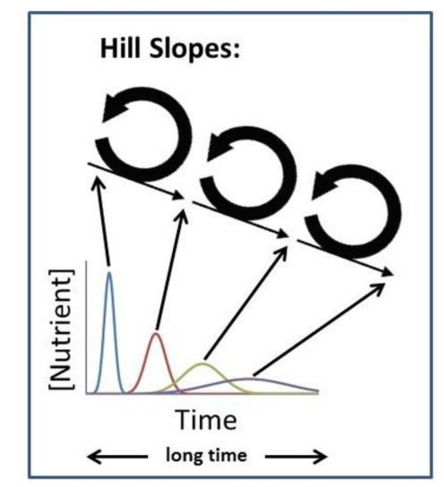
Toolik Field Station is at 68ºN, in north-facing foothills of the Brooks Range, Alaska. The site lies in formerly-glaciated rolling hills and includes an array of tundra ecosystems, streams, and oligotrophic lakes up to 20 m depth

CLIMATE

Air Temp		
	May	0.6 ºC
	June	8.1
	July	11.9
	August	7.4
	Annual Ave	- 8.4

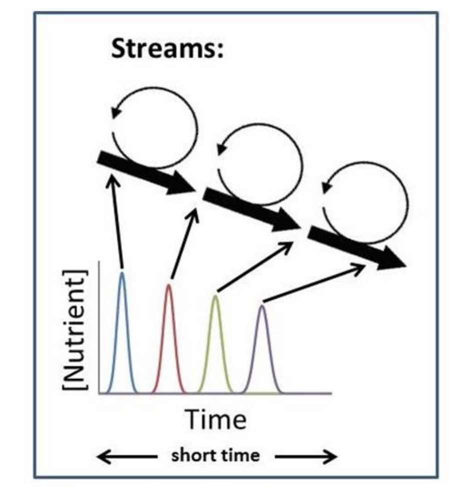
Precipitation 200-300 mm

Within-patch nutrient cycling

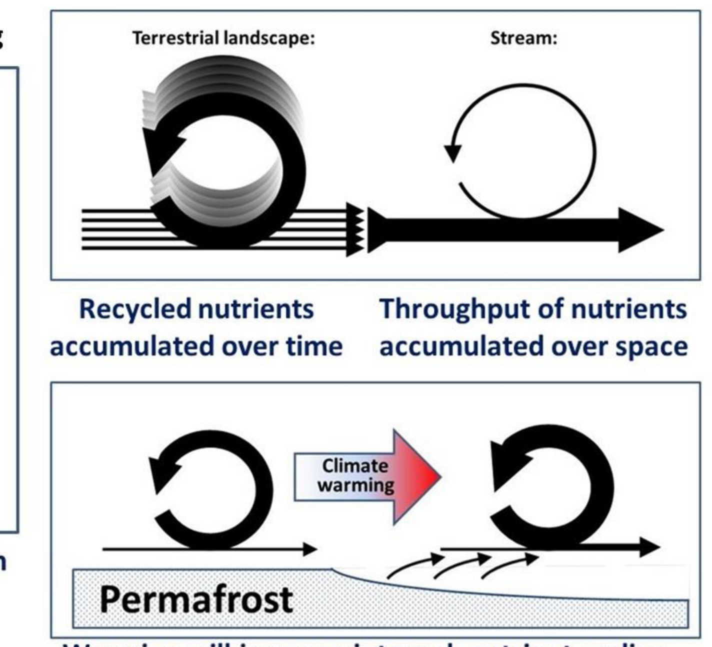


The nearly closed ecosystems on hill slopes are poorly connected and therefore delay and attenuate signals moving down slope (e.g., nutrient pulse)

Downstream nutrient spiraling



The more open ecosystems in streams are well connected and therefore propagate signals moving downstream (e.g., nutrient pulse)



Warming will increase internal nutrient cycling, nutrient inputs from thawing permafrost, and downslope nutrient losses (leakiness).

TERRESTRIAL RESEARCH

Arctic terrestrial ecosystems are closed biogeochemically but warming is "opening" nutrient cycling by allowing greater nutrient inputs from thawing permafrost and potentially opening the community by allowing novel species to establish. Our long-term fertilization experiments provide insights into how the tundra will continue to respond to warmer temperatures and increased nutrient availability.

Increased nutrients cause greater NPP in tundra plant communities while reducing species diversity (Fig. 1). After 24 years of fertilization, arthropod abundance and biomass did not differ from control plots but arthropod community composition significantly changed in moist acidic tundra (Fig. 2, Asmus et al. 2017 *Oikos*).

In addition to affecting consumers and NPP, increased nutrient availability can alter other ecosystem characteristics in complex ways (Gough et al. 2016 *Oecologia*). In some arctic streams, greater phosphorus resulted in a shift to moss cover which provided habitat for an assemblage of invertebrates not normally found. In lakes, greater nutrients caused eutrophication without altering the physical habitat, while in terrestrial ecosystems the new plant community (Fig. 1) affected microclimate and use of the plots by both invertebrates and vertebrates.

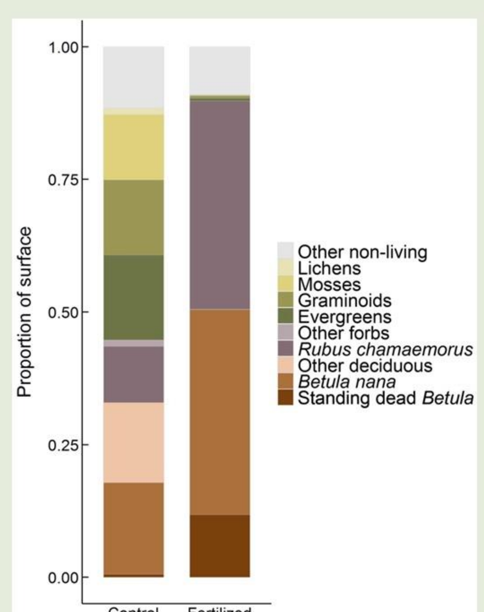


Fig. 1 Moist acidic tundra response to 24 years of added N+P. (Asmus et al. 2017)

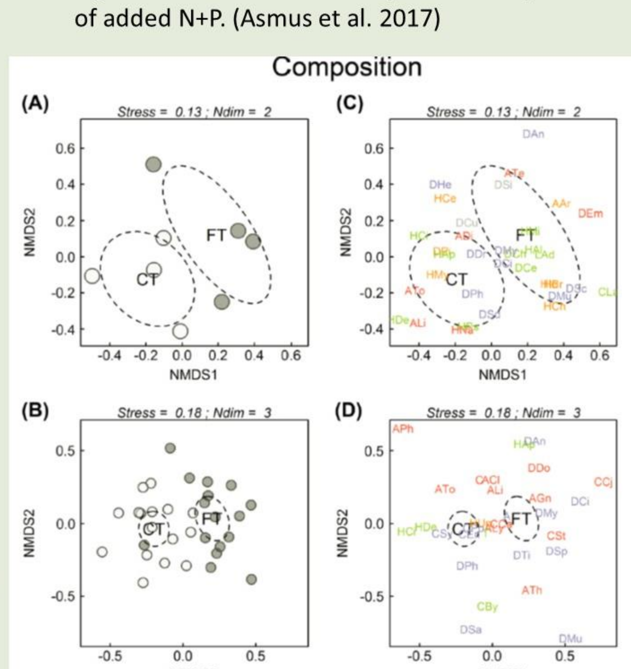


Fig. 2 Arthropod community response to 24 years of added N+P. (Asmus et al. 2017)

Our models indicate that responses of tundra ecosystems to fire are strongly responsive to warming because warming accelerates the cycling of nutrients through soils (Fig. 3; Jiang et al. 2017 *Ecological Applications*). Our simulations also indicate that tundra reestablishes nutrient cycles quickly after disturbance like fire, which helps close nutrient cycles and retain remaining nutrients in the ecosystem and thereby limits long-term biogeochemical connectivity down slope (Jiang et al. 2015 *Ecological Applications*).

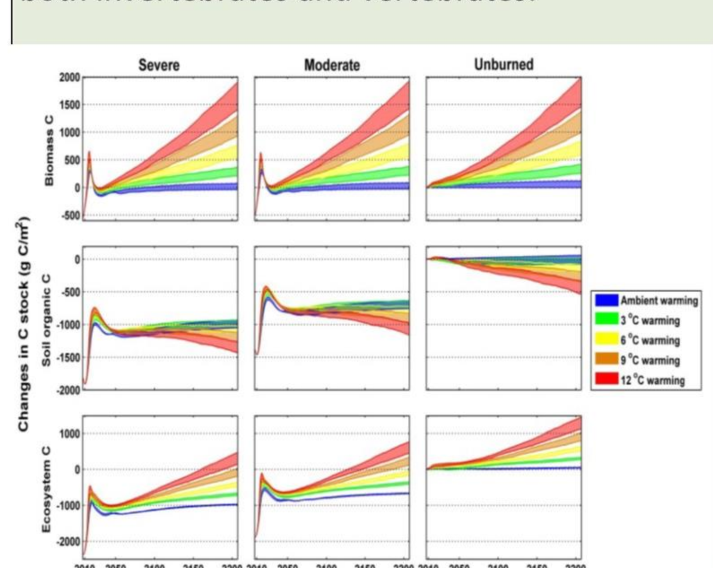
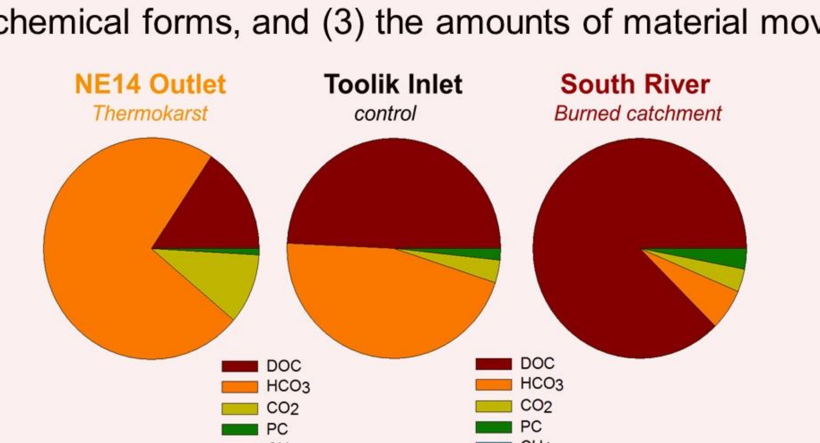


Fig. 3 Modeled C stocks in response to fire, warming, and increased CO_2. (Jiant et al. 2017)

LAND-WATER INTERACTIONS RESEARCH

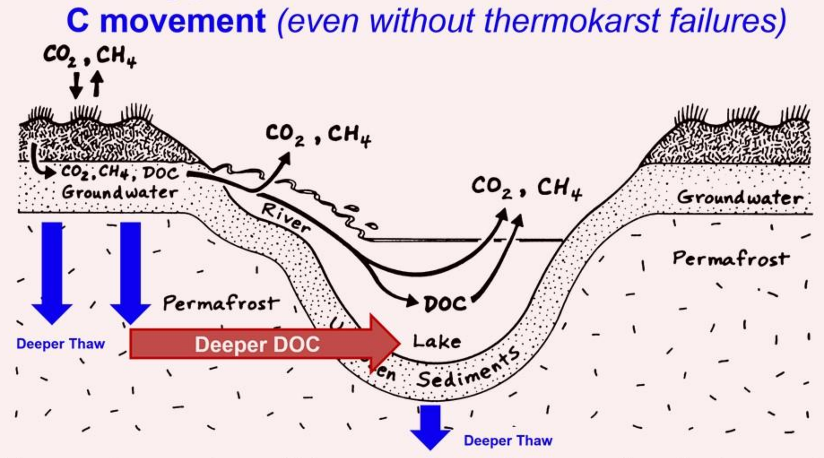
Slow (climate change, permafrost thaw) and rapid disturbance (fires and thermokarst failures) affect connectivity and biogeochemical openness differently, and will determine how the tundra responds to future change.

1. Disturbance type alters carbon species and export from land. Thermokarst failures export mostly mineral forms of carbon (DIC), burned catchments export mostly organic forms (DOC), and undisturbed catchments export equal amounts of DIC and DOC (pie charts below). Thus the biogeochemical "openness" depends on the (1) type of disturbance, (2) the chemical forms, and (3) the amounts of material moving from land to water.



Above – Lake NE-14 changed color due to the mineral inputs from a thermokarst failure. Inputs from the failure to the lake also affected the C species and the C and N export from the lake.

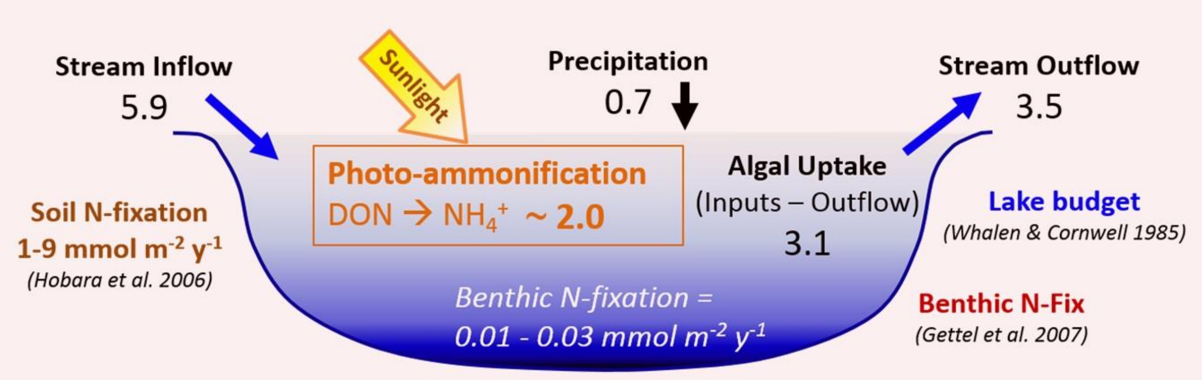
Thawing permafrost will increase openness and C movement *(even without thermokarst failures)*



Above – Deeper thaw will increase the surface area in soils that are leached by water, increasing the amount of materials such as DOC that are exported from soils to surface waters, independent of any changes in the amount of precipitation

2. Photo-ammonification of terrestrial DOM increases landscape connectivity and may strongly contribute to aquatic inorganic nitrogen.

Dissolved Inorganic Nitrogen (DIN) in Toolik Lake ***(mmol N m⁻² y⁻¹)***

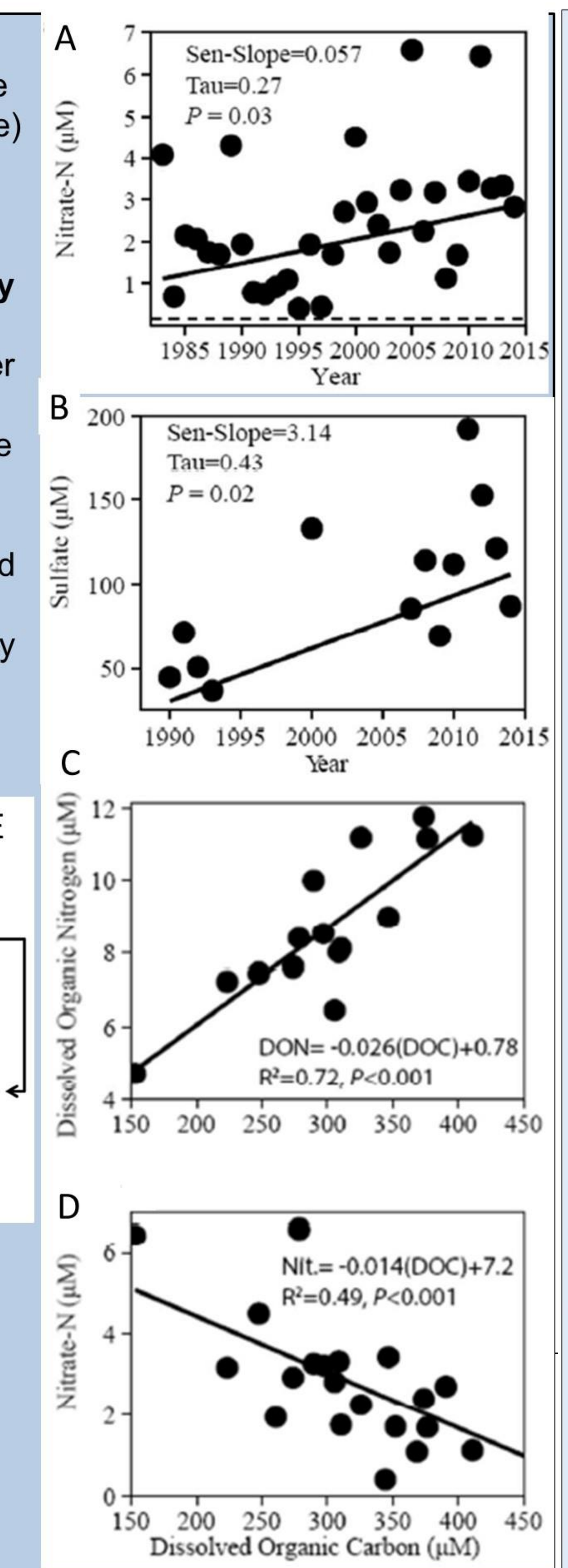


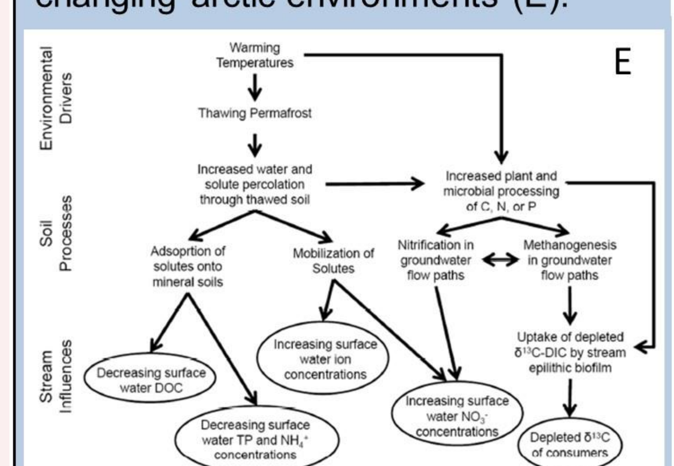
Above – Dissolved organic nitrogen (DON) dominates terrestrial and aquatic N budgets, but dissolved inorganic N (DIN) released from soils is extremely low and limits aquatic system productivity (along with PO_4). However, sunlight can alter DON to NH_4^+ during photo-ammonification, and this contribution of terrestrial DON to aquatic DIN increases overall landscape openness.

STREAMS RESEARCH

The changes noted in the panel to the left (permafrost thaw, thermokarst, fire) impact stream ecosystems.

1. Long-term records reveal changes in stream biogeochemistry and food web resources. Concentrations of nitrate (A) and other indicators of permafrost thaw (e.g. sulfate, B) are increasing. At the same time the relative abundances of nutrient resources are shifting as well (C and D). Physical, geochemical, and biological changes associated with warming permafrost are fundamentally altering linkages between upland and aquatic ecosystems in rapidly changing arctic environments (E).

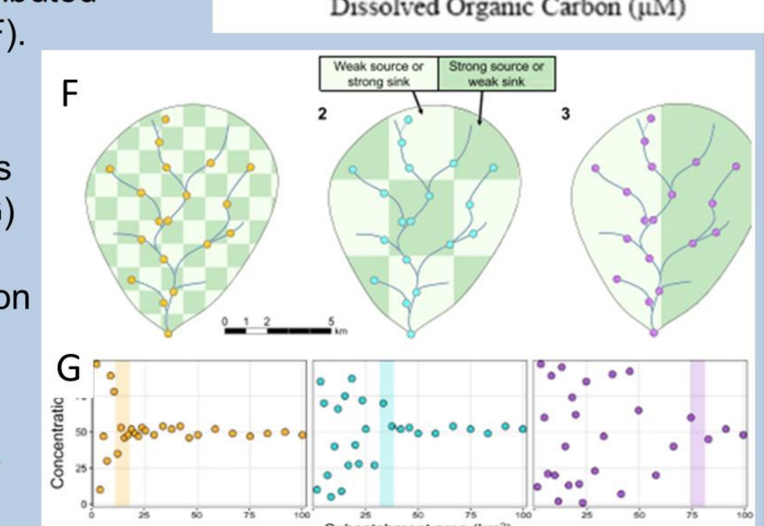




Kendrick et al. (in press) Global Change Biology

2. We are developing and testing frameworks to understand how changes in nutrient loading are propagated through stream networks. Hypothetical patterns of stream solute sources distributed differently in watersheds (F).

Darker areas are stronger sources; lighter areas are weak sources. The patterns of solute concentrations (G) at particular points in the watershed are dependent on the specific distributions of the upstream sources. We can use the concentration patterns in the river to infer the nature and spatial arrangement of solute sources.



Abbott et al. (2018) Ecology Letters 21: 296–308

LAKES RESEARCH

With climate warming, arctic lakes will likely experience increased water temperatures and altered hydrology, which may have varying effects on open (connected) versus closed lakes (isolated). For example, open lakes may be more resilient to change given that species can move more freely between unfavorable and favorable habitats. However, this resiliency requires movement corridors to remain passable (altered hydrology may affect connectivity).

In order to understand how open lakes may respond to disturbance (altered connectivity), we plan to experimentally 'close' off an open system. In preparation for this experiment, two open lakes (I1 & I2) were intensively sampled (fishes, macroinvertebrates, & overall trophic structure) during the 2018 summer. One of these lakes will serve as the experimental lake (closed off) while the other will serve as a reference lake. The population structure and diets of fishes from these two lakes were characterized and found to be very similar (Fig 1), suggesting they are suitable as paired experimental lakes. In the short-term we will continue to monitor movement patterns, trophic changes, vital rates, and relative abundance and biomass, while in the longer term, changes in population size-structure cycles and trends will be examined.

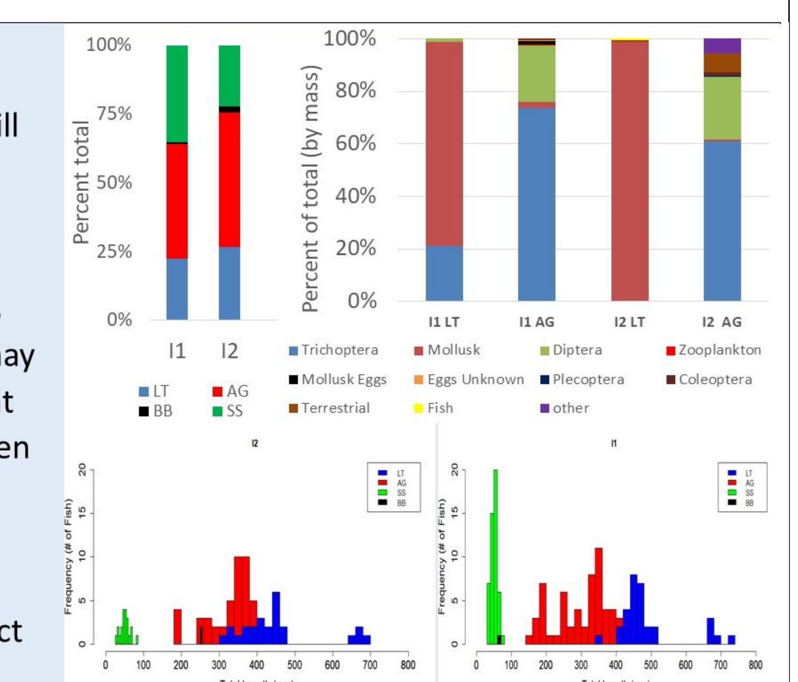
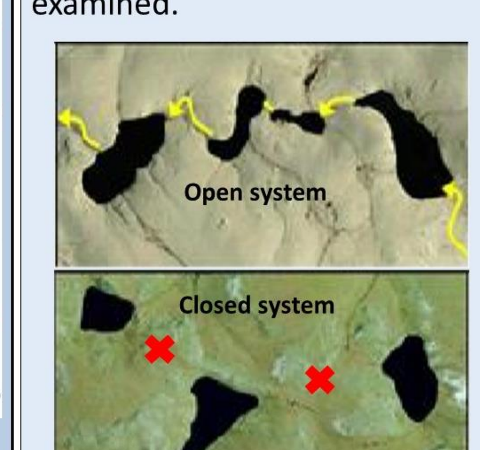


Figure 1. Pre-manipulation data gathered during summer of 2018 on lakes I-1 and I-2. Community composition (top left), diet composition (top right), and length frequency histograms are displayed (bottom panels). LT: lake trout, AG: arctic grayling; BB: burbot; SS: slimy sculpin.

Warming and disturbance may also influence net ecosystem production (NEP; ecosystem metabolism). For example, warming may alter NEP due to the temperature dependence of physiological processes or indirectly (e.g., permafrost thaw) could affect NEP due to altered nutrient input to lakes. Importantly, shifts in NEP may alter the role lakes play as sources or sinks of carbon.

Early results suggest large differences in pelagic (benthos not yet included) ecosystem metabolism among lakes (Fig 2), likely driven by differences in morphology and landscape position. In addition, pelagic ecosystem respiration increases non-linearly with temperature (Fig 2), demonstrating an additional potential affect of lake warming.

Future research and monitoring will continue to focus on understanding how arctic lake ecosystems and their organisms will respond to climate change and disturbance.



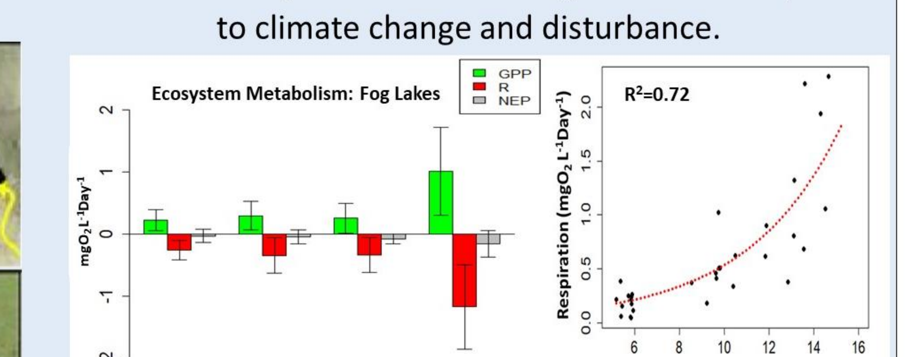


Figure 2. Estimates of pelagic ecosystem metabolism for the fog lakes (top left) and the relationship between daily rates of pelagic ecosystem respiration and temperature in Fog 5 (bottom right). GPP: Gross primary production; R: Ecosystem respiration; NEP: Net ecosystem production or ecosystem metabolism. The benthos is not yet included.