

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

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SUMMARY

Overview: The Arctic is one of the most rapidly warming regions on Earth. Responses to this warming involve acceleration of processes common to other ecosystems around the world (e.g., shifts in plant community composition) and changes to processes unique to the Arctic (e.g., carbon loss from permafrost thaw). The objectives of the Arctic Long-Term Ecological Research (LTER) Project for 2017-2023 are to use the concepts of biogeochemical and community “openness” and “connectivity” to understand the responses of arctic terrestrial and freshwater ecosystems to climate change and disturbance. These objectives will be met through continued long-term monitoring of changes in undisturbed terrestrial, stream, and lake ecosystems in the vicinity of Toolik Lake, Alaska, observations of the recovery of these ecosystems from natural and imposed disturbances, maintenance of existing long-term experiments, and initiation of new experimental manipulations. Based on these data, carbon and nutrient budgets and indices of species composition will be compiled for each component of the arctic landscape to compare the biogeochemistry and community dynamics of each ecosystem in relation to their responses to climate change and disturbance and to the propagation of those responses across the landscape.

Intellectual Merit: The research is organized around the concepts of ecosystem “openness” and landscape “connectivity”: “Biogeochemical openness” is the degree to which ecosystems depend on external sources of nutrients and organic carbon versus nutrients recycled internally and organic carbon fixed locally by photosynthesis. “Community openness” is the degree to which the movement of organisms in and out of the ecosystem determines community and trophic structure. Finally, “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. The proposed research 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. The proposed research 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.

Broader impacts: Historically, research by Arctic-LTER scientists has had broad impacts on the scientific community with over 35,000 citations of the 579 journal publications by Arctic LTER researchers and their collaborators since 1975 (currently ~ 10 citations per day). The 147 publications since 2010 have been cited ~2,500 times (currently ~ 2.5 citations per day). This impact will continue through publications based on ongoing long-term and proposed research. The Arctic LTER actively fosters work by other researchers and their students and postdocs through access to data and encouragement to make measurements and conduct complementary studies in Arctic LTER long-term experiments. This openness is reflected in the number of top-quality assistant and associate researchers now affiliated with the Arctic LTER. The Arctic LTER will also continue to have broader impacts through education and outreach. These activities include: (i) a new schoolyard program that will engage K-12 students at Barrow, AK and K-12 teachers from both Barrow and the Environmental Literacy Program at Colorado State University, (ii) the Polar Hands-on Laboratory for journalists through the Logan Science Journalism Program at the Marine Biological Laboratory, (iii) courses in Arctic Ecology with Arctic LTER investigators serving as faculty, (iv) talks and short courses given by LTER researchers to Alaskan Native communities at Anaktuvuk Pass, Kaktovik, and Barrow, (v) briefings to the US Bureau of Land Management, Arctic National Wildlife Refuge, Alaska Division of Natural Resources, Alaska Fish and Game, and North Slope Borough officials, (vi) serving on national and international advisory boards and panels, (vii) support of two students per year in the NSF REU program, plus providing opportunities for students on other projects to work on Arctic LTER sites and experiments, and (viii) graduate student participation in an open, annual meeting.

INTRODUCTION:

Research on streams, lakes, and tundra has been ongoing near Toolik Lake, Alaska for the past 40 years, including support since 1987 by the NSF Long-Term Ecological Research (LTER) program (Fig. 1; Hobbie & Kling 2014). The Arctic LTER (ARC LTER) is based at the Toolik Field Station in the northern foothills of the Brooks Range on Alaska's North Slope. The Arctic is one of the most rapidly warming regions on Earth (Overland et al. 2015), and thawing of extensive stores of permafrost carbon (C) could provide a positive reinforcement for global warming (e.g., MacDougall et al. 2012, Schuur et al. 2015). The effects of warming also include disturbances from thermal erosion of permafrost and land-surface failures (Bowden et al. 2008), more frequent tundra wildfires (Mack et al. 2011, Hu et al. 2010, 2015), and a lengthening thaw season (Overeem & Syvitski 2010).

Ecosystem response to climate change and disturbance can be either rapid or prolonged, as communities are restructured and the biogeochemical balance is changed and reestablished over years to decades to centuries. For example, Rocha et al. (2012) found recovery of canopy greenness and function within a decade after fire, but Schuur et al. (2007) reported changes in plant community composition five decades after ground surface subsidence following thaw of ice-rich permafrost. Modeling studies indicate that although vegetation and surface soils can recover from disturbance in a few decades, deep soil recovery might require centuries (Pearce et al. 2015). These disturbances and subsequent recovery of terrestrial systems have important consequences for downslope stream and lake ecosystems, primarily associated with the release and transport of C and nutrients and the consequent alteration of aquatic communities (Bowden et al. 2008, Cory et al. 2013, Kendrick & Hury 2015, Daniels et al. 2015). These aquatic systems tend to respond and recover faster than the terrestrial systems (Bowden et al. 2012), but there can also be long lags before new species become established (Slavik et al. 2004, Gough et al. *in revision*).

Given the knowledge developed in our prior research, we believe ecosystem responses to climate change and disturbance are governed to a significant extent by the biogeochemical and community “openness” of the ecosystem and by the connectivity among ecosystems on the landscape. For biogeochemical openness, ecosystem response is strongly controlled by the degree to which these linked systems depend on externally supplied nutrients and organic C versus internally recycled nutrients and locally-fixed organic C. For community openness, the response is controlled by the degree to which community changes are manifest in species migrations and the local establishment of new species versus changes in relative abundance of species already in the community. The spatial arrangement and interactions among these ecosystems determine their connectivity, which governs the movement of nutrients, organic C, and species across the landscape. Quantifying these concepts of ecological “openness” and “connectivity” and relating them to responses to climate change and disturbance is the focus for research in this LTER renewal proposal.

Project History: Research at Toolik Lake began in 1975, and the site became part of the LTER Network in 1987. The overall aim of the ARC-LTER has been to *develop a landscape understanding of ecologi-*

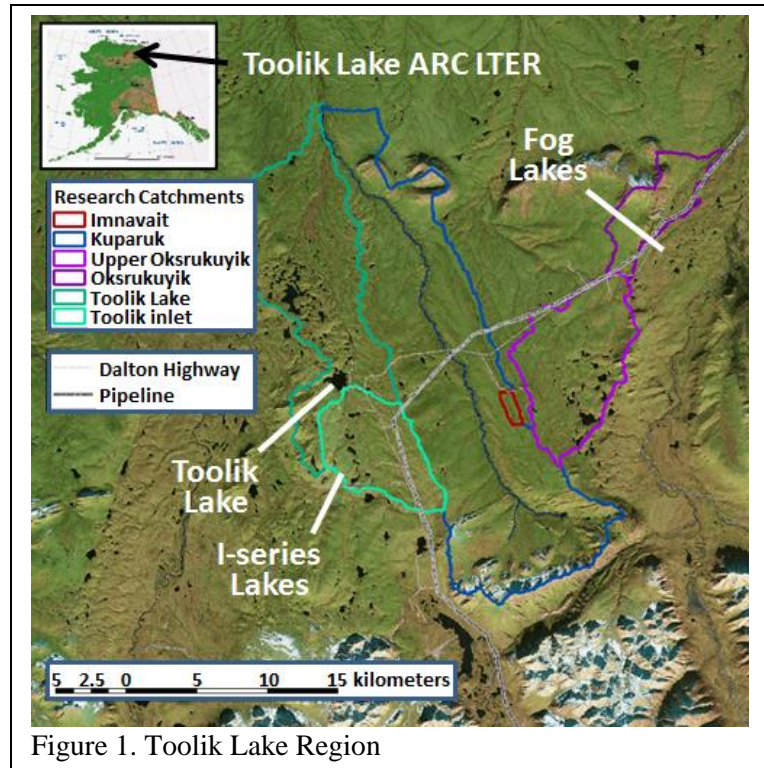


Figure 1. Toolik Lake Region

cal functioning based on the interactions among tundra, stream, and lake ecosystems near Toolik Lake, Alaska. The specific focus evolves continuously and changes with each renewal cycle, as understanding has grown and as new opportunities and questions are recognized:

ARC-LTER I (1987-1992): Descriptions of tundra, stream, and lake ecosystems; long-term change versus short-term controls on ecosystem components

ARC-LTER II (1992-1998): Ecological variability and long-term change; top-down versus bottom-up controls on tundra, streams, and lakes

ARC-LTER III (1998-2004): Prediction of the future characteristics of arctic ecosystems and landscapes; controls by physical, climatic, and biotic factors

ARC-LTER IV (2004-2010): Understanding changes in the arctic system at catchment and landscape scales through knowledge of linkages and interactions among ecosystems.

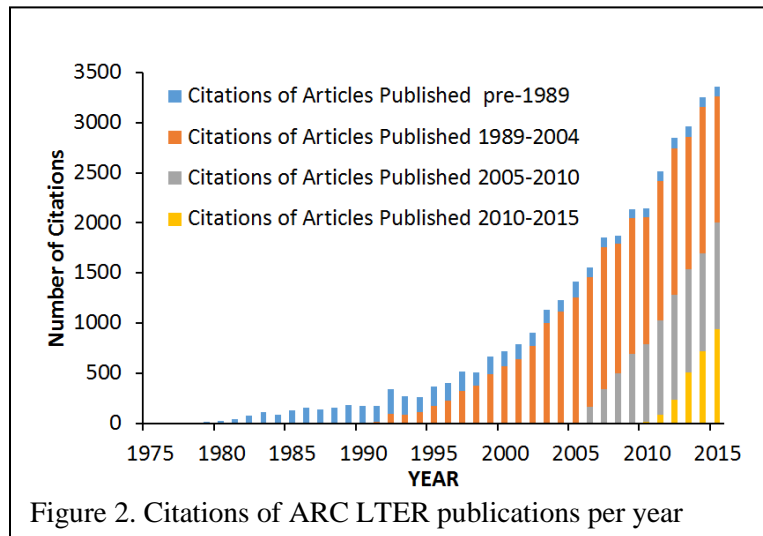
ARC-LTER V (2011-2017): Understanding changes in the arctic system resulting from (i) direct effects of climate change on states, processes, and linkages of terrestrial and aquatic ecosystems, and (ii) indirect effects of climate change on ecosystems through a changing disturbance regime.

This proposed renewal will continue our recent theme of assessing and predicting effects of climate change and disturbance through synthesis and comparison of data from our long-term measurements and experiments. We will also add select new activities related to understanding and quantifying how biogeochemical and community openness and landscape connectivity control ecosystem responses to change.

RESULTS FROM PRIOR RE-SEARCH:

Publications and Other Products:

LTER-related research at Toolik Lake has had significant *broader impacts* in ecology and ecosystem science, with over 35,000 citations of the 579 journal publications since 1975 that include contributions from ARC LTER scientists and their collaborators. These publications are currently cited at a rate of 10 times per day (Fig. 2) with an overall h-index of 101 (Table 1). In addition, ARC LTER scientists have produced 7 books, 95 book chapters,



35 PhD theses, 66 Master's theses, and 15 honor's theses.

Since 2010, ARC LTER scientists and their collaborators have published 147 journal articles that have been cited ~ 2500 times, at a current rate of 2.5 citations per day. Recent major works of synthesis include a book based on ARC LTER research in the Toolik region (Hobbie & Kling 2014) and a field guide to the North Slope (Hurn & Hobbie 2012), which serves as both a scientific resource and as accessible outreach to the general public.

	Table 1. Publications since:				
	1975	1989	2005	2010	
# Journal Articles Publ.	579	490	266	147	
# Articles in Web of Science	528	450	235	235	
Sum of Citations	35,485	30,796	10,030	2,498	
Citations per article	67.2	68.4	42.7	10.6	
h-index of library	101	97	48	48	
Books	7	5	4	3	
Book Chapters	95	86	40	20	
All Theses	116	87	48	29	
	PhD	35	26	17	8
	MS/MA	66	46	19	10
	BS	15	15	12	11

Data sets: Data are archived on the ARC LTER database (<http://arc-lter.ecosystems.mbl.edu>); all have

DOI designations for direct citation purposes (see attached Data Management Plan and list of datasets). As of February 2016, the ARC LTER database contained 650 data sets. As an index of their broader impacts, data files were downloaded 111,182 times in the last 10 years. (This number of downloads is derived from the previous (pre-2013) LTER Network Data Access System and the newer (post-2013) LTER Network Data Portal - data access reports from the newer Data Portal include web crawler downloads.)

Ten significant papers: The ARC LTER is organized into research groups studying four core areas: Terrestrial, Lakes, Streams, and Landscape Interactions. Although we cannot summarize all of this research in the space available, below we annotate ten key papers from these core areas that are products of our current LTER grant (LTER V; 2011-2017) and that highlight our contributions and broader impacts in ecology. Nearly all of these key papers result from long-term studies on our themes of climate warming and disturbance from fire or thermal erosion of permafrost resulting in land-surface failures (which we will call “thermokarst failures”, Gooseff et al. 2009). **More detail on our long-term research in the four core areas is presented in the "Rationale and Background" sections below.**

(1) **Shaver et al. (2013)** reported on a remarkable convergence in ecosystem C metabolism among all major vegetation types in arctic and subarctic tundra in Alaska, Greenland, Svalbard, and Sweden. A single regression model predicts net ecosystem-atmosphere C exchange as a function of only leaf area, air temperature, and photosynthetically active radiation. This result is significant in the context of climate change because it means that as the Arctic warms, biomass increases, and vegetation patterns shift, net ecosystem metabolism can still be predicted based on these three easily and remotely quantified variables.

(2) **Gough et al. (2012)** observed different responses to the interactions between nutrients and herbivory in dry heath and moist acidic tussock (MAT) tundra after 11 years of treatment. In both communities, herbivores exacerbated species shifts caused by greater nutrients, favoring a woody shrub in MAT tundra and a grass in dry heath, but herbivory increased above-ground net primary production only in MAT. Soil food webs responded differently as well. Thus mammalian herbivores may cause different responses to increased soil fertility depending on ecosystem type.

(3) **Sistla et al. (2013)** examined responses to a two-decade warming experiment and found that warming homogenized the soil trophic structure across soil horizons and increased plant biomass and the dominance of woody plants, which indirectly increased winter soil temperature by trapping snow and insulating the ground. Surprisingly, soil C or nitrogen (N) stocks in the surface organic soil layers were unchanged, but increases in mineral-soil C and plant biomass resulted in an increase in total ecosystem C.

(4) **Mack et al. (2011)** reported on how a single, massive tundra fire on the North Slope of Alaska released ~ 2 Pg of C to the atmosphere, an amount roughly equal to the annual net C sink for the entire arctic tundra biome. Climate-driven increases in tundra fire represent a positive feedback on warming, potentially offsetting the effects of arctic greening and influencing the net C balance of the tundra.

(5) **Pearce et al. (2015)** examined recovery from thermokarst failure, which has increased with warming and is exacerbated by fire (Bowden et al. 2008). They used 30 years of LTER data to calibrate the Multiple Element Limitation (MEL) model (Rastetter et al. 2013) to simulate recovery of MAT after thermokarst failures. Vegetation recovers rapidly for 30 to 40 years and then recovery slows as readily available nutrients run out, and after 100 years the vegetation response is still constrained by the initial N and P availability in the soils. This model has also been used to examine recovery from fire (Jiang et al. 2015a) and is an important tool for evaluating biogeochemical “openness” of terrestrial ecosystems.

(6) **Cory et al. (2013)** discovered that dissolved organic C (DOC) released from thawing permafrost soil is labile to microbial respiration to carbon dioxide (CO₂) in the dark, but respiration is almost doubled if the DOC is first exposed to UV light. In addition to this sunlight amplification of microbial degradation of previously frozen organic matter, direct photochemical degradation of DOC from land is the dominant mechanism of DOC oxidation in the water column of arctic streams and lakes (Cory et al. 2014).

(7) **Crump et al. (2012)** showed that moving down the hydrological continuum from soil waters to streams to lakes, microbial community diversity decreased and about half of the most common lake bacteria were first detected in soils and headwater streams. Thus, stream and lake microbial communities are structured by the openness and connectivity of microbial communities on the landscape, with initial inoc-

ulation from soil reservoirs followed by species sorting during downslope dispersal. The implication is that future changes in thaw depth and hydrological flow paths and connectivity will affect downslope microbial communities across the arctic landscape.

(8) **Kendrick and Hury** (2015) studied biofilm accrual and metabolism in the Kuparuk River and found that hydrologic connectivity and nutrients supplied from land strongly impact in-stream processes. Because biofilms are both critical to ecosystem processes and subject to freezing dynamics, discharge, and nutrient supply, the effects of climate warming on arctic river ecosystems might be substantial.

(9) **Daniels et al.** (2015) reported on a 13-year study of responses of deep versus shallow arctic lakes to increased nutrient inputs, as might be expected from warming-induced releases of nutrients from soils and permafrost. The pelagic system is biogeochemically open and depends on externally supplied nutrients. Benthic algae in deep and shallow lakes appear to be limited more by light than by nutrients, and the light availability varies strongly year-to-year depending on light-absorbing DOC inputs from land. This suggests that shifts in land-water connectivity through the transfers of nutrients and DOC could have offsetting impacts on the benthic and pelagic metabolism in lakes.

(10) **Budy and Lueke** (2014) showed direct effects of warming on fish populations that cycle dramatically between dominance by small versus large individuals. Modeled scenarios predict that under warmer climate fish will grow faster and require more food, resulting in even greater amplitude of cycles in population structure as well as an increase in reproductive output and decrease in generation time. Climate change will likely elevate growth rates of small arctic char (*Salvelinus alpinus*), a carnivorous fish found in many lakes near Toolik, and act in a manner similar to a resource pulse allowing a subset of small char to break through a maximum-size barrier, thus initiating cycles in population structure.

Together, these 10 papers highlight a consistent theme of how the function of terrestrial and aquatic ecosystems is driven by climate and disturbance, and modified by internal recycling of materials or changes in relative abundance of species already in the community versus the movement of materials and species across the landscape into and out of ecosystems. This theme is captured in our conceptual model of ecosystem “openness” and landscape “connectivity”, as described in our Proposed Research below.

Education and outreach: The ARC LTER maintains a multifaceted education and outreach program with significant *broader impacts*. Each program component is selected to optimize particular education opportunities. Our strategy is to use carefully-selected activities to reach a diverse audience ranging from kindergarten through graduate students to the general public, and to governmental and scientific planning agencies. Each of these high-impact activities is independently funded but receives support from the ARC LTER in the form of investigator, student, or RA participation, and through access to our field sites, laboratories, and data base. We also assist with travel and logistics costs for participation by LTER students, investigators, and teachers and journalists at the Toolik Field Station.

1. Our **Schoolyard LTER program** focuses on Barrow, Alaska, the nearest large town to Toolik Lake. We foster a strong link with this local community because of its historic involvement with science and its interest in, feeling of ownership of, and responsibility for North Slope science. For ~20 years the activities at Barrow have included: (1) weekly lectures on a wide range of scientific topics and (2) an inquiry-based program that replicates some of our experimental and monitoring activities in tundra and lakes, which have been used as part of the K-12 science program in Barrow schools. Each year 1-4 LTER personnel visit Barrow to lecture in the “Saturday Schoolyard” and in the public schools. Both activities have been well-received. In 2014, however, our partner in this program, the Barrow Arctic Science Consortium (BASC), dissolved and closed. Since then we have been working with the Utgeavik Inupiat Corporation and the Barrow Native Heritage Center to reestablish this program, now in collaboration with the Environmental Literacy Program at Colorado State University. Additionally, in summer 2015 a graduate student and REU working with the ARC LTER participated as instructors in summer “Schoolyard” science programs in the villages of Kaktovik and Arctic Village, Alaska, organized by USGS and USFWS.

2. The **Polar Hands-on Laboratory** is offered each year by the Logan Science Journalism Program of the Marine Biological Laboratory (MBL). Every summer, following a two-week intensive exposure to biology at the MBL, 2-12 science journalists come to Toolik Lake for hands-on experience in the Arctic. Our

aim is to infuse public-communication professionals with excitement for arctic research and with the principles of doing science. The program is a tremendous impact multiplier with the graduates serving as ambassadors of our research to the general public and to others who are unable to visit our remote site.

3. K-12 Teachers visit Toolik Lake to participate in our summer field research. In cooperation with the Environmental Literacy Program at Colorado State University, each summer we host 2-10 K-12 teachers with funding from a range of sources, including ARCUS PolarTREC; ARC LTER typically provides travel and logistics support for some of these teachers. The aim is to provide teachers with experience in scientific research that will inform their teaching and will provide them with access to data, methods, and other materials that they can use in their classrooms. In some summers (2011, 2016) this effort is also supported with NSF-RET (Research Experience for Teachers) Supplemental funds.

4. Courses in Arctic Ecology for graduate and undergraduate students are held at Toolik Lake most summers, with ARC LTER investigators as faculty. These courses are exceptional because few other courses provide opportunities for learning advanced field techniques in the Arctic, particularly in the United States. As with the Polar Hands-on Laboratory, these are “hands-on” courses with an emphasis on field measurements and analyzing and discussing the results in the context of ongoing LTER research.

5. Arctic research experience for undergraduate and graduate students: Each year the LTER supports at least 2 REU students at the Toolik Field Station, and 2-10 others in association with collaborating NSF grants. REU's have their own independent research projects, mentored by a PI. Graduate students supported on collaborating grants make use of our long-term experiments and data sets, and we continue to encourage foreign collaborators to send students. To promote communication among Toolik researchers, including these students, every summer there is a weekly seminar series, "Toolik Talking Shop". REU students present their results at these sessions and at an end-of-summer poster session. Graduate students, and occasionally REU students, are invited to our annual winter workshop in Woods Hole to present their results and to participate in planning for the following summer's research.

6. Outreach to the general public includes occasional talks given by LTER personnel to Alaskan Native communities at Anaktuvuk Pass, Kaktovik, and Barrow. Additionally, Alex Hurn and John Hobbie (2012) published “Land of Extremes”, a book intended for tourists as well as scientists on the natural history of northern Alaska, including the Toolik area. PIs have additional records of outreach to their local communities, newspapers, and magazines plus blogs about science for public consumption; e.g., Natalie Boelman's 15 Jun 2011 *The New York Times* blog, “Eavesdropping on Arctic Birds” and Mark Urban and Linda Deegan's 5 Feb 2016 *The New York Times* Op-Ed “T-Shirt Weather in the Arctic”.

7. Outreach to federal, state, and local management agencies: Research done at Toolik Lake is directly relevant to problems of managing the huge expanse of publicly owned, wild land on the North Slope. We provide regular briefings to Bureau of Land Management (BLM), Arctic National Wildlife Refuge, Department of Natural Resources, Alaska Fish and Game, and North Slope Borough officials; usually this consists of visits to their offices in Anchorage, Fairbanks, and Barrow, as well as tours of our research sites at Toolik Lake. We work particularly closely with these agencies in association with the annual permitting process for our research, and present at local conferences upon request. The Alaska Fish and Game office has used our data and advice to set angling policies and fish catch regulations. Our contacts with the North Slope Borough have increased in frequency as our research increasingly involves helicopter travel through areas where subsistence hunting takes place. Occasionally, Toolik Field Station has invited representatives of these agencies to speak at our weekly “Toolik Talking Shop” seminars, helping to make this a two-way channel of communication.

8. National and International Research Planning and Organization: ARC LTER scientists serve on a wide range of advisory boards and panels. In the past 5 years this has included participation in SEARCH (the Study of Environmental Arctic Change), ISAC (International Study of Arctic Change), the National Academy of Sciences Polar Research Board, and the US Department of Energy's Biological and Environmental Research Advisory Committee (BERAC). We continue to serve as Advisory Committee members of Toolik Field Station (operated by the University of Alaska), and from 2011-2014 ARC LTER PI Gus Shaver served on the LTER Network Executive Committee.

Use of supplemental funding: Since the start of the current award (1 March 2011) we applied for and received three supplemental funding awards (2011, 2012, and 2015); a fourth request for 2016 is currently pending. The 2011 request (\$76,501) included funds for Information Management (participation in LTER Network activities and improvements in the ARC database), Research Experience for Teachers (visits to Toolik Lake and the local schools in Anaktuvuk Pass by a high school teacher from Alabama), and for purchase of a new field truck. The 2012 request (\$100,000) was for further improvements to the ARC data base including linking the data to the LTER Network Information System. The 2015 request (\$55,108) was for two key items of research equipment, a sonde for lake water-column profiling and a scintillation counter for use at Toolik Field Station. All of the funds were used for the purposes for which they were awarded, and the results were described in our annual progress reports to NSF. The 2016 request (\$17,000), if awarded, will be used to support travel to Toolik Lake and Barrow by a high school teacher under the NSF-RET program.

Response to advice from midterm review: The ARC LTER hosted an NSF site review in June 2013 at Toolik Field Station. The review was strongly positive, with many favorable comments about our research design and our productivity. The review team did, however, suggest three areas where there was room for improvement: (1) “Research output has been heterogeneous across the different groups ... recent changes in group leadership ... will help address these issues. The panel encourages ... supporting grant proposals and ... targeting its New Investigator support to help strengthen the science in these areas.” (2) “[T]he site review panel had the definite impression that opportunities for integration across the [four] groups could be further developed. ... The panel encourages the ARC-LTER site to establish some more explicit mechanisms to increase the integration across the four groups.” (3) “Though the written documentation provided many examples of impacts of LTER funding on education and outreach, these were given comparatively little attention during the presentations to the panel. ... It would have been more effective if someone involved in education and outreach at this site had put those facts and figures into an engaging context and gave an impression there was more commitment to Broader Impacts components.”

These are all excellent and appropriate suggestions. We have followed up since the review and in the current proposal by (1) increasing the pace of recruitment of collaborating investigators and projects, reflected in the number of top-quality assistant and associate researchers now affiliated with the ARC LTER, particularly those involving aquatic researchers (e.g., new LTER personnel Mark Urban, Rose Cory, Beth Neilson, Bayani Cardenas), (2) planning on more direct collaborations in our field sampling program and synthesis of earlier results; we have also designed our overall research with a focus on questions and concepts to be addressed by direct comparisons among lake, stream, and terrestrial ecosystems, and (3) we provide a more detailed description of our Education and Outreach activities in this proposal.

PROPOSED RESEARCH

Arctic landscapes serve as models for advancing a general understanding of ecological function and also as unique ecosystems to be studied and understood in their own right. Because the Arctic is one of the most rapidly warming regions on Earth (Overland et al. 2015), it also serves as a harbinger of changes to come in other ecosystems around the world. Over the past 40 years, including 28 years supported through the LTER program (Hobbie & Kling 2014), we have developed an understanding of long-term dynamics and controls in the five core areas of the LTER program: (1) production, (2) population dynamics and community structure, (3) the movement and accumulation of organic matter, (4) the movement of inorganic nutrients, and (5) responses to disturbance, including chronic changes in the environment (e.g., climate warming) and acute events and their ongoing effects (e.g., fire and thermokarst failures).

Based on our long-term monitoring and experimental studies, and especially on our more recent investigation of responses to fire and thermokarst failures, we are ready to synthesize this information using an integrated, conceptual framework based on the “openness” of ecosystems and the closely related concept of “connectivity” among ecosystems on the landscape. We define two types of openness: (1) “**Bio-geochemical openness**” is the degree to which the ecosystem depends on external supplies of nutrients and organic C (allochthonous C) versus internally recycled nutrients and locally fixed organic C (autochthonous C), and (2) “**Community openness**” is the degree to which the ecosystem depends on the move-

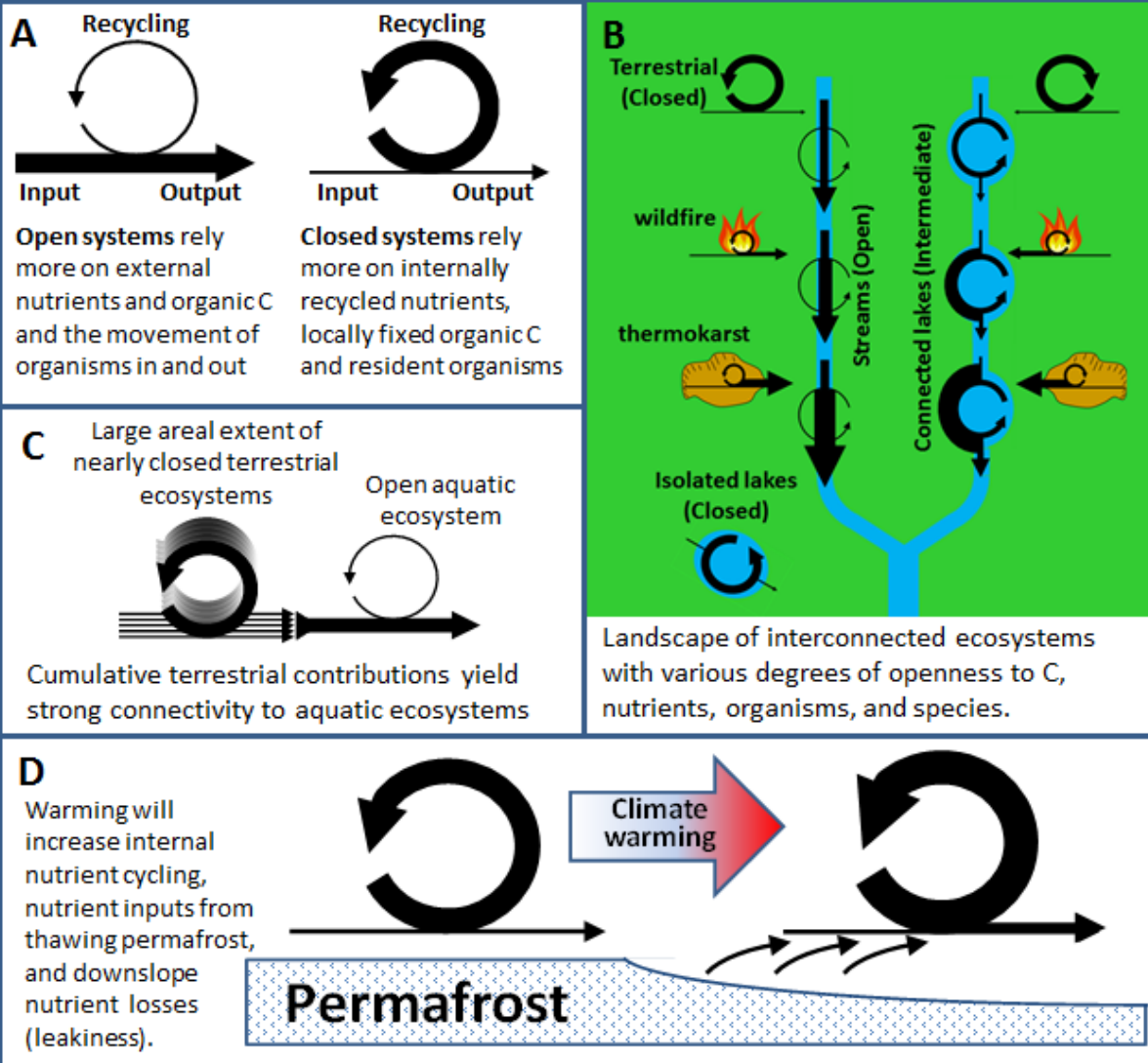
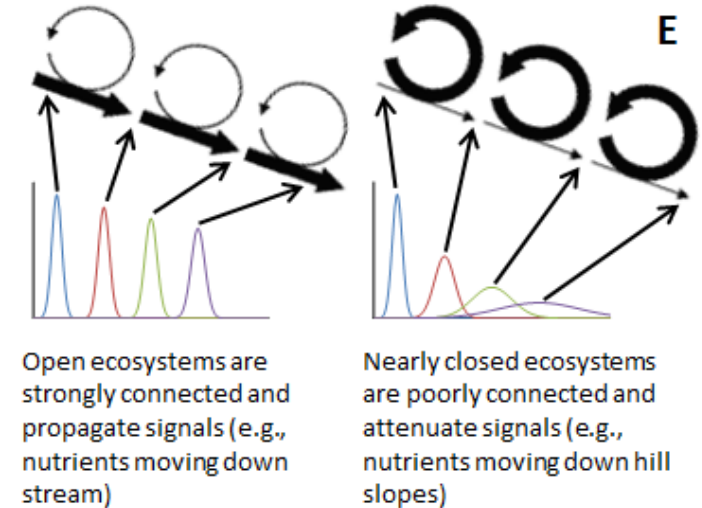


Figure 3. Conceptual diagram. Arctic landscapes are made up of a mosaic of terrestrial, stream, and lake ecosystems with varying degrees of openness and connectivity. Climate warming will release C and nutrients from permafrost, accelerate nutrient cycling and leaching, and will result in species resorting and new colonization. Disturbances such as wildfire and thermokarst failures will result in the loss of C and nutrient capital locally and release a pulse of nutrients and DOM that will propagate across the landscape.



ment of organisms in and out to maintain its community and trophic structure. These two definitions of openness focus inward on the function of the ecosystem. The related concept of connectivity focuses outward on the interactions among ecosystems. “**Landscape Connectivity**” is the degree to which the spatial arrangement and interactions among ecosystems in the transfer of nutrients and organic matter or in the exchange of organisms fosters the propagation of ecological signals across the landscape.

In this renewal of the ARC LTER for 2017-2023, our goal is to use the concepts of *biogeochemical and community openness* for arctic terrestrial and freshwater ecosystems and the *landscape connectivity* among these ecosystems to develop a predictive understanding of the response of arctic landscapes to climate change and acute disturbance.

Conceptual Framework:

Below we describe our conceptual framework based on a gradient of “openness” of ecosystems and “connectivity” among ecosystems on arctic landscapes (Fig. 3). In general, this conceptual framework is grounded on the biogeochemical ideas originally put forth by Lindeman (1942) and Odum (1969) about nutrient and organic matter cycles and movement through organisms and ecosystems, and on the community ecology ideas originally put forth by Summerhayes and Elton (1923) and MacArthur and Wilson (1967) about the movement of species among ecosystems and changes in species relative abundance and turnover in communities. These early biogeochemical and community concepts are well-known and widely applied, and recent applications include the ideas of individuals moving among populations (Levins 1969) that occupy patches of differing quality (Gilpin & Hanski 1991), and species moving among communities or colonizing new habitats (e.g., Leibold et al. 2004). Here we re-specify and re-interpret these foundational ideas using the concepts of openness and connectivity, defined above. For example, we add a broader spatial component by explicitly incorporating the linkages among ecosystems across the landscape (e.g., landscape ecology principles, Turner et al. 2001), we examine those spatial linkages among qualitatively different kinds of ecosystems (terrestrial, streams, and lakes), we broaden the temporal perspective from one of slow changes over succession (Odum 1969) to one incorporating rapid responses to disturbances, and we consider drivers of change not originally specified, such as shifts in climate. Overall, we believe that this revised framework can help unify our understanding of the integrated functions of arctic landscapes and can be applied to other ecosystems as well.

(1) *Biogeochemical openness - Externally supplied nutrients and organic matter versus recycled nutrients and autochthonous organic matter* - Components of the arctic landscape differ widely in their dependence on externally supplied versus internally recycled nutrients. For example, tussock tundra has nearly closed nutrient cycles where primary production relies almost exclusively (95-98%, Shaver et al. 1992, Pearce et al. 2015) on the recycling of N and P that have accumulated within the ecosystem over thousands of years. In contrast, arctic streams have open nutrient cycles where primary production relies almost exclusively on externally supplied N and P from the slow leakage of materials by the surrounding terrestrial ecosystems over large catchment areas (several km²). Lakes are intermediate in biogeochemical openness between terrestrial and stream ecosystems, relying on the accumulation of nutrients from the catchment (87%) but also relying heavily on recycling of nutrients in the water column (11%), and to a lesser extent on recycling from sediments (2%; Whalen & Cornwell 1985). We will quantify biogeochemical openness to nutrients as the ratio of nutrients supporting primary production that are supplied from external sources versus sources recycled locally within the ecosystem; e.g., this information can be derived directly from ARC LTER harvest and process data from which we build nutrient budgets (e.g., McKane et al. 1997a, Pearce et al. 2015, Whalen & Cornwell 1985, Whalen et al. 1988).

Similar landscape patterns apply to organic C. Virtually all the organic C metabolized in terrestrial ecosystems is derived from local photosynthesis, and losses of DOC plus dissolved inorganic C (DIC) in soil water are very small (~1% of photosynthesis, Shaver et al. 2014). Nevertheless, these dissolved C losses are substantial relative to the *net* rate of C accumulation in these terrestrial ecosystems (Kling et al. 1991). Furthermore, accumulated over large catchment areas, the downslope loss of organic matter from terrestrial ecosystems is a major source of organic C to aquatic systems, which are generally net hetero-

trophic in the Arctic (Kling et al. 1991, 1992, 2000) and elsewhere (Cole et al. 1994, 2007, Raymond et al. 2013). Because of longer residence times of water in lakes than streams, lakes are intermediate in their biogeochemical openness to organic C between closed terrestrial ecosystems and open streams, paralleling their relative openness to nutrients (Whalen et al. 1988). We will quantify biogeochemical openness to organic C as the ratio of organic C supporting secondary production that is supplied from external sources versus locally photosynthesized by plants in the ecosystem (allochthonous: autochthonous C); this information can be derived from measurements of ecosystem C metabolism, DOC and DIC movement in soil and water, and secondary production by microbes (e.g., Whalen & Cornwell 1985, Kling et al. 1991, 2000, Crump et al. 2007, Luecke et al. 2014, Moore & de Ruiter 2012).

The contrast in openness between terrestrial and aquatic systems in the Arctic is a critical consideration in ecosystem connectivity. Although the downslope losses under undisturbed conditions are only a minor component of the budgets for terrestrial ecosystems, these losses, accumulated over a large landscape, are the major source of nutrients and organic matter in the budgets for streams and lakes. Aquatic systems are therefore strongly connected to terrestrial systems, a connectivity that is likely to increase as permafrost thaws and currently frozen organic matter and nutrients are released and move downslope.

These characteristics should greatly influence how individual ecosystems respond to climate change and disturbance. For example, we predict that climate warming should affect ecosystems with closed nutrient cycles more than ecosystems with open nutrient cycles. Warming is predicted to stimulate the rates of mineralization and uptake and therefore the rate of internal nutrient cycling, but might not affect the external nutrient supply (e.g., atmospheric N deposition). Similarly, a disturbance that resulted in a major loss of nutrient capital, such as fire and thermokarst failures, should have a longer-lasting effect on a more-closed system because the slow external supply rate would significantly prolong replacement of the lost nutrient capital unless a large, new source of nutrients became accessible (e.g., from thawing permafrost). The large throughput of nutrients in an open system should make the recovery from an analogous loss of nutrients easier and faster. Therefore, we predict that more-open systems will be more resilient to a loss (or gain) of nutrient capital than more-closed systems. Finally, we recognize that especially with C, the chemical characteristics of the inputs from land to surface waters might be more critical to aquatic ecosystem function than the absolute amounts alone. For example, disturbance and climate change could alter whether C inputs are more inorganic or organic (DIC vs. DOC), and the light absorption by DOC might in turn limit primary production (e.g., Daniels et al. 2015). Thus, changes in system openness as well as changes in the nature of the inputs will control element budgets and more importantly system metabolism and function (production and respiration). In our proposed renewal we will test these ideas and advance knowledge of biogeochemical budgets in a landscape with a wide diversity of terrestrial and aquatic ecosystem types for which we have long time series of data and are performing whole-ecosystems experiments.

(2) Community openness - Movement of species in and out of the ecosystem versus changes in relative abundance among species already in the ecosystem - Components of the arctic landscape differ widely in their susceptibility to species colonization. For example, tussock tundra is composed of long-lived, densely overlapping, low-stature plants with little space available for new seedlings to become established, either for species already in the community or those in the regional species pool (Gartner et al. 1983, Chapin & Shaver 1985, Gough 2006, Gough et al. 2015); "community openness" is therefore low. In contrast, heath tundra and streams have ample space for new organisms to become established and so "community openness" could potentially be high. The likely reason that these systems have not been colonized by other species is that the dispersal distance, physical conditions, and low fertility preclude the establishment of most species (Moulton & Gough 2011). Nevertheless, if there is a change to more favorable conditions for these potential colonizers, then new species would eventually be expected to become established (e.g., moss colonization of the Kuparuk River after 10 years of P fertilization, Arscott et al. 1998, Slavik et al. 2004; fireweed colonization of fertilized heath plots, Moulton & Gough 2011).

As with the biogeochemical characteristics, we predict that community openness should influence how the individual ecosystems respond to climate change and disturbance. Because plant functional

types significantly affect biogeochemistry (e.g., Austin & Zanne 2015 and associated *J. Ecology* Special Feature), understanding controls over species composition in a changing environment is an important endeavor. For example, community structure of open systems should change if chronic environmental shifts make the site favorable to new species within a given dispersal range. If the new species have different characteristics (e.g., the shift from algae to moss in long-term stream fertilization, Slavik et al. 2004), they might significantly alter ecosystem function (e.g., Ehrenfeld 2010). In contrast, closed systems should respond to chronic shifts in the environment by a change in the relative abundance of species already present (e.g., change to shrub dominance in fertilized moist acidic tundra, Shaver & Chapin 1986, Gough et al. 2012, or shift to the large morph of char in closed lakes, Budy & Luecke 2014), but should be resistant to changes involving new species. Acute disturbances to closed systems might actually facilitate climate-induced changes in species composition by opening space for new species to become established (e.g., Connell 1978, Gough 2006).

Community openness has two important components. The first is the simple movement of organisms in and out of the ecosystem (e.g., grayling seasonal migration between lakes and streams, Bowden et al. 2014; bacteria dispersal from soil water to streams to lakes, Crump et al. 2012). This movement of organisms can be quantified using a “budget” based on numbers of individuals, biomass, or gene abundance. The second component is a change in species composition or trophic structure in response to an environmental change. In the research proposed here, we focus on species that contribute significantly to ecosystem function (e.g., terrestrial plants and carnivorous fish) and that are also responsive to environmental change and disturbance. We will use changes in community similarity indices (e.g., Jaccard [1912] coefficient, which quantifies the overlap in species between sites relative to the total number of species in both sites) or measures of Beta diversity (e.g., Crump et al. 2012) as appropriate for the taxa being studied to quantify this component of community openness. If there is no change in community similarity (or trophic structure, which implies a change in species present) in response to climate change, disturbance, or experimental manipulation, then that community is closed and resistant to change. On the other hand, if there is turnover in species composition, the response will reflect reduced similarity indicating community openness. Similarly, an increase in similarity can be used to quantify recovery from a disturbance.

(3) Landscape connectivity - Arrangement and linkages among landscape components - At a landscape scale, the arrangement of open versus closed ecosystems influences the current state of these ecosystems and should also influence how they respond to climate change and disturbance (Fig. 3). Quantifying the connectivity in the landscape is more difficult than quantifying openness because the exchanges of nutrients, organic C, or organisms are not equally important among the component ecosystems. For example, nutrient loss from terrestrial ecosystems is small relative to internal recycling; they are therefore biogeochemically nearly closed. Nevertheless, cumulatively this loss from terrestrial ecosystems is vital to the receiving aquatic ecosystems; the connectivity between terrestrial and aquatic components of the landscape is therefore strong. Connectivity can also change in response to disturbance. For example, although most terrestrial ecosystems are nearly closed biogeochemically and might resist nutrient and organic matter losses in response to the relatively slow change in climate, acute disturbances like fire and thermokarst failures can open these systems to biogeochemical losses and thereby intensify the connectivity to downslope ecosystems, at least temporarily (Bowden et al. 2008, Larouche et al. 2015). Landscape connectivity should also affect how responses to climate change and disturbance propagate across the aquatic portion of the landscape through the flow of nutrients, organic matter, and organisms, with open systems (e.g., streams) acting as conductors that rapidly propagate responses, and more closed systems (e.g., lakes) acting as capacitors that buffer and slow the propagation of the disturbance response across the landscape.

From a community perspective, lakes with inlet or outlet streams that allow the free migration of fish typically have biota and trophic structures that differ from isolated lakes (e.g., Luecke et al. 2014). If climate change or disturbance results in a change in the connectivity among lakes and streams, the responses might take these lakes beyond a “tipping point” that completely changes the community and biogeochemistry. For example, dry conditions can prevent migration of grayling to over-wintering lake ref-

uges before the streams freeze. Conversely, wet conditions can allow fish migration into usually isolated streams and lakes and alter their community composition and trophic structure (Betts & Kane 2015, Golden et al. 2015).

Synthesis - Interactions among biogeochemical openness, community openness, and landscape connectivity – Biogeochemical, community, and landscape responses to climate change and disturbance obviously interact. The biogeochemical characteristics of a system set the stage on which community processes act, the community structure of a system sets the potential for various biogeochemical processes, and spatial connectivity of both biogeochemical and community processes tie the landscape together. We propose to develop a synthetic understanding of the arctic landscape based on these principles, which have application to most landscapes around the world. The Arctic has several advantages for this type of study: (1) Low-stature and fine spatial scale of the terrestrial systems means that whole ecosystems can be enclosed and manipulated, with appropriate replication, within experimentally tractable plots. (2) A diversity of terrestrial ecosystem types (upland heath, tussock tundra, shrub-dominated water tracks, wet sedge meadows, river-side willows) interact with one another, and with aquatic ecosystems, over a relatively small landscape area (ha to a few km²). (3) There is an abundance of streams and lakes of various sizes and characteristics including lakes that completely freeze in the winter and others that do not, stream networks that include lakes and those that do not, and isolated lakes with no stream connections. (4) There are lakes with and without fish and a resulting diversity of trophic structures and dynamics.

In the following sections for each of our four core research areas (terrestrial, streams, lakes, and landscape interactions) we present (1) our rationale and ongoing research findings to set the background for and illustrate the importance of these organizing questions, and (2) the new studies we propose to answer these questions.

Terrestrial Research:

Rationale and Background. The landscape around Toolik Lake includes several distinct types of tundra ecosystem (Shaver & Chapin 1991, Walker et al. 1994, Shaver et al. 2014). The dominant land cover is moist acidic tundra (MAT) on surfaces older than ~66k years and moist non-acidic tundra (MNT) on younger surfaces. Hill crests and rocky outcrops are typically covered with upland dry heath and low-lying flat areas by wet sedge meadows. Areas along stream edges and where water tracks develop on hillslopes are covered by shrub tundra. In our past work we (1) compared and contrasted the community structure and biogeochemical function among these different tundra types (Shaver & Chapin 1991, Gough et al. 2000, Hobbie et al. 2005), (2) monitored their key properties in relation to weather and climate (Shaver et al. 2014), and (3) conducted long-term, whole-ecosystem experimental manipulations of factors related to climate change including N+P factorial fertilization, greenhouses with and without N+P fertilization, and shade houses (Gough et al. 2002, Mack et al. 2004, Bret-Harte et al. 2008, Sistla et al. 2013). We also experimentally altered mammalian herbivore pressure to examine the role of herbivores (e.g., Gough et al. 2012). More recently we focused on the responses of tundra to two climate-related disturbances, wildfire (e.g., Mack et al. 2011, Rocha & Shaver 2011a,b, Jiang et al. 2015a) and thermokarst failures (e.g., Bowden et al. 2008, Pearce et al. 2015). Our aim has been to develop a predictive understanding of the distribution of these tundra types on the landscape and the controls on their structure and function so that we can model their responses to climate change and their recovery from disturbance. Here we describe our main findings and future research *within the framework of the biogeochemical and community “openness” and “connectivity”*.

Biogeochemical openness and connectivity. Based on our monitoring, experiments, and modeling, we know that these ecosystems are remarkably closed biogeochemically for nutrients like N and P and for organic C. Inputs from outside the ecosystems can supply less than 2% of the macronutrient requirements of the plants (Shaver et al. 1992, 2014, Pearce et al. 2015); virtually all productivity on this landscape is therefore supported through the recycling of nutrients that have slowly accumulated over thousands of years. This biogeochemical closure has major implications for how these ecosystems respond to climate change and their recovery from disturbance. Because of the slow supply of nutrients from outside these

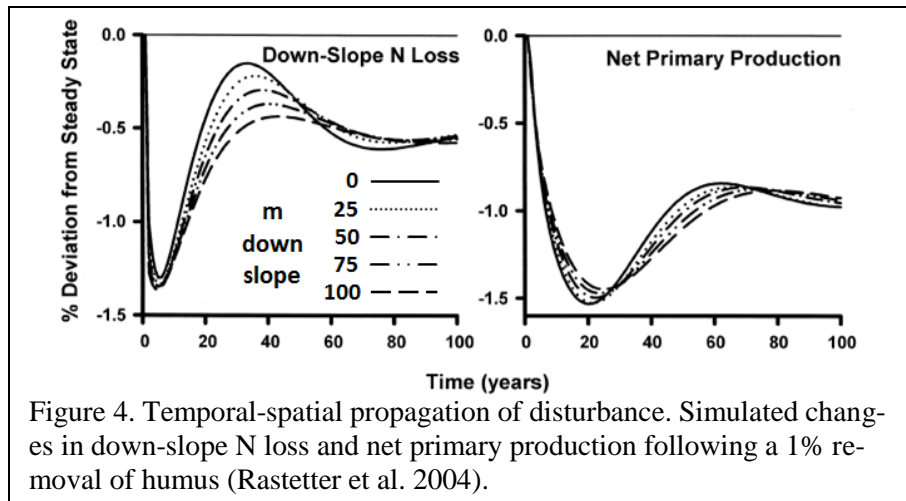


Figure 4. Temporal-spatial propagation of disturbance. Simulated changes in down-slope N loss and net primary production following a 1% removal of humus (Rastetter et al. 2004).

severe constraints on the response to disturbance because it means that recovery has to be supported almost exclusively by residual nutrients left at the disturbance site (Pearce et al. 2015, Jiang et al. 2015a); full recovery of any nutrient capital lost in the disturbance could take thousands of years. For both the response to climate change and the recovery from disturbance, the release of nutrients from thawing permafrost could significantly stimulate plant growth and represents an "opening" of nutrient supply to these ecosystems. *In fact, because of accelerated soil nutrient and C cycling, we predict that in a warming climate, the terrestrial ecosystem will become more open and "leak" more into aquatic ecosystems* (Fig. 3). This general expectation is supported by our past work (e.g., Abbott et al. 2014, 2015, Larouche et al. 2015, Vonk et al. 2015) and is the starting premise of our research on streams, lakes, and landscape interactions described below.

The biogeochemical closure of terrestrial ecosystems also has important ramifications for the interconnectivity among ecosystems on the landscape. Through hydrological transport in soil water, nutrients gradually spiral downhill much as they do in streams (Newbold et al. 1981, 1982, Yano et al. 2010). Rastetter et al. (2004) estimated that N on a tundra hillslope spirals downhill at a rate of about 0.25 m every 325 years. This rate is very slow, but can nevertheless have important cumulative effects when integrated over time or space (Fig. 4). Shaver et al. (2014) estimated an average loss of inorganic plus organic N from MAT of about $0.085 \text{ g N m}^{-2} \text{ yr}^{-1}$, which is about the rate of N fixation in these ecosystems (Hobara et al. 2006). If this N is moving downslope in a form that is accessible to plants or can be made accessible to plants by soil processes (e.g., mineralization), then an increase in N demand at the top of the hill (e.g., from elevated CO_2) will very slowly propagate down slope as a decrease in N supply. Thus the biogeochemical connectivity can be altered by, e.g., changes in climate and CO_2 concentration. On the other hand, if the N is moving in a recalcitrant organic form, it might move past the ecosystems on the hillslope but become activated by UV light as it enters adjoining surface waters (Vähätalo & Zepp 2005, Cory et al. 2013). This biogeochemical connectivity and its landscape ramifications on streams and lakes are further discussed in the Landscape Interactions section below.

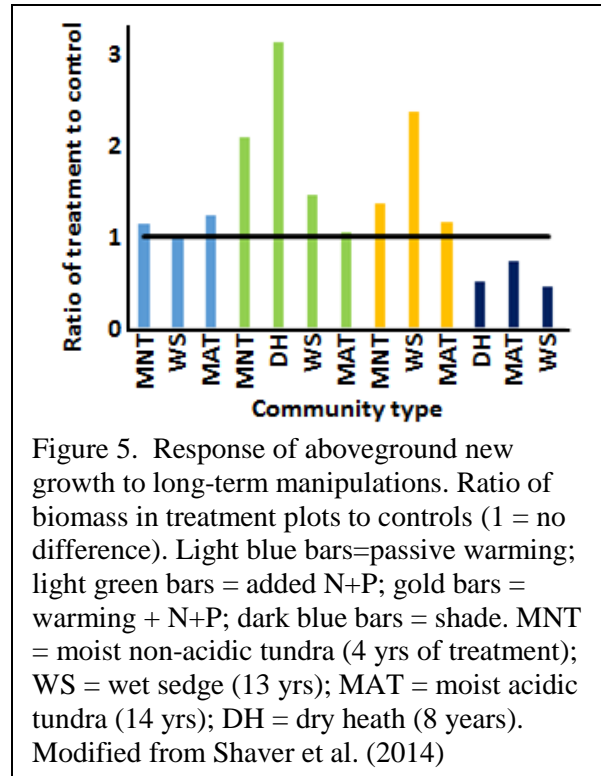
Community openness and connectivity. The plant communities in these ecosystems are remarkably closed even to seed propagation by species already in the ecosystem (Gartner et al. 1983, Chapin & Shaver 1985; Gough 2006; Gough et al. 2015). In response to fairly strong manipulations (fertilization, warming), the relative abundances of established species in these ecosystems have changed dramatically and some lower-stature species have been lost (Shaver & Chapin 1986, Gough et al. 2012); however, the experimental plots have mostly resisted invasion by species new to the local area for at least 25-35 years. Two exceptions have occurred after multiple years of fertilization: some of the dry heath plots were colonized by fireweed (*Epilobium angustifolium*; Moulton & Gough 2011), and some MAT plots were colonized by an arctic grass (*Calamagrostis lapponica*), but this latter colonization appears to be associated with small disturbances on the plots (e.g., frost boils). *We therefore predict that more frequent disturbance (fires, thermokarst) might help "open" these plant communities to colonization* (Gartner et al. 1983,

ecosystems, any increased growth associated with elevated CO_2 has to be supported by nutrients already in the ecosystem, resulting in a net transfer of nutrients from soils to vegetation (Rastetter et al. 1992, Jiang et al. 2015b). Warming facilitates this net transfer by speeding up the rate of soil nutrient cycling (e.g., Rustad et al. 2001). Similarly, the slow nutrient supply puts

Gough 2006) and potentially accelerate the ultimate response to climate warming. Recent sampling of aboveground arthropods in the fertilized MAT plots indicates that some arthropod taxa favor patches of greater soil nutrients and associated vegetation (data not shown), suggesting that the aboveground arthropod community might be open to colonization as soils warm and nutrients turn over faster and become more available. In addition, tundra voles were found at greater abundances in areas that had been burned in the Anaktuvuk River fire compared with areas that were not burned (R. Rowe, unpublished), suggesting disturbance might increase the openness of vertebrate communities. The seasonal migration of songbirds (e.g., Boelman et al. 2014) and caribou (Cameron et al. 2002) through this region suggests a substantial openness of the tundra to migratory vertebrates.

Ongoing Activities. Terrestrial research of the Arctic LTER includes experimental and descriptive studies on tundra ecosystems of the effects of climate, biota, geology and geomorphology, and fluxes of water and nutrients within and through ecosystems. The research design incorporates these controls through a combination of long-term manipulations of climate and nutrient inputs with comparisons among sites that differ in their biota and their topographic position, geology, and landscape age. Over the past 40 years we have developed a suite of experiments in which contrasting tundra types, dominated by different plant functional types and located on different geological surfaces, are subjected to identical manipulations of nutrient inputs (with N and P fertilizers), air temperature (plastic greenhouses), light (shading), and other treatments such as herbivore exclusion (Fig. 5).

Over the next six years, we will maintain most of our existing suite of long-term observations, experiments, and comparisons, with periodic harvests as in the past. Because these ecosystems continue to respond to treatments, with each harvest we gain new insights about ecosystem regulation and we expect to continue to do so as long as the experimental plots continue to change. We focus particularly on experiments on landscapes that are also studied by the aquatic and landscape interactions research teams, which allows us to quantify inter-system connectivity as nutrients and C in soil waters move into surface waters. We will intermittently monitor the vegetation response to fire (Bret-Harte et al. 2013) in conjunction with a recently funded LTREB grant to A. Rocha. We will also continue long-term monitoring of plant growth and flowering in relation to weather (Shaver et al. 1986a,b) and implement a new protocol to explicitly track seedling establishment in the long-term plots as a measure of community openness. To track inter-annual changes in above ground biomass we now routinely make NDVI (“greenness”) measurements of all plots using a hand-held spectroradiometer (Shaver et al. 2007). This provides a complete data set from all of our long-term treatments and is allowing us to see how greater soil nutrients alter the phenology of the plant canopy, which can have additional implications for C cycling (Sweet et al. 2015). Finally, with our collaborators we seek complementary funding for related grants to continue process studies. For example, J. Schimel and M. Mack currently have separate NSF funding to investigate N biogeochemistry that requires sampling from our long-term plots. In addition, we will continue simulation modeling to integrate the results of field experiments and observations (Pearce et al. 2015, Jiang et al. 2015a) and to develop predictions about long-term and large-area changes (Rastetter et al. 2003, Jiang et al. 2015b) and compare across both the Arctic and the LTER network.



New activities.

Question and Activity #1: Does warming alter the biogeochemical and community openness of arctic terrestrial ecosystems? Passive greenhouses were established in three tundra types in 1989: shrub, MAT, and wet sedge, and in MNT in 1997. These treatments mimic increases in air temperature as predicted by global climate models (Chapin et al. 1995). The houses were set up in a factorial design with nutrient addition, and much has been learned from them (e.g., Chapin et al. 1995, DeMarco et al. 2014). However, their small size and the large interest of the science community in warming have meant that we are running out of space to sample. Because of cost and power constraints, we cannot implement an active warming experiment, but here we propose to establish a new suite of larger greenhouses at two locations: on the ~66k year-old surface where our current MAT studies are centered near Toolik Lake and in the Imnavait Creek watershed (~250k years old). At each site we will establish six greenhouses and six control plots of the same size. We propose to install greenhouses for the first time at Imnavait Creek to link with ongoing studies by the Landscape Interactions group who will sample soil water in the greenhouses for landscape connectivity studies including catchment export of C, N, and P.

Question and Activity #2: Are terrestrial consumer communities open under changes in arctic climate? Arctic tundra supports vast numbers of migratory birds (Boelman et al. 2014) and caribou (Cameron et al. 2002) in the summer, which by definition demonstrates the importance of seasonal openness of these animal communities. However, resident consumers, including small mammals and arthropods, may comprise relatively closed animal communities. In the past few years we have sampled the aboveground arthropod communities in several long-term experiments and at the Anaktuvuk River fire site (Asmus et al. submitted). Continuing to monitor and calculating similarity indices as described earlier will allow us to determine if the arthropod community is open to new species. We will also further investigate a potentially important aquatic to terrestrial nutrient subsidy, that of aquatic insects (particularly mosquitoes). In other arctic ecosystems, mosquitoes and midges have been found to provide crucial subsidies to terrestrial ecosystems (e.g., Gratton et al. 2008), but this has yet to be investigated in the Alaskan Arctic. In addition, we will maintain a set of small mammal exclosures in MAT and dry heath tundra (Gough et al. 2012). As appropriate, we will coordinate our sampling and protocols with that of both the Toolik Field Station monitoring program and the nascent NEON site to be established at Toolik Lake in 2016-2017.

Question and Activity #3: How do terrestrial ecosystems respond first to biogeochemical opening through long-term N and P fertilization and then to closure when fertilization stops? In July 2015 we quantified in detail the current state of our longest-running fertilization experiment in MAT (established in 1981). The goal of this data collection was two-fold: (1) to compare results with prior data collections in 2000 and earlier (Fig. 6) to determine changes in the trajectory of ecosystem response, and (2) to set up the experimental plots for monitoring of system recovery once we stopped adding

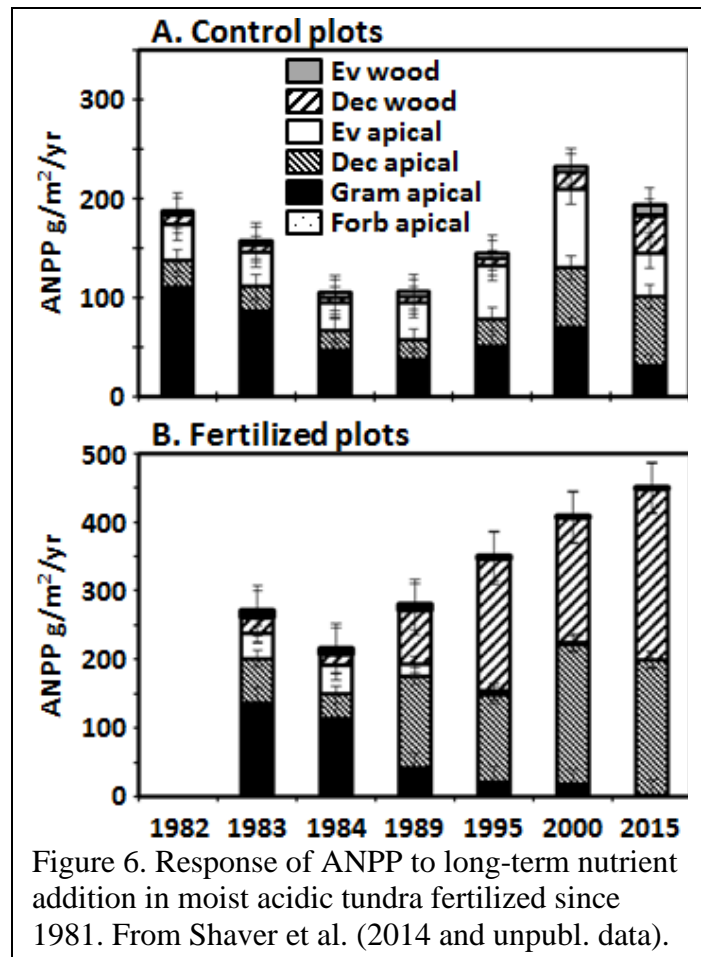


Figure 6. Response of ANPP to long-term nutrient addition in moist acidic tundra fertilized since 1981. From Shaver et al. (2014 and unpubl. data).

nutrients. Beginning in 2016, only half of each fertilized plot will continue to receive nutrients, while the other will not. We will thus reduce the biogeochemical “openness” by eliminating fertilizer nutrient inputs to half of each plot. This will provide an important opportunity to monitor the trajectory of ecosystem response following dramatic change in species relative abundance and nutrient loading. This same approach has been taken in the Stream and Lake fertilization studies, allowing us to compare the transient response of decreased openness between terrestrial and aquatic ecosystems. We propose to annually monitor NDVI and species composition (non-destructively) and to conduct a biomass harvest in year 4 to determine how the previously fertilized system has changed after 5 years without fertilization.

Question and Activity #4: How do changes in plant biomass and species composition affect connectivity and losses of nutrients and C to aquatic ecosystems? To complement studies by the aquatics groups near Toolik Lake and at Imnavait Creek, we will conduct vegetation sampling to estimate plant biomass and production non-destructively (using NDVI) and determine vegetation community composition. Working with the Streams, Lakes, and Landscape Interactions groups, we will determine if there are correlations between terrestrial production and aquatic metabolism and nutrient concentrations.

Streams Research:

Rationale and background. As part of the ARC LTER and related NSF-funded research, we have studied the structure and function of the primary stream types on the North Slope of Alaska, especially in the vicinity of the Toolik Field Station, for over 30 years. These streams include meandering tundra streams, cascading mountain streams, and “beaded” streams that are a particular feature of ice-rich, tundra landscapes (Bowden et al. 2014). In our previous research we characterized benthic autotrophic (e.g., Miller et al. 1992) and invertebrate (e.g., Hiltner 1985, Hershey et al. 1988, Hinterleitner-Anderson et al. 1992, Huryn et al. 2005) communities. We developed and applied methods to measure key ecosystem processes including nutrient dynamics (Peterson et al. 1985, 1997, 2001, Harvey et al. 1998, Peterson 1999), primary production (Bowden et al. 1994, Finlay et al. 1994, Arscott et al. 1998, Bowden et al. 1999), secondary production (Deegan & Peterson 1992, Deegan et al. 1997, 2005, Huryn et al. 2005, Benstead et al. 2007), and decomposition (Peterson et al. 1986, Bowden et al. 1999, Benstead et al. 2005). Results of this long-term stream research are summarized in several key journal articles (Peterson et al. 1986, 1993, Slavik et al. 2004) and in our recent synthesis volume (Bowden et al. 2014).

Our primary objectives in this past research were to compare the structure and function of arctic stream systems to streams in other biomes and to identify how arctic streams are likely to respond to climate change. Streams are open, flow-through systems that connect terrestrial ecosystems to downstream coastal ecosystems. In addition, stream networks connect a substantial portion of the lakes and ponds on the arctic tundra. Because streams transform nutrients and convey organisms, landscape connectivity mediated by streams can strongly modify aquatic biogeochemical and community dynamics on a landscape scale.

We expect these influences to be different depending on the type of terrestrial ecosystem adjacent to streams and the degree to which streams are connected or not connected to lakes. Furthermore, as the arctic climate changes we expect the connectedness of arctic stream ecosystems to change, which may alter aquatic biogeochemical dynamics and community structure. Here we describe our main findings and future research within our framework of the biogeochemical and community openness and connectivity of the arctic system.

Biogeochemical openness and connectivity. Consequences of climate change on the biogeochemistry of arctic streams are strongly influenced by the connectivity of streams to lakes and the na-

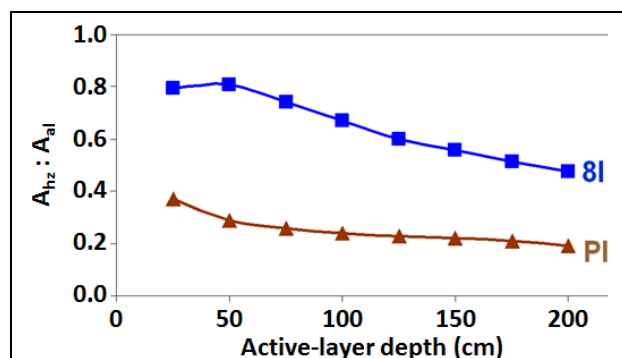


Figure 7. Simulations showing fraction of active layer (A_{al}) occupied by the hyporheic zone (A_{hz}) in coble (8I) and silt (PI) bed streams under different future active layer thickness due to climate warming. From Zarnetske et al. (2008).

ture of the watersheds that these streams drain. Permafrost-dominated arctic soils contain large amounts of C, N, and P that may be introduced into actively cycling pools when permafrost thaws. Previous research directly related to the ARC LTER project investigated how nutrient processing might change in the future if the zone of permeable sediments in streams (the hyporheic zone) thickened as a consequence of climate warming (Greenwald et al. 2008,

Zarnetske et al. 2007, 2008). This research showed clearly that thickening of the hyporheic zone during the season was less important for biogeochemical transport of solutes than the lengthening of the flowing water season (Fig. 7). In the Kuparuk River, increased annual NO_3 flux (McClelland et al. 2007), as well as increased NO_3 concentration at higher flows relative to observations during the previous decade (Townsend-Small et al. 2011), indicate that these climate-related changes to the N cycle may already be increasing N export. Autumn is a particularly important season that may significantly increase the pool of available N in the Arctic because previously frozen N likely enters the actively cycling pool for the first time in autumn, when thaw is deepest. It is more difficult to identify increases in P flux because this limiting nutrient is rapidly taken up by benthic algae, which are then quickly assimilated into the stream food web. However, our long-term monitoring suggests that benthic stocks of total P (and total N) have increased, differently, over the last decade or more (Fig. 8). *We predict that in the future, the conditions conducive to continued microbial activity and hydrologic transport (i.e., warmer temperatures) will dominate the conditions conducive to greater plant uptake (i.e., light remains the same), resulting in greater mass flux of nutrients and organic matter to streams.* There are several mechanisms that could explain this greater mass flux of nutrients (Fig. 9), and the conceptual framework of this proposal allows us to explore how late-season dynamics influence interconnected lake and stream ecosystems.

Community openness and connectivity. Mobile consumers such as fish can transport large quantities of energy and nutrients (C, N, and P) across ecosystem boundaries (Deegan 1993, Polis et al. 1997, Vanni 2002, Lundberg & Moberg 2003, Flecker et al. 2010). These cross-system transfers by migrating fish may be particularly important in nutrient poor, low productivity Arctic ecosystems. Many lakes do not have enough in-situ productivity to support a large resident population of fish feeding at lower trophic

levels, forcing grayling to move from lakes into rivers to feed in the summer. However, with the onset of winter, large numbers (and biomass) of stream-dwelling Arctic grayling travel long distances to concentrate in those few lakes that are sufficiently deep to have liquid water below the ice (West et al. 1992, Parkinson et al. 1999). These large and deep lakes also support resident populations of potentially piscivorous fishes such as lake trout (Lake char) and Arctic char. In many lakes, summer gut content analysis indicates that lake trout primarily consume snails and insects (Hershey et al. 1999, Keyse et al. 2007). However, Sierszen et al. (2003) used stable isotope anal-

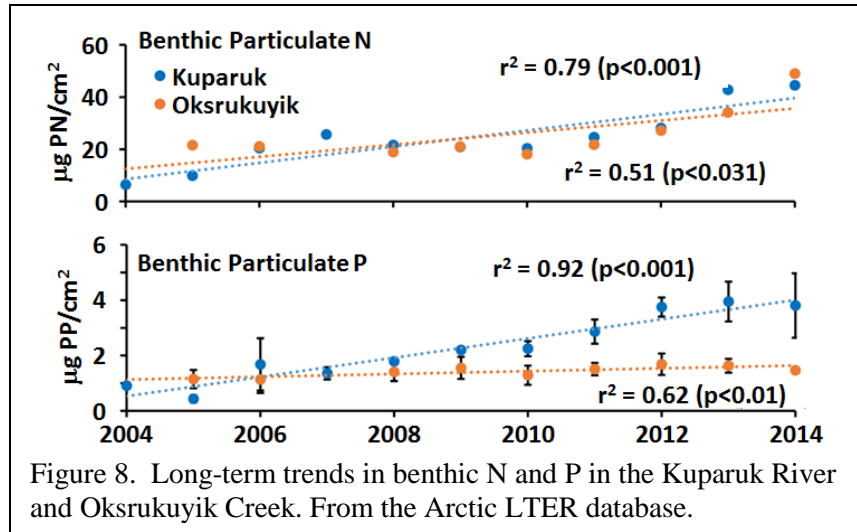


Figure 8. Long-term trends in benthic N and P in the Kuparuk River and Oksrukuyik Creek. From the Arctic LTER database.

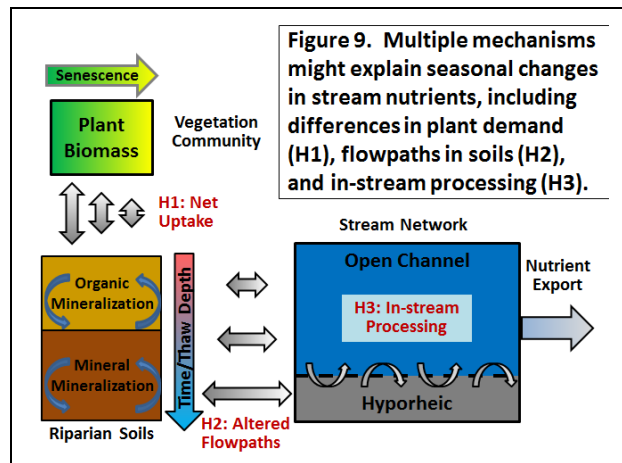


Figure 9. Multiple mechanisms might explain seasonal changes in stream nutrients, including differences in plant demand (H1), flowpaths in soils (H2), and in-stream processing (H3).

yses to examine the food webs in two lakes near Toolik and suggested that in one lake, migrating grayling might contribute a portion of the diet for the resident lake trout. Calculating a similarity index for the fish community in streams and lakes at different times of year and across years will allow explicit comparison of community openness across ecosystems.

Most of this earlier work on lake trout diets was done when migrating grayling would be absent or at very low densities in these lakes. Green Cabin Lake in the headwaters of the Kuparuk River supports a large portion of the seasonal migrant population of Arctic grayling in this river, which has been a major focus of our long-term research. Recent data from this lake regarding the seasonal importance of grayling in lake trout diets (Fig. 10) and stable isotope analysis of food webs (Fig. 11), suggest that grayling support almost 90% of lake trout production. In comparison to in-situ benthic or pelagic invertebrate prey sources, migrating grayling represent a larger pool of energy and nutrients and a higher quality of food (Table 2). Thus we suspect that this trophic subsidy is more important and widespread than previously thought. For example, new collaborative research with the Lakes group in the Oksrukuyik Creek watershed on “leaky” lakes (lakes that have intermediate or intermittent surface connectivity with other lakes) suggests that very large-sized Arctic char may be using grayling as a trophic subsidy when compared to more closed lakes in which char generally remain small and are rarely piscivorous.

The urgency to understand the linkages between streams and lakes by grayling migration stems from the rapid rate and broad extent of changes in the Arctic that could affect this connectivity. The importance of trophic subsidies supported by migration of grayling from streams to lakes is expected to be-

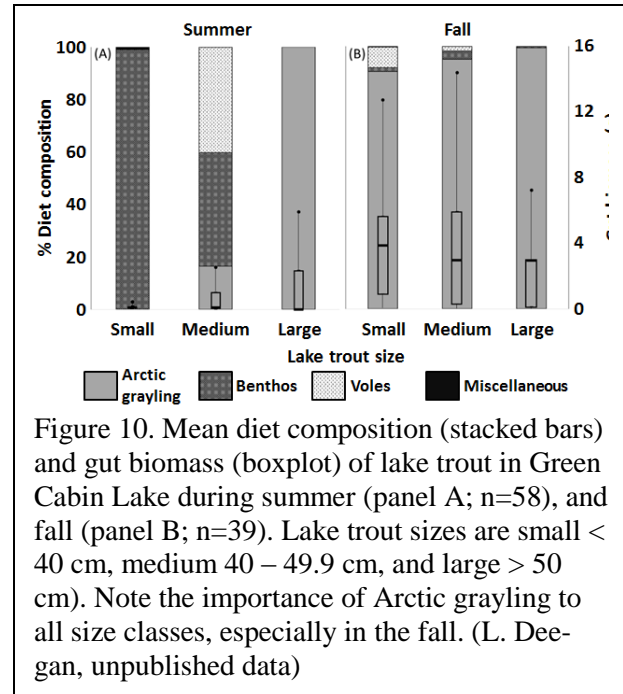


Figure 10. Mean diet composition (stacked bars) and gut biomass (boxplot) of lake trout in Green Cabin Lake during summer (panel A; n=58), and fall (panel B; n=39). Lake trout sizes are small < 40 cm, medium 40 – 49.9 cm, and large > 50 cm). Note the importance of Arctic grayling to all size classes, especially in the fall. (L. Deegan, unpublished data)

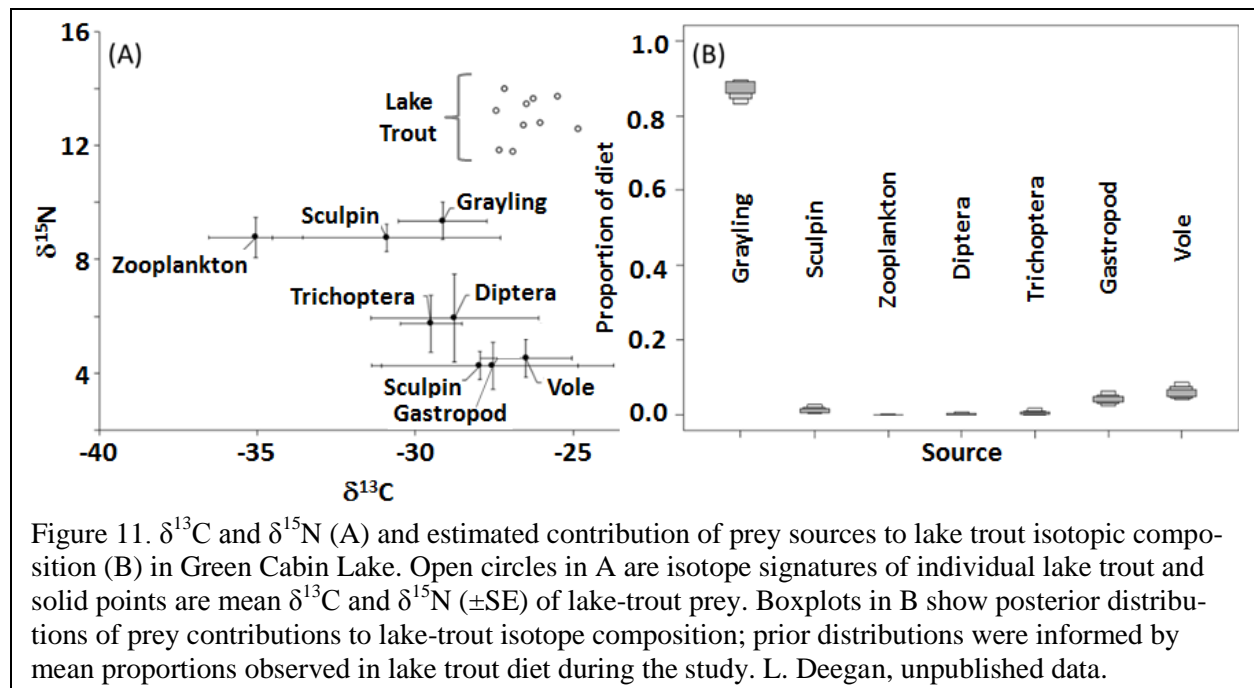


Figure 11. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (A) and estimated contribution of prey sources to lake trout isotopic composition (B) in Green Cabin Lake. Open circles in A are isotope signatures of individual lake trout and solid points are mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\pm\text{SE}$) of lake-trout prey. Boxplots in B show posterior distributions of prey contributions to lake-trout isotope composition; prior distributions were informed by mean proportions observed in lake trout diet during the study. L. Deegan, unpublished data.

Table 2. Carbon required to meet observed annual lake trout production in Green Cabin Lake and the potential C supply available through predation on migrant grayling and benthos. Lake trout (C:N 3.7 ± 0.04) predator demand was estimated via independent bioenergetic models, assuming exclusive foraging on grayling (C:N 4.05 ± 0.03 SE) and gastropods (i.e. predominant benthic prey; C:N 5.07 ± 0.2).

	Prey	kg dry mass yr ⁻¹
Predator Demand	Migrant grayling	12
	Benthic Production	31
Prey Supply	Migrant grayling	208
	Benthic Production	139
Supply:Demand	Migrant grayling	17.3
	Benthic Production	4.5

come more important to lake predators but may also become more imperiled by climate change. The energetic demands of top predators in lakes will increase with higher lake temperatures (Budy & Luecke 2014), but the longer autumn open-water season may allow grayling to return later, thus shortening the period of vulnerability to top predators in lakes. Additionally, climate-induced changes to stream productivity could either enhance grayling productivity if stream primary and secondary productivity increase, or decrease grayling productivity if hydrological discontinuities in the late-season trap grayling in rivers for ex-

tended periods or over the winter. *In either case, we predict that changes to environmental conditions that alter system openness or connectivity are likely to also alter the production of grayling or the timing of their migration in ways that significantly affect resident lake piscivores. Collectively, these changes might also influence the community and biogeochemical characteristics of aquatic systems downstream from these lakes.* Current aquatic resource management rarely takes into account the ecosystem functions performed by organisms that move between systems, yet they are essential components of resilience to change (Lundberg & Moberg 2003). The Arctic may be one of the last remaining opportunities to study a spatially extensive region where many of the ecological processes and feedbacks are still intact (Chapin et al. 2006).

Ongoing Activities. We propose to continue the following long-term activities.

Long-term sentinel river monitoring. We will continue long-term monitoring of the Kuparuk River and Oksrukuyik Creek, which have been focal rivers since the start of the ARC LTER. Our monitoring includes fundamental aspects of the structure and characteristics of these streams, including nutrient concentrations (NH₄, NO₃, PO₄, plus dissolved and particulate organic C, N, and P), benthic chlorophyll *a*, benthic cover by aquatic bryophytes, benthic macroinvertebrates (abundance and diversity), and fish abundance (young-of-the-year and adult grayling).

Estimate whole-stream metabolism and nutrient dynamics. In recent years we have added measurements of whole-stream metabolism and 24-h, high-frequency nutrient sampling in the Kuparuk River to examine fundamental ecological functions operating on short-time scales.

Synthesize results of the long-term experimental fertilization of the Kuparuk River. The results from the groundbreaking 33-year low-level P fertilization of the Kuparuk River experiment have been summarized in several publications (Peterson et al. 1985, 1993, Slavik et al. 2004, Bowden et al. 2014). Recently we have not seen any large changes suggesting this is an appropriate time to start a new whole-river recovery experiment (stop fertilizing) that will address the role of community openness (specifically of primary producers) in the biogeochemical functions (phosphorus uptake) of stream ecosystems. In the final phase of this experiment we reintroduced phosphate to a reach of the Kuparuk River that had been fertilized for many years but was allowed to recover before we resumed fertilization. The ongoing activities we propose are to complete the analyses of this experiment and publish the results. We will follow the post-fertilization recovery process as a complement to our earlier work on stream recovery (Benstead et al. 2007, Kendrick & Huyrn 2015) and to compare with recovery work and its effects on openness being done by the Terrestrial and Lake groups. This change in effort allocation will also allow us to pursue new work on the openness and connectedness of streams and lakes described below.

New activities. Our proposed new monitoring and research activities have three objectives: (1) to stimulate further integration of our historic research on lakes and streams, (2) to extend our research into

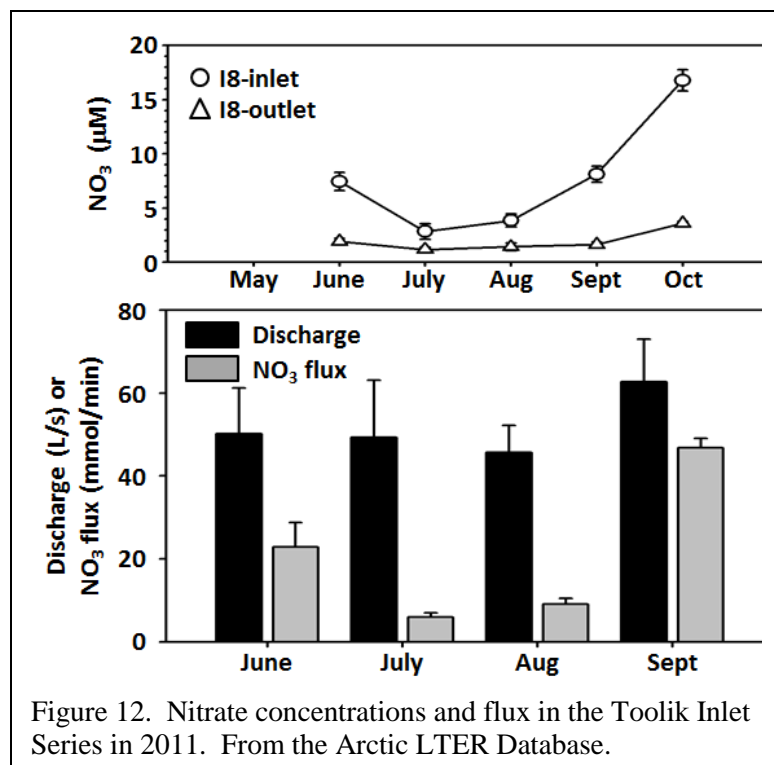


Figure 12. Nitrate concentrations and flux in the Toolik Inlet Series in 2011. From the Arctic LTER Database.

gests that despite decreasing discharge in the arctic fall, the substantial increase in nitrate concentrations results in an overall increase in nitrogen mass flux as well. We propose to increase sampling in the early spring as well as the late fall to quantify the nutrient losses during these two critical seasons that have been relatively under-studied. Ending the long-term P fertilization experiment will free resources needed to do this extended-season monitoring.

Question and Activity #2: Do Arctic grayling provide an important nutrient or energy subsidy to piscivorous fish in larger arctic lakes? We will work with the Lakes group to monitor a set of connected lake-stream systems in the Oksrukuyik watershed including the Fog lakes. We have worked in these watersheds for many years and developed a considerable body of knowledge about the hydrology, biogeochemistry, and productivity of the streams that can complement the new data collected by the Lakes group. With the Lakes group, we will monitor grayling movement between rivers and lakes using PIT tags and weirs during migrations. Where necessary we will supplement existing information about lake and stream food webs and productivity by measuring diet and stable isotope composition and the demographics of secondary consumers. We will use bioenergetics and ecological stoichiometry modeling to determine the relative contributions of in-situ versus migrating grayling to lake communities.

Question and Activity #3: How do geospatial characteristics interact with river network connectivity to influence biogeochemical and community dynamics in arctic rivers? Geospatial analyses are already a major focus of some of our previous and current research, for example the effect of landscape factors on fish distribution in lakes near Toolik (Hershey et al. 2006) and the observation of “synchrony” among connected lake and stream systems (Kling et al. 2000). In the associated ‘FISHSCAPES’ project, L. Deegan, M. Urban and colleagues are exploring how spatial river continuity affects the distribution of fish populations in the Kuparuk River and Oksrukuyik Creek. In another associated project (SCALER), W.B. Bowden and colleagues have been exploring how stream network configurations, including the influences of lakes, affect nutrient concentrations, nutrient uptake rates, and stream metabolism.

In continuing our geospatial work to examine the relationship between landscape structure (i.e., connectivity) and biogeochemical characteristics, we propose to use image resources from the Polar Geospatial Center (Univ. Minnesota) to identify times and places where hydrologic discontinuities occur. These discontinuities tend to recur in the same places, but we do not yet know the factors that combine to create

the “shoulder” seasons of early spring and especially late fall, periods that we increasingly think are important and about which we know relatively little, and (3) to increase our understanding of biogeochemical and community “connectivity” among these open, aquatic systems.

Question and Activity #1: Does the mass flux of nutrients (notably nitrogen) increase during the early autumn season? Through our current monitoring program we have observed that in late summer and early autumn there is often a substantial increase in nitrate concentrations that appears to be common among tundra and mountain streams in the Toolik area (Fig. 12). However, flux estimates are harder to determine because we have fewer discharge records after the main summer field season is over. Recent evidence sug-

these conditions. Preliminary indications suggest that this imagery could help us determine variability in landscape connectivity over space and time. This geospatial aspect of our proposed research explicitly links the efforts of the Terrestrial group to those of the Streams and Lakes groups.

Question and Activity #4: *Does the genetic composition of fish communities change over time in response to changes in connectivity among aquatic ecosystems?* Changes in the connectivity among aquatic systems will likely change the flow of genetic information as well, isolating some populations and mixing others. How altered hydrological connectivity changes biodiversity is an important question that will take a long time and considerable effort to address. In the context of this question we propose to conduct a feasibility study of using environmental DNA (eDNA) analyses (Thomsen et al. 2012, Rees et al. 2014) as a first step. We will compare current community composition against eDNA analyses and established benchmarks. LTER data taken from 1996 to 2003 for many lakes (Hershey et al. 2006, O'Brien et al. 2004) and streams (Bowden et al. 2014) near Toolik provide benchmarks from which to assess community compositional changes, but were sampled via traditional methods (i.e., nets and traps). Analysis of eDNA is a potential alternative approach to assess current and future community composition of lakes and streams. With eDNA, we might be able to determine species presence/absence for comparison to our benchmarked lakes with less effort and with better detection of rare species for which we have primers (Biggs et al. 2015, Evans et al. 2016, Kelly 2016). Samples of eDNA are obtained from filtered water and represent DNA naturally released into the environment (Takahara et al. 2013). We have access to PCR primers for key fish species in the Toolik area to test the feasibility of this approach. Using these primers, we will sample a subset of streams and lakes with traditional and eDNA techniques to compare accuracy and sensitivity (Roussel et al. 2015) prior to embarking on more extensive investigations. Advances in eDNA technology might eventually allow us to assess species abundances using either quantitative PCR (qPCR) or droplet digital PCR (ddPCR) (Doi et al. 2015). If successful, this eDNA will allow us to assess more lakes and streams more frequently and thereby enhance our ability to detect colonization and community shifts. We can also use these data to calculate similarity indices or other measures of Beta diversity to look at annual and spatial patterns of community openness.

Lakes Research:

Rationale and Background. Our first lake studies showed that strong regional variation in lake chemistry was driven by different land surface ages reflecting past glaciations (Kling et al. 1992, 2000), which emphasized the importance of landscape connectivity. But nearly all lakes in the area are extremely nutrient poor, leading to low biological production and low species diversity (e.g., Hobbie 1984, Luecke et al. 2014). Fertilization experiments of varying scale and loading rates confirmed pelagic pro-

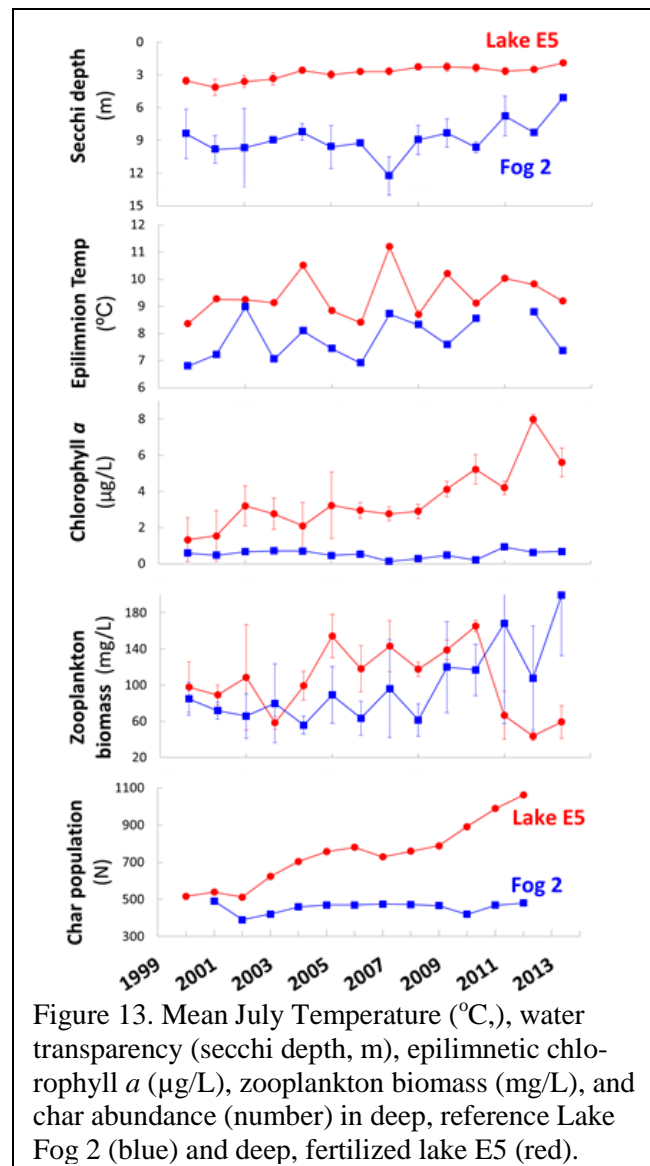
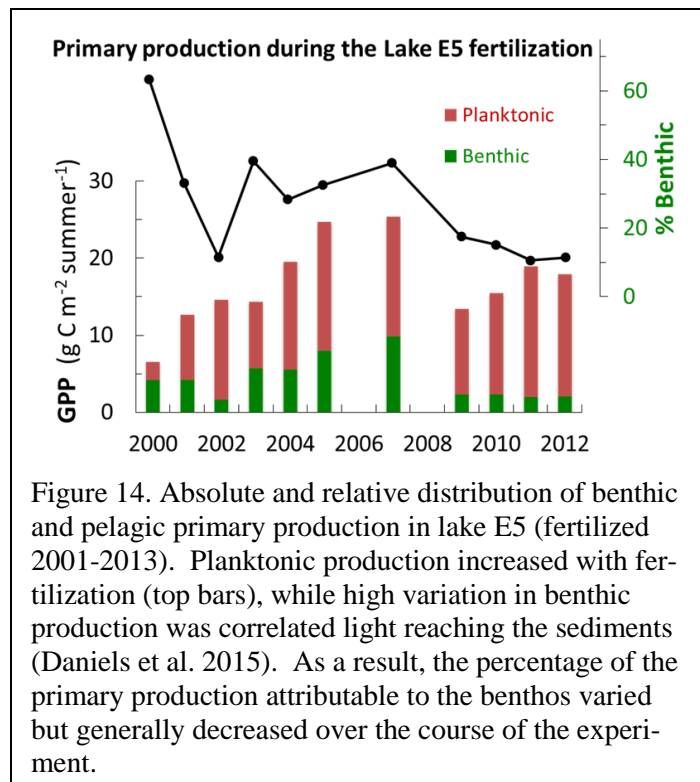


Figure 13. Mean July Temperature (°C), water transparency (secchi depth, m), epilimnetic chlorophyll *a* (µg/L), zooplankton biomass (mg/L), and char abundance (number) in deep, reference Lake Fog 2 (blue) and deep, fertilized lake E5 (red).

duction was co-limited by N and P (e.g., O'Brien et al. 1992, 2005, Levine & Whalen 2001) and benthic algal production was limited more by light (e.g., Daniels et al. 2015). However, the influence of nutrient additions and food-web manipulations on secondary producers was mixed, showing varying responses to both bottom-up and top-down controls (e.g., Hershey 1992a,b, Johnson et al. 2010). Part of this variable response is likely due to the direct impacts of climate change and disturbance on lake biogeochemical processes and food-web dynamics (e.g., Luecke et al. 2014, Budy & Luecke 2014, Daniels et al. 2015, Kling et al. 2014). However, it is also clear that changes in the hydrologic connectivity and openness of lakes to movements of materials and species across the landscape (e.g., Hershey et al. 1999, 2006) control how internal lake processes respond to climate change and disturbance. For example, increased runoff of DOC from land is causing "brownification" of many lakes (Kritzberg et al. 2014) and altering patterns of primary production and heterotrophy. Conversely, increasing intermittency of streamflow prevents fish from moving among habitats and into lakes, likely lowering fish survival (Betts & Kane 2015, Golden et al. 2015). *Our goal is to develop a predictive understanding of how the openness and connectivity of lakes controls their responses to climate change and disturbance.*

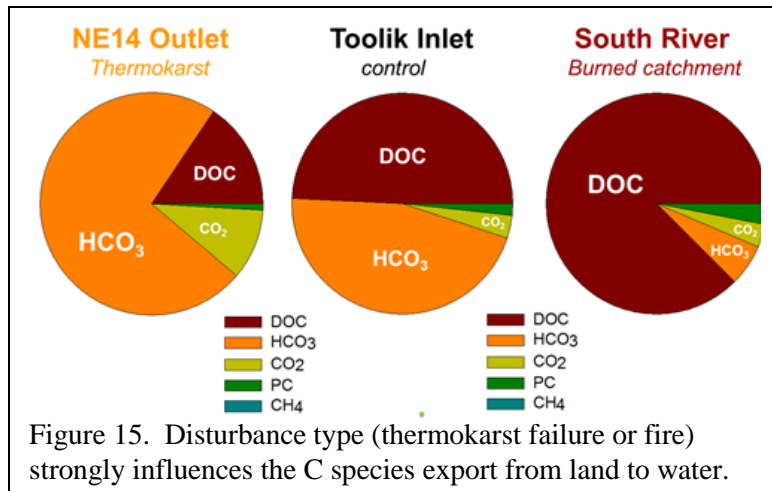
Biogeochemical openness and connectivity – Lakes with more stream inputs are more open than isolated lakes, but the impact of this biogeochemical openness on lake ecosystems is modified by seasonality in the Arctic. The majority of annual nutrient input to lakes comes from snowmelt runoff in May, but retention of these nutrients is low at that time because lakes are ice covered and the nutrients are in organic forms less available to phytoplankton (Whalen & Cornwell 1985). However, in spite of this low nutrient retention, runoff is critical because it leaves a legacy in summer and fall when productivity relies on recycling of the nutrients ultimately derived from land that were retained in the lake. The high reliance on water-column recycling in summer and fall is due to low nutrient release from very closed terrestrial systems (Whalen et al. 1988, Kling 1995), and very low or no nutrient return from lake sediments (Kipphut 1988, O'Brien et al. 2005, Gettel 2006, Luecke et al. 2014).

We mimicked long-term changes in land-to-lake connectedness with low-level fertilization experiments, designed to simulate an expected increase in nutrient export from land due to deeper soil thaw and a longer growing season (Hobbie et al. 1999). These experiments showed increased pelagic primary production but no change in benthic production, which continued to vary strongly with changes in light availability. While fertilization increased chlorophyll *a* content, zooplankton biomass, and fish abundance and biomass, lake clarity was reduced (Fig. 13), but this change in transparency was minor compared to inter-annual variation in ambient light and DOC concentrations (Daniels et al. 2015). Thus, increased biogeochemical openness of lakes is likely to increase pelagic production because of nutrient inputs, but may decrease benthic production because of elevated DOC (Fig. 14). Further, if warming is concentrated in autumn when benthic production is already light limited and when nutrients from thawing permafrost are most likely to become available, we would predict a long-term shift away from benthic and toward pelagic production (Fig. 14).



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Short-term disturbances like tundra fires and thermokarst failures can also alter



the openness of lakes by dramatically increasing land-to-lake connectivity. These terrestrial disturbances result initially in particulate C washed into surface waters, but over time they strongly affect the relative amounts of dissolved organic versus inorganic C released to surface waters (Fig. 15). Specifically, burning appears to release more organic C while thermokarst failures reach deeper into the underlying mineral soil and release more inorganic C (DIC, Fig. 15). In general, disturbance increases system openness (e.g., light, nutrients, DOC,

etc.), which should strengthen downstream connectivity. We will test this idea with experiments manipulating DOC and light input, and by monitoring the impacts of a recent thermokarst failure on Wolverine Lake, one of our long-term LTER monitoring lakes.

The response to changes in biogeochemical openness (e.g., fertilization) in our lakes was not immediately carried up the food web. Zooplankton were only able to respond to increased food availability when summer temperatures were high enough to allow for a second generation, and without passing this threshold there was no response (Budy & Luecke 2014; Fig. 13). As a result, it also took 5 years to see a consistent fish response, but then the increase was strong and continued beyond that initial threshold (Fig. 13). Thus, predicting the propagation of bottom-up nutrient responses through arctic food webs is complex even in relatively closed systems. We expect that in more open systems, the responses will be muted and only become apparent with fairly large, persistent changes in nutrient inputs. *Therefore, overall we predict that both long-term changes in climate as well as short-term disturbances will make lakes more open, lead to a shift toward more pelagic versus benthic primary production, and increased inputs and variation in solute chemistry (nutrients, DOC, DIC).*

Community openness and connectivity. Community openness and connectivity in arctic lakes varies from completely closed (isolated lakes) to extremely open (strings of lakes connected by flowing streams; Fig. 16). Our previous studies showed that lake morphometry and landscape position predict the presence or absence of fish, and provided a prediction of fish and invertebrate species composition of those lakes sampled at a coarse scale (e.g., Hershey et al. 1999). As discussed above in the Streams group section, we have tracked the large-scale movement of grayling into several lakes, where in some cases they provide an important trophic subsidy to top predators. Relative to closed lakes, lakes open to contemporary colonization and fish movement are characterized by different fish communities, trophic structures, and pathways of energy flow (biomass). Lakes with fish may be categorized as: (1) open lakes with high diversity and a common, moderately-sized top predator, (2) closed lakes with low diversity (2 fish species), population regulation by internal and density-dependent processes, and small fish body size, and (3) “leaky lakes” with intermediate diversity, unique and very large top predators, and seasonal influxes of grayling (Fig. 16). Associated with the degree of openness (quantified using a similarity index or other measure of Beta diversity), *we predict that trophic subsidies from highly mobile fish such as grayling determine, in part, the total biomass and community composition of open and leaky lakes.*

Under a warmer climate, altered stream hydrology, increased lake temperatures, and longer growing seasons will have varying effects on open versus closed lakes. Open lakes may be more resilient to climate change effects because species can move from unfavorable to favorable habitats, but that resilience requires movement corridors to remain navigable to fishes with varying movement tendencies and swimming abilities. For example, highly-mobile grayling may serve to recolonize lakes after a disturbance, and whether or not grayling are available as a trophic subsidy may determine the food-web response to

warmer lake temperatures. Fish will likely grow faster and need more food under warmer temperatures (Budy & Luecke 2014), potentially enhancing the importance of trophic subsidies from streams in open lakes. Based on our long time-series measures of fish population dynamics, we predict the relative contribution of internal regulation is much greater in closed versus open lakes. Closed lakes have strong intra-specific population cycles, cannibalism, and cohort organization (e.g., Power 1978, Finstad et al. 2006). In contrast, open systems may be buffered by immigration, emigration, and interspecific interactions and thus be more stable over time (e.g., a ‘portfolio effect’, Schindler et al. 2010). Considered collectively, these characteristics indicate that climate change and disturbance should have much more pronounced impacts on fish population structure, dynamics, and probability of persistence in closed systems relative to open systems. *We predict that open systems will have greater total fish abundance and local persistence, while closed systems will respond to change by altering species composition and life-history expression.*

Ongoing Activities. Our LTER lake research consists of long-term sampling and process-level measurements and modeling in: (1) Toolik Lake and the Inlet Series lakes (I-lakes; Fig. 1), (2) several control and experimental lakes (in recovery) sampled less frequently, plus sentinel lakes on landscapes of different ages; our monitoring of the fertilized lakes will allow us to determine how system function changes when a lake is switched from more open (nutrients added) to more closed (nutrient addition stopped), (3) periodic and opportunistic sampling of lakes undergoing change due to disturbance (e.g., fire and thermo-karst), and (4) lakes added to address New Activities described below.

Long-term measurements include a complete suite of physical and chemical parameters, chlorophyll a, and zooplankton. In many lakes we also measure pelagic and benthic primary production and sample microzooplankton, bacteria, and benthic invertebrates. Long-term monitoring of fish communities includes comprehensive mark-recapture studies, associated annual measurements of vital rates (e.g., growth, survival, condition), and estimates of population trends. On a subsample of fish, we also measure diet, analyze trophic position and pelagic versus littoral contributions to diet using isotopes, and age fish using otoliths. These long-term data are critical for understanding the effects of interannual variation and long-term changes in arctic lakes, for example, by synthesizing information on fish growth or pelagic ver-

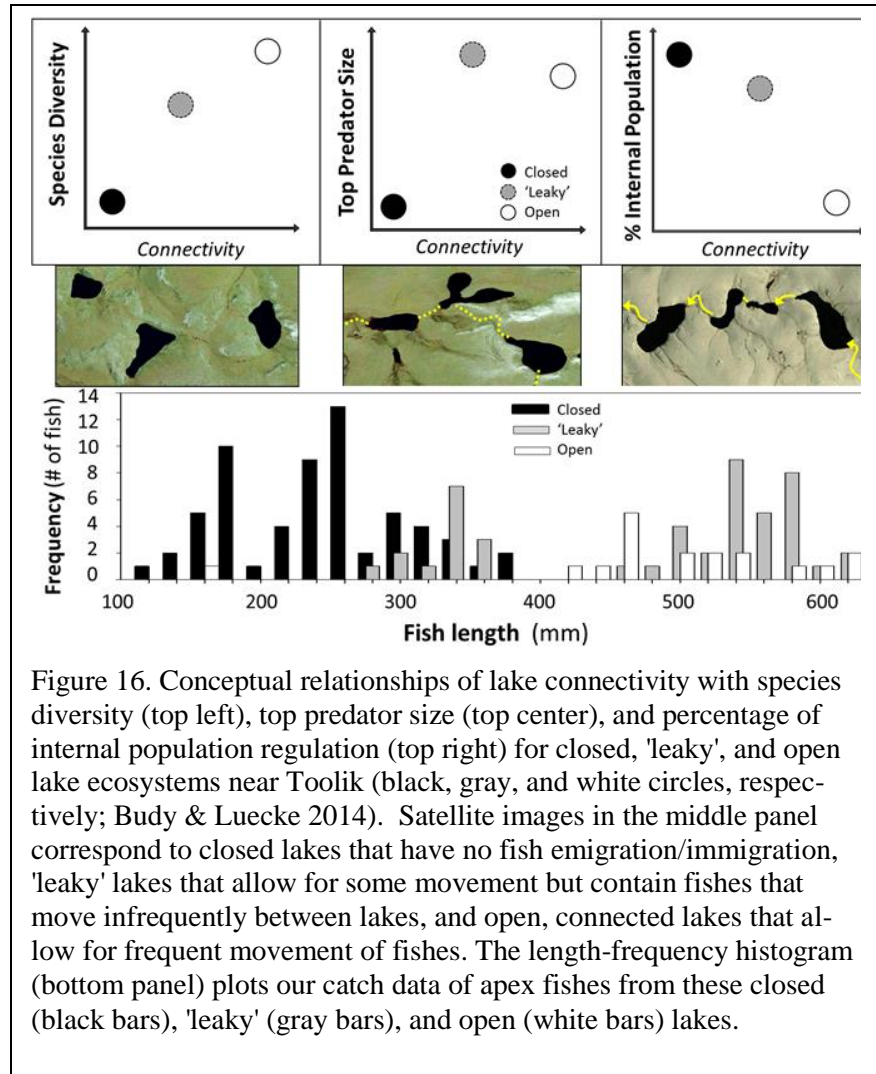


Figure 16. Conceptual relationships of lake connectivity with species diversity (top left), top predator size (top center), and percentage of internal population regulation (top right) for closed, 'leaky', and open lake ecosystems near Toolik (black, gray, and white circles, respectively; Budy & Luecke 2014). Satellite images in the middle panel correspond to closed lakes that have no fish emigration/immigration, 'leaky' lakes that allow for some movement but contain fishes that move infrequently between lakes, and open, connected lakes that allow for frequent movement of fishes. The length-frequency histogram (bottom panel) plots our catch data of apex fishes from these closed (black bars), 'leaky' (gray bars), and open (white bars) lakes.

sus benthic productivity in warm and cold years. Finally, tracking parallel efforts by the Streams group, we propose to increase focus of on-going and future research on late summer and early fall, which is the time period that climate warming is predicted to have the greatest effect on lakes.

New Activities. In this renewal proposal we will focus on two new inter-related research activities linked to the core proposal questions, one focused on biogeochemical openness and one focused on the effects of connectivity on aquatic community structure and function. We will answer these questions in part on a new comparison of four lakes; two very closed lakes (Fog lakes) relative to two very open and connected lakes (I-lakes; Fig. 1). Both sets of lakes have been part of our long-term sampling. The Fog lakes are isolated, on a younger-aged surface, have low watershed inputs and DOC concentrations, and have a closed, char-dominated community common in isolated lakes (Budy & Luecke 2014). The I-lakes are highly inter-connected and DOC rich, and have diverse and more mobile, grayling-dominated (with lake trout) communities common in connected systems (see Streams section; Kling et al. 1992).

Question and Activity #1. *How will the relative openness of lakes determine the biogeochemical response to climate change and disturbance?* We will answer this question with experiments on nutrient versus DOC inputs controlling productivity, and by using our long-term data to construct nutrient and C budgets for lakes that vary in their openness and location on different-aged surfaces (i.e., surrounded by key vegetation types, see Terrestrial section).

First, the in-situ experiments will shade part of the benthic zone to decouple the impact of DOC on reducing light to the bottom from the possible role of DOC supporting bacterial respiration and releasing nutrients, or UV light converting DOC into ammonium (see Landscape Interactions section). Shade cloth will be placed 1 m off the bottom to shade an area of 5 m² in each of the four lakes. Three times each summer we will remove the cloth, take sediment cores, and compare the benthic primary production and sediment chlorophyll concentrations to nearby unshaded areas of the same depth. To evaluate the importance of DOC mineralization providing nutrients supporting pelagic production, we will measure primary production in limnocorrals with the following treatments (and appropriate controls): (1) DOC added, (2) shielded from UV but not PAR using plastic screening, (2) inorganic nutrient additions, and (3) nutrients plus UV shielding.

Second, we will target five lakes for more intensive study on element budgets, including Toolik plus two Fog lakes and two I-lakes of similar depths (Fig. 1). New activities will focus on understanding how warm and cold years differ in (1) nutrient inputs and retention, (2) the balance of benthic and pelagic production (Fig. 13), and (3) carbon (inorganic and organic) inputs, sediment respiration, burial, and export (studied together the Landscape Interactions group). A special emphasis will be put on late-season (Sept. – Oct.) processes, which have only recently received attention due to logistical constraints. We predict primary production will respond more strongly to inter-annual differences in temperature in the closed Fog lakes where production is more dependent on internal nutrient recycling, and in the open I-lakes production will respond more to variation in precipitation and runoff that alters inputs of nutrients and DOC. To test these predictions, we will collect the full suite of physical, chemical and biological data described above at 7-10 day intervals through the growing season until ice up.

Question and Activity #2. *How will closed (isolated) versus open (connected) lakes differ in trophic structure and species composition and in their response to disturbance?* To answer this question we will rely on the Fog lakes and I-lakes (closed vs. open comparison) and use (1) long-term monitoring of fish growth and vital rates, (2) measurements of trophic subsidies and ecology (diets, isotopes), and (3) a whole-lake manipulation (only in Years 4-6). We will continue our routine LTER sampling in the Fog lakes and will initiate fish sampling in the I-lakes. After collecting pre-manipulation data, in year 4 we will block fish movement in and out of an open I-lake and add grayling and lake trout to a closed Fog lake. In the short term we will monitor trophic changes, vital rates, and relative abundance and biomass, and in the longer term we will monitor population size-structure cycles and trends (Budy & Luecke 2014).

We will also work closely with the Streams group and expand our trophic sampling into the Oksrukuyik lakes (these are “leaky lakes” as described above), as well as gather new information on spe-

cies diversity using eDNA techniques (*see Streams section*) that will assist in quantifying community openness. The recent discovery of very large Arctic char in the Oksrukuyik lakes (2-fold larger than in closed lakes) strongly suggests they are using grayling as a trophic subsidy; however, the timing and mechanisms of this subsidy are unknown. In the Oksrukuyik basin the Streams group will tag and monitor grayling and monitor movement in streams and in and out of lakes, while the Lakes group will determine the contribution of grayling to predator diets, determine the source of grayling consumed, and quantify tagged, stream grayling mortality due to lake predation. As discussed above, the trophic structure (e.g., food web assembly, food chain length) and energetic demand are predicted to be strongly determined by lake openness, a feature which is predicted to change in a warmer climate (e.g., lake temperatures, growing season, connectivity, and timing of grayling migration).

Landscape Interactions Research:

Rationale and Background. Our “Landscape Interactions” research focuses on how inputs of materials and species from upland or upstream systems (land to streams, streams to and from lakes) affect downstream ecosystem structure and function. The hydrologic catchment provides a framework for studying biogeochemical exchanges among ecosystems (e.g., Likens et al. 1967, Bormann et al. 1974), yet it is challenging to quantify the downslope flow of materials and species, relate them back to the structure and function of the upstream system, and assess the consequences on downstream systems. To study these complex interactions we examine the controls on production of dissolved C, N, and P on land (e.g., Giblin et al. 1991, Judd & Kling 2002, Judd et al. 2007), and how hydrological and biological processing exert a strong control on materials moving downslope (e.g., Stieglitz et al. 2000, Rastetter et al. 2004, McNamara et al. 2008), including the processing of materials in surface waters (e.g., Merck et al. 2011, Cory et al. 2014, 2015). Disturbances such as thermokarst failures, and interactions among ecosystems on the landscape such as land-stream-lake transfers of materials or species, can also strongly modify ecosystem function (e.g., Kling et al. 2000, Crump et al. 2007, 2012, Cory et al. 2013). Here we describe our main findings and future research within the framework of the biogeochemical and community openness and connectedness of the arctic system.

Biogeochemical Openness and Connectivity. Our LTER research in landscape interactions initially focused on C cycling. We found that C loss from land was $\sim 4 \text{ g C m}^{-2}$ of land surface per year, $2/3^{\text{rd}}$ as DOC and $1/3^{\text{rd}}$ as CO_2 and CH_4 subsequently released from surface waters to the atmosphere (Kling et al. 1991, 1992). The release of C to the atmosphere from all inland waters has a substantial impact on the global C cycle (“Evasion” on Fig. 17, Kling et al. 1991, Cole et al. 1994), and is driven by the large flux of C from land to water (2.7 Pg y^{-1} , red circle in Fig 16). This nexus of C exported from land, processed in surface waters, then released to the atmosphere is especially important in the Arctic, where current warming of permafrost soils can move huge amounts of “newly-thawed” C from land to the atmosphere as CO_2 on short timescales, thus providing a fast, positive reinforcement for global warming (e.g., MacDougall et al. 2012). Thus, although terrestrial ecosystems are fairly closed to C losses, the cumulative losses over vast areas are large, resulting in a strong connectivity from terrestrial to aquatic systems, and from aquatic systems releasing CO_2 to the atmosphere.

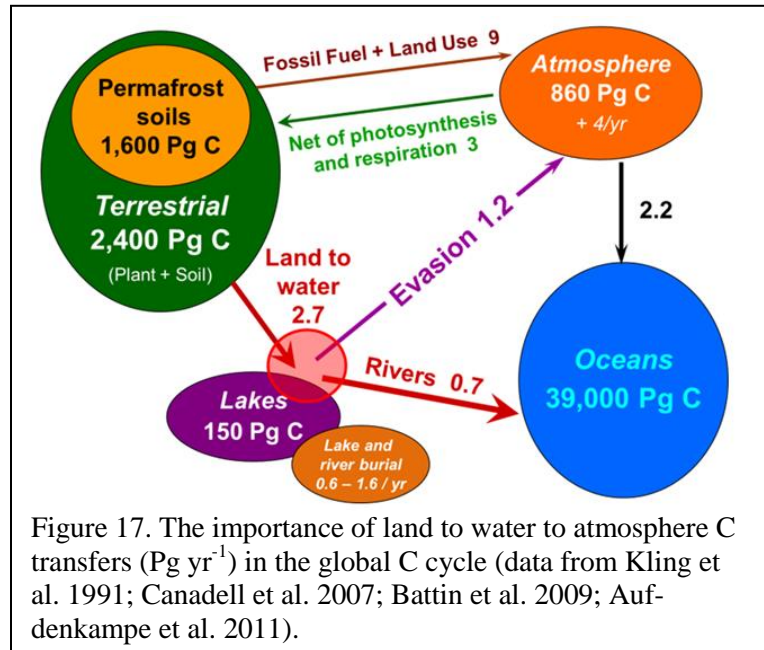


Figure 17. The importance of land to water to atmosphere C transfers (Pg yr^{-1}) in the global C cycle (data from Kling et al. 1991; Canadell et al. 2007; Battin et al. 2009; Aufdenkampe et al. 2011).

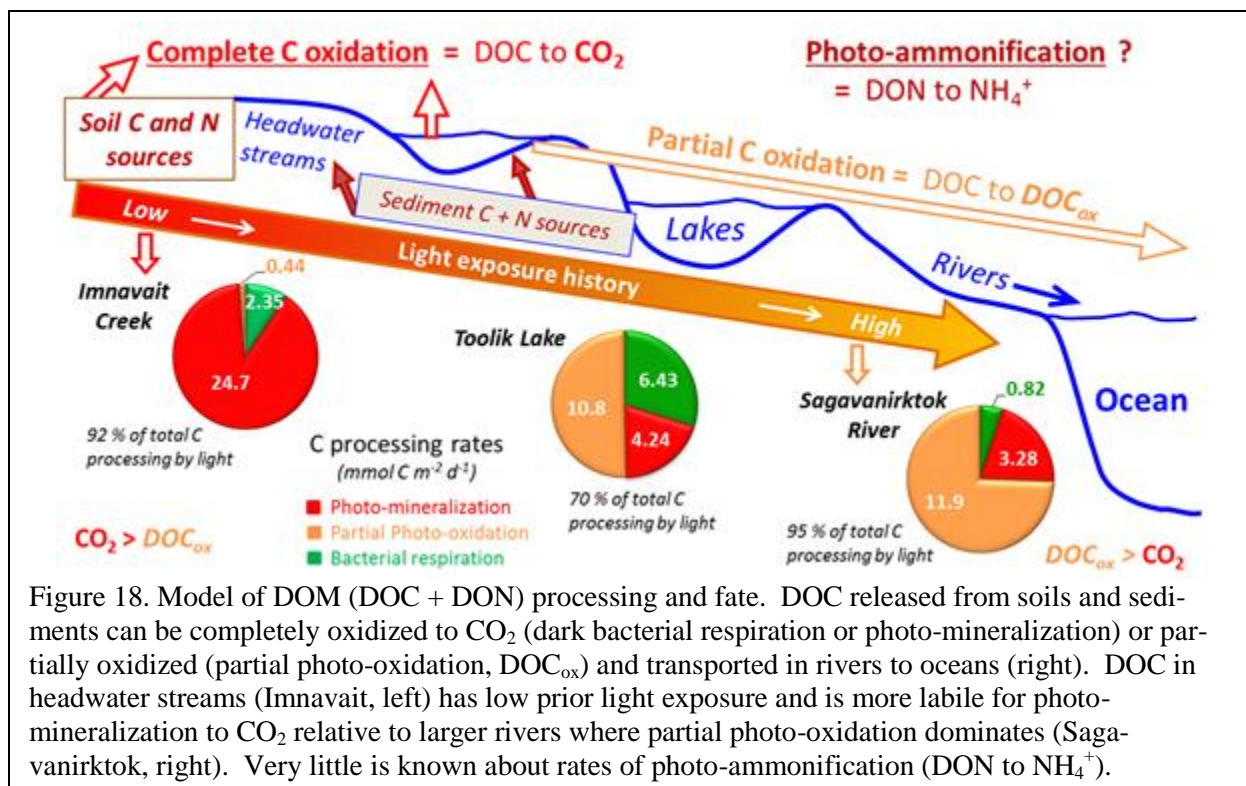


Figure 18. Model of DOM (DOC + DON) processing and fate. DOC released from soils and sediments can be completely oxidized to CO₂ (dark bacterial respiration or photo-mineralization) or partially oxidized (partial photo-oxidation, DOC_{ox}) and transported in rivers to oceans (right). DOC in headwater streams (Imnavait, left) has low prior light exposure and is more labile for photo-mineralization to CO₂ relative to larger rivers where partial photo-oxidation dominates (Sagavanirktok, right). Very little is known about rates of photo-ammonification (DON to NH₄⁺).

Overall, we have *three main findings* on controls of ecosystem connectedness at this nexus of material exported from land and processed in aquatic systems. First, we found that DOC from formerly frozen soils (“permafrost C”) released during thermokarst failures was labile to bacterial oxidation, but was 40% more labile when first exposed to sunlight (Cory et al. 2013). Second, we found that, contrary to expectations, photochemical oxidation of DOC dominated over bacterial oxidation (respiration) in the water column of lakes and streams, and 83% of total DOC processing was by photochemistry (Cory et al. 2014). Essentially sunlight is “outcompeting” bacteria for labile DOC substrates that can be oxidized partially to a degraded form of DOC and moved downstream, or oxidized fully to CO₂ (“photo-mineralization”) and released to the atmosphere. Our conceptual model of the integrated photo-bio degradation of dissolved organic matter (DOM) in lakes and streams suggests that the amount of prior light exposure is critical in determining the relative importance of partial or complete oxidation of DOM (Fig. 18, Cory et al. 2014). This model also highlights three potential controls we know too little about: (1) the DOM degradation in lake and stream sediments, (2) the photo-degradation of DON to NH₄⁺ (photo-ammonification), which could have major implications for N budgets given how closed terrestrial systems are with respect to N cycling and how dependent aquatic systems are on the cumulative N losses from the catchment, and (3) the hydrological connection and processing of DOM at the land-water interface (the riparian zone) where soil waters first see light. In our new activities we will work with the Streams and Lakes groups to measure sediment contributions to landscape C cycling, to determine photo-ammonification rates in surface waters, and to better characterize the connectedness of hydrological and biogeochemical processes at the land-water interfaces in streams and lakes.

Using our long-term data, the third finding on the controls of ecosystem connectivity shows 40 years of geochemical change in Toolik Lake (Fig. 19, and similar responses in other lakes). It is clear that changes on land release inorganic as well as organic C, and the observed increase in alkalinity results from rock weathering in the catchment (Keller et al. 2007, 2010). But this dramatic change has occurred despite the lack of a detectable increase in air temperature (Fig. 19 top), and a lack of detectable increases in lake water temperature or mean catchment thaw depth (Kling et al. 2014). What we *have* found is a correlation between the alkalinity increase and an increase in the permafrost temperature measured in

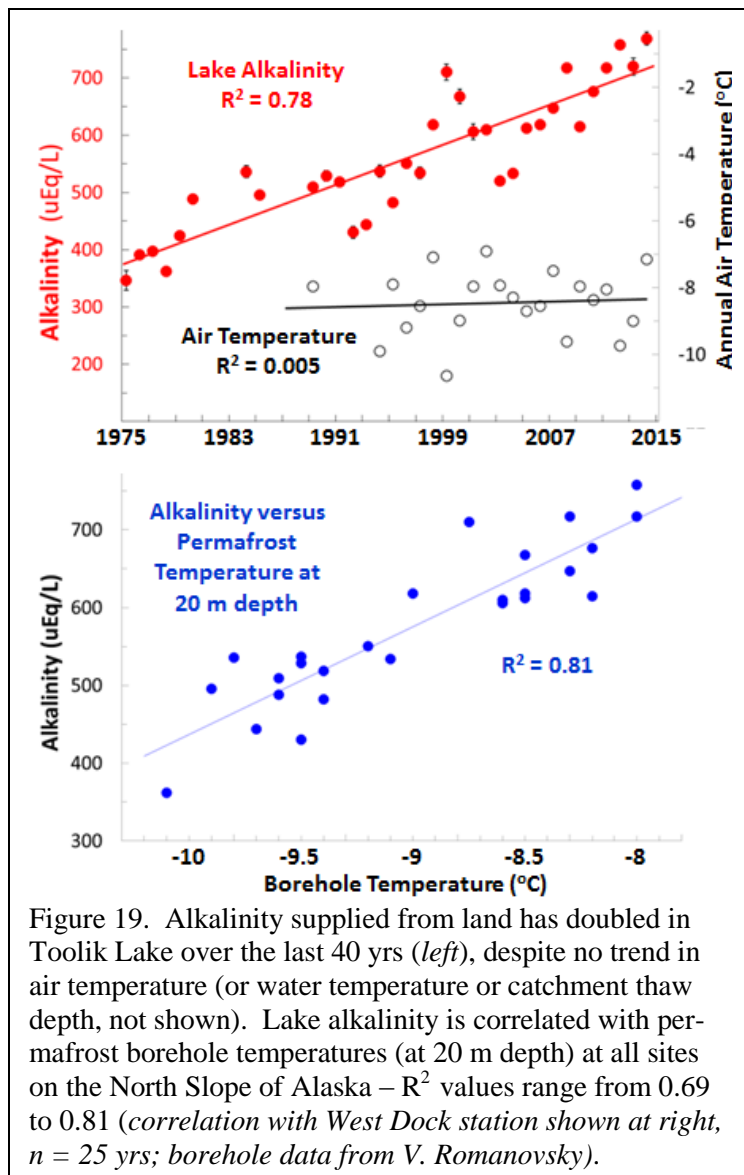


Figure 19. Alkalinity supplied from land has doubled in Toolik Lake over the last 40 yrs (*left*), despite no trend in air temperature (or water temperature or catchment thaw depth, not shown). Lake alkalinity is correlated with permafrost borehole temperatures (at 20 m depth) at all sites on the North Slope of Alaska – R^2 values range from 0.69 to 0.81 (*correlation with West Dock station shown at right, $n = 25$ yrs; borehole data from V. Romanovsky*).

boreholes at 20 m depth (Fig. 19 *bottom*). Given that there has been no detectable change in factors that drive weathering including air and water temperature, thaw depth, and precipitation (not shown), our measurements would have failed to predict the dramatic geochemical changes in Toolik Lake. Clearly this land-water system has high biogeochemical connectivity, and the openness of the aquatic systems make them vulnerable to change. But, the specific ecosystem stressors causing change are either hidden from our observational capabilities or as yet undiscovered. One hypothesis is that these changes are integrating the effects of the climate signal on multi-year to decadal time scales; that is, they act as a medium-pass filter that reduces the signal variability yet allows the effects of long-term warming to emerge, as seen in the alkalinity and permafrost temperature records. It will be useful to test and apply this idea of a medium-pass filter to identify, or devise, other long-term data sets that will detect early climate warming signals in other ecosystems (Hobbie et al. *submitted*).

Community Openness and Connectivity. In studying the ‘Inlet Series’ of streams and lakes (the I-Lakes) feeding Toolik Lake, we showed that landscape-level connections among terrestrial, stream, and lake ecosystems affect patterns of chemistry and biology among sites (Kling et al. 2000, Crump et al.

2007), and we found that downslope transport and inoculation of soil bacteria strongly influence stream and lake microbial community composition (Crump et al. 2012, Adams et al. 2014, 2015). In other words, there is surprising openness of the microbial community and high “community connectivity” moving downslope across the landscape, and the genomics of microbes indicate that many bacteria and Archaea species (OTUs) found in Toolik Lake were initially observed in upland soils and small headwater streams (Crump et al. 2012). For example, in Toolik Lake 58% of the bacterial taxa and 43% of the archaeal taxa were first observed in upland habitats, and the 39 most common species of these groups in Toolik Lake were also found higher on the landscape in the soils or headwater stream. Because most of these common taxa in the lake were classified as “rare” in upslope environments (<0.1% of sequences), it is clear that the rare taxa transferred into the lake must undergo species sorting processes (e.g., competition and predation) in order to form the resultant lake community. These results suggest that terrestrial environments serve as critical reservoirs of microbial diversity, and that the patterns of diversity in surface waters are structured by initial inoculation from upslope habitats. However, we also found that larger, eukaryotic organisms were less likely to originate or be found first in upslope waters, and were more likely to be specific to the lake or stream environment where they were dominant (Crump et al. 2012). Thus, the degree of microbial community openness and landscape connectedness may vary by habitat, or

by typical organism size. One implication of our findings is that environmental changes on land (e.g., permafrost thaw from climate warming) that affect microbes will propagate to surface waters, and understanding freshwater microbial diversity and dynamics must include the study of diversity and dispersal of terrestrial communities. *We will next study the activity and “function” of these taxa across the landscape continuum using metagenomic approaches in order to test whether this community openness translates into functional importance for ecosystem processes (e.g., metabolism of DOC and DON), or if the openness is mainly a passive transfer of inactive microbial species.*

Ongoing Activities. In support of the continuing and new questions derived from prior results, we will continue the long-term monitoring needed to understand the processes that control current and future changes in the Arctic, especially with respect to the biogeochemical and community openness and connectedness and the role this plays in system function. Specifically, our ongoing activities and locations, many shared with other ARC-LTER groups, include:

Thaw depth measurements. We will continue to characterize permafrost thaw at Toolik and in the Imnavait basin.

Monitor chemical budgets. We will continue to monitor changes in chemical budgets in Toolik Lake and the Inlet Series lakes in its catchment, and in Wolverine Lake (a recent thermokarst site) jointly with Lakes group. We will continue working with a funded project (R. Cory, NSF) to integrate measures of DOM photo-degradation with microbial activity.

Monitor microbial species distribution and movement on the landscape. We will continue measurements on the Toolik ‘Inlet Series’ of lakes and streams microbial species distribution and movement on the landscape. Note that to free-up resources for new activities, we will reduce our chemical and microbial monitoring frequency of the entire Inlet Series by one third (still providing the necessary long-term data), and drop our monitoring of Lake NE14 (an old thermokarst disturbance site).

Catchment C balance. We will continue to collect data to determine the catchment C balance in Imnavait Creek (in conjunction with terrestrial projects), including investigations of the chemistry of soil waters in the Terrestrial group’s experimental plots, and the hydrological connectivity and C degradation by microbes and photochemistry in the critical riparian zone connecting soil waters to the stream.

New Activities. We have four new questions to answer with new research activities in this proposal:

Question and Activity #1. *What is the biogeochemical openness of lake and stream sediments for C?* We know that lake sediments in the Toolik region are ‘closed’ with respect to N and P (minor N flux and no P flux from the sediments, Luecke et al. 2014), but we have few direct measurements of CO₂ fluxes in either lake or stream sediments. Measurements of inorganic and organic C inputs to and returns from sediments including whole-stream metabolism studies, on time scales similar to concurrent measures of photo-bio degradation of DOM, will be made in Toolik Lake, Imnavait Creek, and selected lakes and streams of the Toolik Inlet Series in coordination with the Lakes and Streams groups. This research will contribute the last piece needed to construct landscape-level C balances (terrestrial plants, soil waters, sediments, and surface waters, Fig. 18) and to allow predictions of how the tundra C balance might change given future warming and permafrost thaw.

Question and Activity #2. *How important for N cycling is the photo-production of NH₄⁺ from DOM?* Exposing DOM to UV light can produce NH₄⁺ (Bushaw et al. 1996, Mopper & Kieber 2002), which can contribute substantially to the inorganic N required by microbes and algae in surface waters (Smith & Benner 2005, Vähätalo & Zepp 2005). In contrast to the relatively open C cycles in arctic ecosystems, plants and microbes on land are extremely N limited (Shaver et al. 2014), resulting in a closed N cycle, very low connectedness and inorganic N loss, and N limitation in surface waters. Yet the DON concentrations in soils and surface waters are relatively high (Hobbie & Kling 2014), creating the opportunity for photo-ammonification to ‘open’ the N cycle and help alleviate N-limitation in aquatic ecosystems. We will test this idea by measuring photo-ammonification rates concurrently with our DOM photo-bio degradation experiments, and during the Lakes group experiments on benthic shading (lowering UV).

Question and Activity #3. *How is the genomic potential and metabolic functioning of microbial communities altered as species move from soils to streams to lakes?* This research will be done in the

Inlet Series of lakes and streams, and will use genomics approaches to test whether the openness of microbial species moving from soils to streams to lakes is merely a passive transfer, or if this community openness translates into functional importance in terms of ecosystem processes and especially the metabolism of dissolved organic matter (DOM) to produce inorganic C, N, and P. We will experimentally alter environmental conditions to replicate moving between ecosystems (e.g., different DOC character in soil water compared to stream water), and measure the metatranscriptomic response to assess which species respond. These experiments will also allow us to measure the similarity of microbial communities among ecosystems (e.g., Crump et al. 2012) as an index of community openness. Our sampling will be coordinated with the eDNA sampling of the Streams and Lakes groups.

Question and Activity #4. *How will altered DOM flux from riparian zones affect aquatic C and N processing?* Hydrology drives the flux of DOM across the land-water riparian interface, and we will continue to collaborate with hydrology modelers studying this flux (e.g., Merck et al. 2011, Cory et al. 2015). We will also measure soil water nutrients in newly-established terrestrial plots (see Terrestrial Section) to improve our measures of downslope C and N transport. In addition, given the importance of sunlight and light history in DOM degradation on the landscape (Fig. 18), and the fact that DOM in surface waters is both absorbing light and acting as a “substrate” for CO₂ or NH₄⁺ production, we will determine the relative balance of light and substrate availability. We propose that the amount and lability of colored DOM (CDOM) entering surface waters from the riparian zone, and the subsequent light attenuation by CDOM, control DOM degradation.

Specifically, high CDOM concentrations attenuate the available light at a shallower depth, but result in no change or an increase in the overall amount of light absorption in the entire water column (Cory et al. 2015). If CDOM leached from soils increases (a more open terrestrial system), then there is more CDOM than can be degraded by the available light and photo-degradation rates in the water column are more likely to be “light-limited” (*left side of Fig. 20*). On the other hand, if riparian inputs of CDOM are low (a more closed terrestrial system), then there is enough light to degrade the CDOM and photo-degradation is more likely to be “substrate-limited”. When photo-degradation is substrate limited, even a short exposure to UV will cause rapid photo-degradation, and thus exposing more DOM even over short residence times increases the overall photo-degradation (*right side of Fig. 20*). The lability of DOM to photo-degradation also acts as a control on processing rates (*solid versus dashed line in Fig. 20*), and at the scale of a stream reach or catchment the hydrologic residence time affects the total amount of UV exposure. In a range of our currently monitored sites, we will test whether photo-degradation in surface waters is limited by light or substrate, and relate that limitation to potential changes in the response of terrestrial systems (more open or more closed) to climate warming, permafrost thaw and deeper hydrological flow paths, or thermokarst failures.

Models in Support of ARC-LTER Research:

Models have served and will continue to serve several important roles in the ARC LTER: (1) examine theoretical constraints on biogeochemistry and community structure (Rastetter et al. 1992, 1997a, 2005,

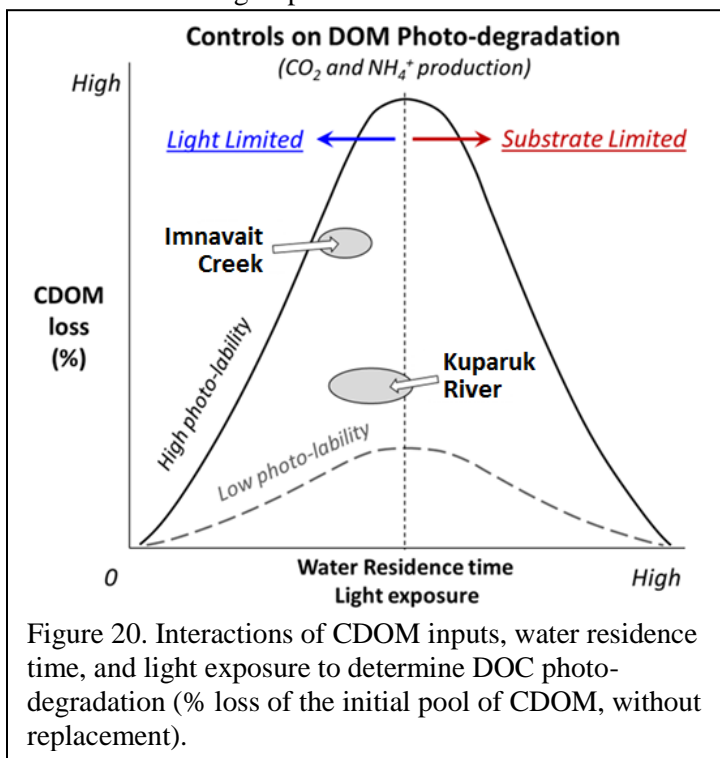


Figure 20. Interactions of CDOM inputs, water residence time, and light exposure to determine DOC photo-degradation (% loss of the initial pool of CDOM, without replacement).

Rastetter & Shaver 1992, Moorhead et al. 1999, Herbert et al. 1999, 2004, Rastetter & Agren 2002); (2) compare canopy function among arctic tundra types and link that analysis to eddy covariance data (Williams et al. 2000, Shaver et al. 2007, Rastetter et al. 2010); (3) analyze effects of primary productivity on trophic structure (Moore et al. 2005, de Ruiter et al. 2005, Moore & de Ruiter 2012); (4) analyze hydrological and biogeochemical connectivity on arctic hillslopes (Stieglitz et al. 1999, Rastetter et al. 2004); (5) integrate ARC LTER results to assess responses to climate change (Rastetter et al. 1991, 1997b, McKane et al. 1997a&b, Clein et al. 2000, Sistla et al. 2014); (6) extrapolate biogeochemical properties of ecosystems regionally (Hobbie et al. 1998, Williams et al. 2001, Le Dizes et al. 2003, Jiang et al. 2015b); (7) predict fish bioenergetic responses to climate change at the individual and population levels (Budy & Luecke 2014), and (8) simulate recovery from disturbance (Pearce et al. 2015, Jiang et al. 2015a, Kranabetter et al. in press).

We will continue to use models to guide and synthesize our research, test hypotheses, make predictions, and to assess uncertainty. The assessment of uncertainty is particularly important. O'Neill (1973) identified two sources of model uncertainty, "systematic bias" associated with under-representing underlying mechanisms and "measurement error" associated with parameter estimation. Both are exacerbated by extrapolation into an unknown future (Rastetter 1996). The dominance of one or the other of these error sources depends on the model and its application. For example, *to assess the parameter error*, Shaver et al. (2013) calibrated the PLIRTLE model, a model of net ecosystem CO₂ exchange with the atmosphere, to each of five sites across the Arctic and tested the calibrations on the other four sites; all calibrations worked equally well and provided the same uncertainty estimate on all sites, indicating a robust calibration and remarkable convergence of function across the Arctic. *To assess the systematic bias*, Rastetter et al. (2010) embedded PLIRTLE in an Ensemble Kalman Filter (EnKF) and applied it to eddy covariance data. The EnKF generated confidence intervals around the eddy covariance time series, and by incorporating an auxiliary variable in the EnKF, they identified a structural deficiency likely associated with afternoon stomatal closure not being incorporated in the model. In some cases uncertainty is so large that *the main aim of modeling is heuristic* (Oreskes et al. 1994). This uncertainty must nevertheless be assessed. For example, Pearce et al. (2015) simulated a wide range of conditions and rates to bracket the range of recovery responses of tundra to thermokarst erosion. Although the range of simulated responses precludes any accurate prediction of the true response, they provide heuristic value for interpreting observed recoveries and for guiding future research.

Related Research Projects:

The ARC LTER has a long history of attracting complementary projects to Toolik. Funding for these projects varies greatly from year to year. In the past, total funding for all collaborating projects has averaged between \$4-8M per year. Most of these complementary projects are funded through NSF, supported by the NSF-GEO Polar Programs and the Division of Environmental Biology; in recent years a number of NASA projects have begun working at Toolik Lake with the ARC LTER. More importantly, though, these complementary projects greatly extend the intellectual significance and applications of LTER research; they contribute additional context and greatly enhance the value of LTER data and knowledge. Most of these projects use the ARC LTER data base as a repository for their data. Thus, not only does the LTER leverage its monetary investment by attracting a 3- to 6-fold increase in research dollars, it also greatly leverages its knowledge base.

In the past a broad array of collaborations with complementary research projects enhanced the LTER's overall productivity and impact, and we welcome such collaborations in the future. None of these collaborations, however, are essential to completion of the specific work of data collection, experimentation, and monitoring proposed here. The core project objectives are to be met using core project resources.

Summary, Intellectual Contributions, and Links to Conceptual Framework:

Our goal for ARC LTER 2017-2023 is to use the concepts of biogeochemical and community openness, and landscape connectivity to develop a predictive understanding of how arctic landscapes respond to climate change and disturbances like wildfire and thermokarst failures. The Arctic is one of the fastest warming regions on earth and, in northern Alaska at least, there is evidence that the frequency of wild fire

and perhaps of thermokarst failures is increasing. Both warming and disturbance have the potential to mobilize globally important stores of C currently sequestered in permafrost. It is less clear how arctic ecosystems will respond to these environmental changes and the role they will play in mitigating the effects of climate warming, in retaining C and nutrients on the landscape, or in releasing C to the atmosphere and transporting C and nutrients through the landscape from land to streams and lakes and ultimately to the Arctic Ocean. Key to understanding this role is an assessment of the openness of arctic ecosystems of all types, and the connectivity among these ecosystems across arctic landscapes.

Biogeochemical openness is a measure of ecosystem dependence on external sources of nutrients and organic C relative to its dependence on internally recycled nutrients and autochthonous organic C; as described above, openness can be calculated directly from the nutrient and C budgets of an ecosystem. We already know a great deal about the budget pieces and will compile full budgets for representative examples of all the major ecosystems near Toolik. We also continue to collect data on how these budgets change in response to climate warming, disturbance, and experiments designed to uncover mechanisms of response to changes in climate and disturbance. As a result of our work over the next six years, we will calculate indices of biogeochemical openness (e.g., ratio of input to recycling rates) for each ecosystem type in our study area and relate openness to the magnitude of response to climate warming and the rate of recovery from disturbance. For example, we will complete measurements of carbon (DOC, DIC) inputs and outputs on the tundra by combining the components of terrestrial and surface water fluxes and including key new measurements of C fluxes in aquatic sediments. From these joint terrestrial, stream, and lake investigations we can calculate the C openness and connectivity for any system on the landscape.

Community openness is a measure of how readily organisms move in and out of an ecosystem and how readily new species can colonize the ecosystem in response to a change in the environment. We know a great deal about openness for key components of the terrestrial and aquatic communities we have intensively studied. We continue to study the role of migrating organisms and species colonization in the response of arctic ecosystems to warming and disturbance and, as described above, will quantify community openness for key groups of taxa (e.g., vascular plants, microbes, and fish). As boreal taxa move north into the Arctic, assessing community openness will be an increasingly important part of our long-term research. Based on past research and our work over the next six years, we will quantify community openness for each ecosystem type on the landscape around Toolik Lake and relate openness to the magnitude of response to climate warming and the rate of recovery from disturbance. Meeting this objective will require quantification and comparisons of species and trophic composition, turnover, and connectedness in contrasting systems. These descriptions and comparisons will be important products in themselves as well as being essential to testing core project questions.

Landscape connectivity is a measure of interdependence among ecosystems on the landscape based on the movement of C, nutrients, organisms, and species. Connectivity relates to both the magnitude of the exchanges among ecosystems and to the arrangement of these ecosystems on the landscape. Connectivity is closely related to openness, but the two are not the same. For example, terrestrial ecosystems in a catchment that are biogeochemically nearly closed can be strongly connected to the stream by virtue of their cumulative losses of nutrients and C to the stream. As a result of our work over the next six years, we will assess the importance of both biogeochemical and community connectivity in the arctic landscape, relate that connectivity to the magnitude of response of different ecosystems to climate warming and to the rate of recovery from disturbance, and estimate catchment-scale budgets of C, N, and P.

Broader Impacts:

Intellectual contributions. The Arctic is one of the fastest warming regions on Earth and serves as a harbinger of future changes in other ecosystems around the world, as a globally important biome deserving study in its own right, and as a potential accelerator of climate warming as permafrost thaws. The objectives of the Arctic Long-Term Ecological Research (LTER) Project for 2017-2023 are to develop a better predictive understanding of the responses of arctic terrestrial and freshwater ecosystems to climate change and climate-induced disturbances such as more frequent wildfires and thermokarst failures. The

research is organized around the concepts of biogeochemical and community “openness” and landscape “connectivity” as described above in our **Conceptual Framework**. The proposed research will compare key component ecosystems of the arctic landscape to determine if their degree of openness and connectivity governs their responses to climate change and acute disturbance such as fire and surface slumping associated with permafrost thaw. The concepts and methods developed here will have broad application to other biomes and landscapes, and the results will be disseminated through continuation of the excellent history of publication and data sharing by the ARC LTER.

Education and outreach. The ARC LTER project will continue to maintain all parts of its current education and outreach program as described in the “Previous Research” section of this proposal. Each component of this program is selected to optimize the particular education opportunities available to this project and its institutional resources. With a few carefully-selected activities, our strategy is to reach a diverse audience ranging from kindergarten through graduate students to K-12 teachers, the general public, and governmental and scientific planning agencies. Core LTER funding is used to support the REU students (two students each summer) and our Schoolyard activities in Barrow; the other activities are independently funded but receive support from the ARC LTER by providing access to our field sites, laboratories, and data base, and through the unreimbursed participation of ARC investigators, students, or RAs. We also provide small subsidies from LTER research or supplemental funds for travel and logistics costs of participation in these activities. **Anticipated changes, 2017-2023:** Overall, we believe our education and outreach program has been well received and we expect to continue all components in 2017-2023. The only major changes will be in the Schoolyard Program, where we will (1) formally identify a new partner at Barrow to replace our former partner, the (now defunct) Barrow Arctic Science Consortium, (2) expand the participation by K-12 teachers from both Barrow and the CSU Environmental Literacy Program (directed by John Moore of CSU, an ARC LTER Senior Collaborator), and (3) commit to continued participation in summer science programs for Native Alaskan school children based at Kaktovik and the Arctic Vilage, Alaska in collaboration with the USFWS.

We are already moving to establish this new and expanded program, with visits by two teachers from the CSU program to Barrow in the summer of 2015 to meet with teachers and administrators at the Barrow Native Heritage Center to set up reciprocal visits in 2016 and beyond, and we have been invited to participate for a second year in the Kaktovik summer science program (managed by the University of Texas Marine Science Program, directed by Ken Dunton). The eventual product of this effort will be a Schoolyard Program that includes (1) a regular series of popular science lectures (a continuation of the “Schoolyard Saturday” series we sponsored for many years with the Barrow Arctic Science Consortium), (2) a program that brings K-12 teachers from Barrow and the lower 48 states to Toolik Lake, where they can work with researchers in the field and develop new programs to apply in their own classrooms, and (3) a program in which scientists from Toolik Lake visit schools in local towns such as Barrow, Kaktovik, and Anaktuvuk Pass to participate in summer science programs for K-12 students.

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