Conceptual ecosystem model of sub-Arctic river response to climate change: Kobuk River, Alaska

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ABSTRACT

The Kobuk River watershed is highly vulnerable to changes in climate due to its sub-Arctic location, unique geography, and discontinuous permafrost. Because of this and its pristine condition, it is an ideal system upon which to build a conceptual model for predicting the ecosystem effects of climate change. We established a baseline of conditions on the Kobuk River which, when combined with the available literature on Arctic and sub-Arctic rivers, allowed us to build a predictive conceptual model. In general, we find that while the mainstem Kobuk has low biological productivity, it provides spawning habitat and connectivity for large resident and migratory fish that rely upon off-channel habitat for food resources. System function is largely dependent upon intermittent pulse flows that regulate connectivity between habitats, and allow periods of high off-channel primary and secondary productivity in late summer. Spring break-up and permafrost processes are critically important in maintaining the habitat complexity and interconnectivity of this system. We examine the vulnerability of these geomorphic drivers to climate change to make predictions for habitat and biota. Using predictions from available climate change models, we assume the region will experience an increase in average air temperature, the number of ice-free days, and annual rainfall. Spring break up may either become more or less severe, depending upon its response to increased air temperature and precipitation. Permafrost is expected to melt, producing an increase in active layer thickness and/or thermokarsting. The interaction of these potential changes gives four different scenarios: 1) increase in break up severity + increase in active layer; 2) increase in break up severity + thermokarsting; 3) decrease in break up severity + increase in active layer; 4) decrease in break up severity + thermokarsting. Decreasing predictability and increasing ecosystem disruption characterize the progression toward decreasing break up severity and increasing incidence of thermokarsting. Under Scenario 1, we expect that overall productivity and fish abundance may increase, although late season connectivity between habitat may be impaired by low flows. In Scenario 2, we predict increasing vulnerability of spring spawning fish to seasonal habitat loss and decreasing off-channel productivity. In Scenario 3, persistent loss of off-channel productivity may lead to long-term declines in spring spawners. Finally, in Scenario 4, we expect heightened vulnerability of both

spring and fall spawners habitat loss, leading to population declines and local extinctions. This model can serve as a conceptual framework for understanding ecosystem changes in response to climate change on the Kobuk River.

INTRODUCTION

Arctic climates have warmed at approximately twice the global rate over the last several decades, likely making Arctic ecosystems more sensitive to the effects of climate change than those in temperate regions (Anisimov 2007). A number of studies have examined the effects of change on Arctic and sub-Arctic river systems (Beltaos and Prowse 2001; Beltaos and Burrell 2003; Hinzman, Bettez et al. 2005; Prowse, Wrona et al. 2006; Pohl, Marsh et al. 2007), but none to date have developed an integrated ecosystem conceptual model to form the basis for predicting possible outcomes. We present here the results of an interdisciplinary study on the sub-Arctic Kobuk River, as an example of such a model. The Kobuk River is of particular utility for climate change study because of its relatively pristine condition, which allows us to isolate the effects of climate from other anthropogenically driven impacts. The Kobuk River is also a little-studied river, despite its size and importance for indigenous fisheries.

In August 2008, we surveyed the upper river from near the headwaters at Walker Lake in Gates of the Arctic National Park, to Kobuk Village (Fig 1), characterizing physical habitat, water quality, invertebrate communities and fish assemblages. In addition, we collected general information on the natural history of the upper Kobuk, including birds and mammals, vegetation and succession patterns, and permafrost condition. The results of our survey were combined with a literature review to create a model of potential hydrologic and geomorphic responses to climate change in the upper Kobuk basin over the next 100 years.

We hypothesize that the river's ecology will be governed most prominently by climate-driven changes to three physical factors: 1) the timing and magnitude of the winter freeze and spring break-up, 2) the degradation of permafrost, and 3) the effect of increased precipitation on the hydrograph. Uncertainty regarding the interaction of these physical drivers gives us four very different scenarios for the development of river morphology and habitat over the next century. Each scenario has a different biological outcome, which can be observable with appropriate monitoring. The model developed here provides a framework for understanding the implications of observed changes in the system.

METHODS

Physical and biological data were collected from August 11-22, 2008 during an raft expedition that began at the Walker Lake outlet (RKM 190) and ended at Kobuk Village (RKM 0). Data collection sites were selected to include a variety of habitats in addition to the Kobuk mainstem, including tributary confluences, backwaters, oxbow lakes, and tundra ponds ("off-channel" habitat). A core group of seventeen sites were characterized for physical characteristics, water quality, invertebrates, and fish (Fig 2). Additional water quality, invertebrate and fish samples were taken at points of interest between core sample locations. These data were used to describe current river conditions in the conceptual model.

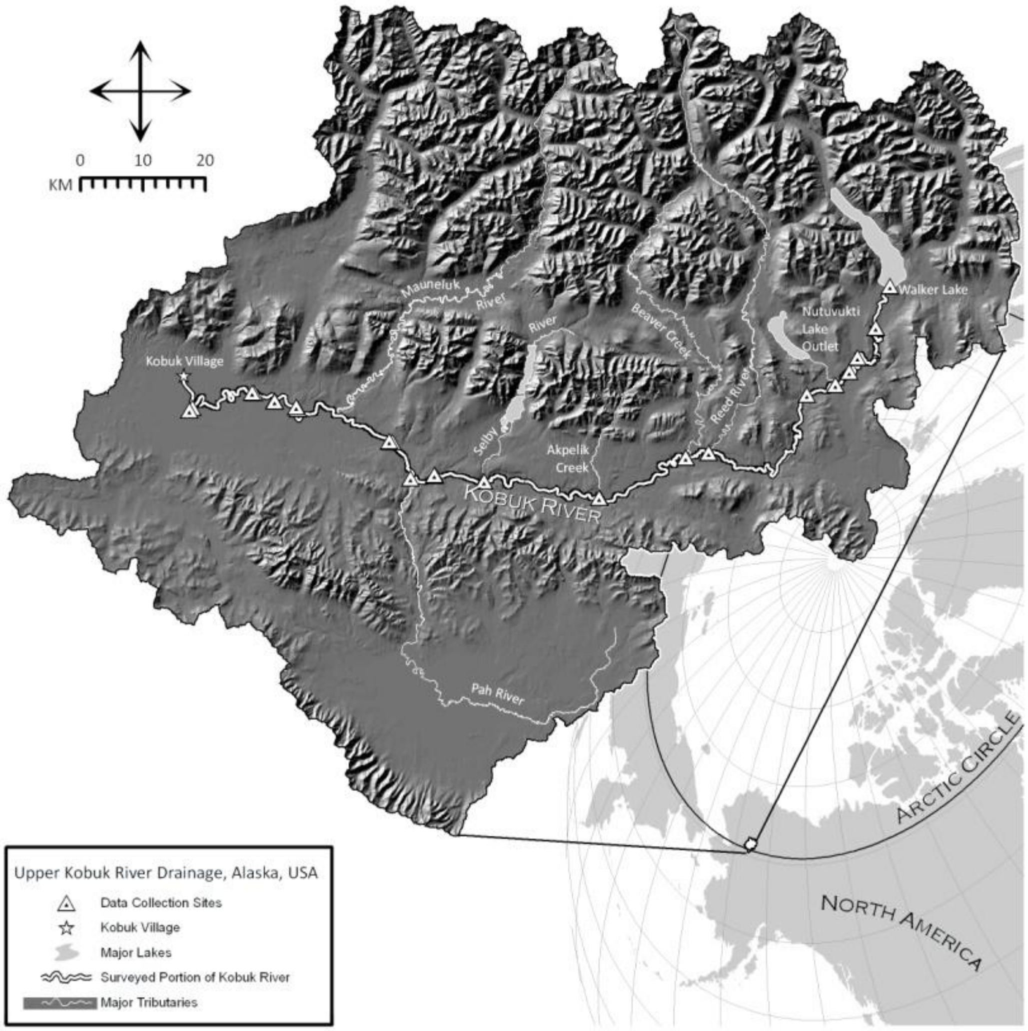


Figure 1. Location of study area and data collection sites along 190 km of the Upper Kobuk River, Alaska. The Kobuk River Basin is located just north of the Arctic Circle and provides important habitat for Arctic and sub-Arctic species.

Scenarios of future climate change are based on predictions from the IPCC Fourth Assessment Report: Polar Regions (Anisimov 2007), the Arctic Climate Impact Assessment (2004) and the Scenarios Network for Alaska Planning (SNAP 2008). For the purposes of developing a conceptual model based on general predictions of climate change in this decade, we chose to consider the areal weighted average composite predictions of the five best performing Global Climate Models (GCMs) for Alaska (ECHAMS, GFDL21, MIROC, HAD, CGCM3.1) simulating a mid-range greenhouse gas emission trend (A1B scenario) from 2000 to 2100. Table 1 presents the predicted change in climate parameters including temperature, precipitation, length of growing season, date of freeze up and date of thaw which have been broken down into decadal averages.

Physical site characteristics were recorded on maps geo-referenced using a Trimble Nomad GPS receiver. For each core site, geomorphic features, grain size distribution, substrate, and vegetation type were mapped, and measured with a LaserTech Impulse 200 where appropriate. The GPS unit tracked water surface elevation and course of travel along the mainstem of the Kobuk River, in addition to locating off-channel habitats. In conjunction with USGS topographical maps, these data were used to measure sinuosity and meander belt width.

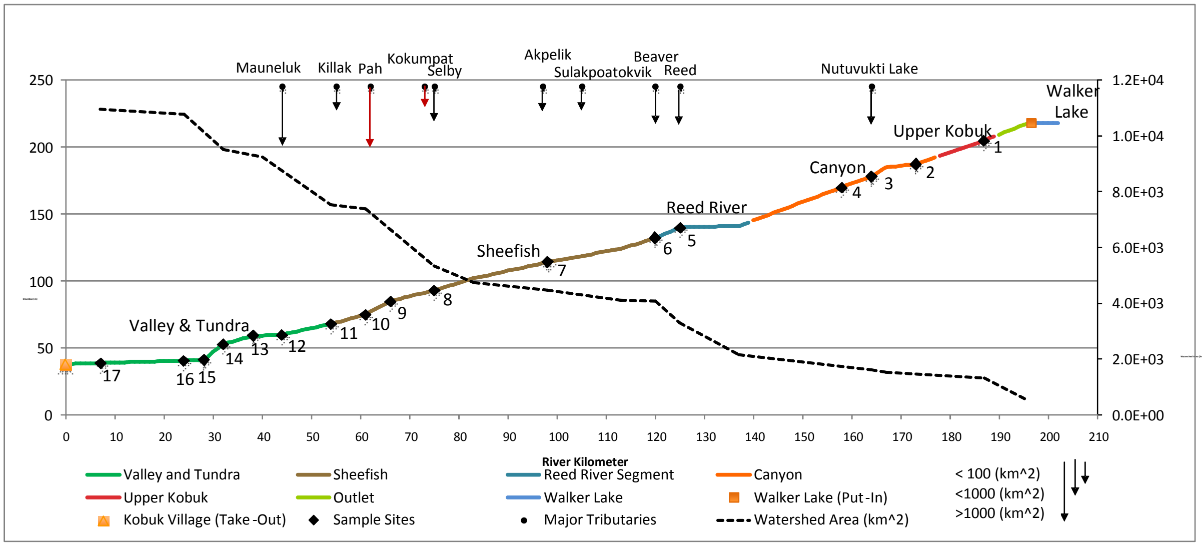


Figure 2. Long profile of Upper Kobuk River with breakdown of river segments having similar characteristics. Watershed area is represented with the dotted line and tributary location and relative size are also depicted. Red tributary arrows indicate southern tributaries.

Decade	Mean Temperature (˚C)		Precipitation (mm)		Length of Growing Season	Date of Freeze Up	Date of Thaw
	Summer	Winter	Summer	Winter	(# of Days)	Ordinal Date	Ordinal Date
2000-2009	12.5	-22.2	77.7	26.4	146.4	270.0	123.5
2030-2039	12.8	-21.0	83.0	29.3	149.8	272.5	122.6
2060-2069	13.9	-17.4	89.7	32.2	160.0	277.8	117.9
2090-2099	15.0	-14.6	86.5	37.6	167.9	282.2	114.4

Table 1. Decadal averages of five GCM predictions for the A1B scenario. Summer is considered to be the months of June, July and August. Winter is considered to be the months of December, January and February. Predictions are given as the average of the model output raster value. (SNAP 2008)

Basic water quality parameters for temperature, conductivity, pH and dissolved oxygen were measured with a Hydrolab Quanta probe. Nutrient availability was assessed by measuring phosphate (P), nitrogen (N), silicon (Si), iron (Fe), manganese (Mn), calcium (Ca)/magnesium (Mg), and tannin/lignin concentrations using a Hach DR890 handheld colorimeter. Phosphate, nitrogen, and silicon were measured because of their importance as limiting nutrients in Arctic ecosystems (Prowse, Wrona et al. 2006). Iron and manganese are able to bind phosphate, potentially stripping nutrients from the water column. Calcium and magnesium concentrations were measured as an indication of the acid neutralizing capacity of the water. Finally, tannin/lignin concentrations were measured to provide clues about sources of refractory C and low pH water. Procedures followed Standard Methods for the Evaluation of Water and Wastewater (APHA 1992) and HACH Methods (2006).

Benthic macroinvertebrates were collected using a 250 µm mesh D-frame kick net. Samples were collected in the mainstem Kobuk and tributary confluences, and in off-channel backwater habitats. Site selection for each sample was based on riffle habitat availability, sediment size, and canopy cover. Each sample consisted of two 30 cm x 30 cm areas, taken within a riffle where possible. Where riffles were unavailable, a multi-habitat approach was used which consisted of sampling marginal habitat and emergent vegetation. The most downstream sample location was always sampled first. The resulting composite was placed in a sorting tray and organisms were counted and identified to family or genus. Invertebrates that could not be identified in the field were placed in 95% ethanol for later identification in the laboratory.

Drift insects and zooplankton (mesoinvertebrates) were collected from mainstem, tributary and off-channel sites using a 30 µm mesh plankton net with a ring diameter of 0.25 m^2. In the channels, samples were collected by holding the net on a 10 m tether mid-stream, approximately 0.5 m below the surface, for 5 minutes without measuring flow rate. Samples collected in slow moving off-channel sites were collected by a sub-surface tow across 10 m. Samples were filtered to reduce water volume and placed in a sorting tray to identify and count organisms. Extremely dense samples were sub-sampled by homogenizing them and then removing a fraction. The inverse of this fraction was used as a multiplier to determine sample abundance. All relative density counts are standardized to number per time or number per volume, depending on the method of collection. All samples were estimated using live organisms in the field, although a few voucher specimens were preserved in 40 percent alcohol for later identification in the lab.

Fish were sampled by seining and hook-and-line. Basic sampling procedures followed Overton et al (1997) and Moyle et al (2003). Small fish were targeted using a 10 x 1.2 m beach seine, with a 1 x 1 x 1 m bag and 5 mm mesh. All fish were removed from the net immediately and placed in buckets of water before being identified, measured to fork length and returned to the water. If more than 25 individuals of any species were collected, only the first 25 were measured. Larger predatory fish were captured using hook-and-line, then identified, measured and weighed. Time of capture was used to infer location on the continuous GPS log. All fish distributions were mapped onto a longitudinal profile of the Kobuk River using this geo-referenced data.

Fish diets were assessed by examining the stomach contents of Arctic grayling (*Thymallus Arcticus*) using gastric lavage. Stomach contents of lake trout (*Salvelinus namycush*) and sheefish (*Stenodus leucichthys*) were analyzed by dissection (all sacrificed fish were eaten). Contents were partitioned into terrestrial animals, aquatic macroinvertebrates, fish, and debris, and each category was estimated as a percentage of the total.

We integrated our findings from the field with an extensive literature review of Arctic and sub-Arctic rivers from both peer-reviewed journals and the grey literature of reports, dissertations, etc. This integration is presented below under Results as a model of ecosystem function on the upper Kobuk River. This model was then used as a baseline to understand how projected changes to the region's climate will be manifested biologically. These predictions are presented in our Discussion.

STUDY AREA

The Upper Kobuk River

The Kobuk River is a gravel and sand-bedded wandering river, located just north of the Arctic Circle running from east to west at around latitude N67° and between longitude W161°45' and 154°03' (Figure 1). From Walker Lake Outlet to the Reed River tributary (RKM 139), the Kobuk is semi-confined by glacial moraine or bedrock, with two narrow canyon stretches both less than 3 kilometers long. The gradient is consistent, with no major knick points or bed steps. There are relatively straight stretches with a striking lack of cross-sectional bathymetric variability. These stretches are wide and shallow, with gravel substrate.

After the Reed River—a major tributary—enters the mainstem, the gradient decreases and river character changes significantly. Anabranching begins directly downstream of the Reed confluence, and island complexes reappear several times for the remainder of the river's course down to Kobuk Village. At RKM 119 the mixed sand-gravel bed fines to a sand bed, the meander belt widens, and backwater sloughs and oxbow lakes become more prominent. At RKM 35 (just above Kobuk Village), the river enters an extensive tundra floodplain that ends only at the Kobuk River Estuary at Hotham Inlet, off Kotzebue Sound to the west, about 240 km downriver.

Because the Kobuk is a sub-Arctic river, the region through which it flow is characterized by short, warm summers and long, cold winters, with a mean annual temperature of -6°C in the middle and upper Kobuk Valley (Mann 2002). Average winter temperatures range from -20 to -25°C, causing near complete freezing of the Kobuk River (SNAP 2008).

The annual average precipitation in the Kobuk River basin is 53 cm with a range of 40-100 cm. Precipitation is greater in the upper reaches of the river basin (Brabets 2001). The unique pattern of annual precipitation on the Kobuk is reflected in a dual-peaked hydrograph (Brabets 2001), which is driven by the mountainous physiography of the region. The Brooks Range shields the river basin from polar storms, distinguishing it from more studied rivers of the north slope of the Brooks Range, like the Colville, the Porcupine and the Kuparuk (Hamilton and Porter 1975) . Because of this rain shadow effect, the Kobuk River basin is comparatively arid throughout the year (Cooper 1986). However, the Kobuk is exposed to late summer storms that move inland from the Chukchi Sea (Mann 2002). As a result, the Kobuk's annual average hydrograph (Fig 3) shows one peak during the spring flood, and another occurring in late summer, with concomitant flow variability throughout the late summer (Brabets 2001; USGS Accessed Aug 21, 2007).

In July 2008, prior to our field study, the basin experienced an above average discharge in terms of magnitude and duration, as measured from the hydrograph near Kiana, AK. This small summer peak occurred earlier than usual, in July, but by our arrival in August the river stage had declined to below average, with a small rise observed during the sampling period associated with characteristic afternoon thundershowers. In general the basin experienced a drier than average year in 2008 (mean annual discharge was 370 cms, placing it in the 35th percentile of water years), particularly in the late summer encompassing the time of our expedition (USGS, accessed Aug 21, 2007).

Changes in river stage (due to flow variability) control connectivity between off-channel habitats and the mainstem Kobuk, regulating exchange of nutrients and biota. For example, spring floods dramatically increase the extent of the river, allowing inputs of allochthonous nutrients and carbon that initiate seasonal biological production. As spring flows decline, off-channel habitats become isolated from the surface flow of the mainstem, increasing residence time and water temperature, and creating sources of primary and secondary production (Malard, Uehlinger et al. 2006). It is likely that episodic high summer flows reestablish connectivity with the mainstem, providing refuge and allowing transfer of nutrients and food for foraging fish (Fig 4).

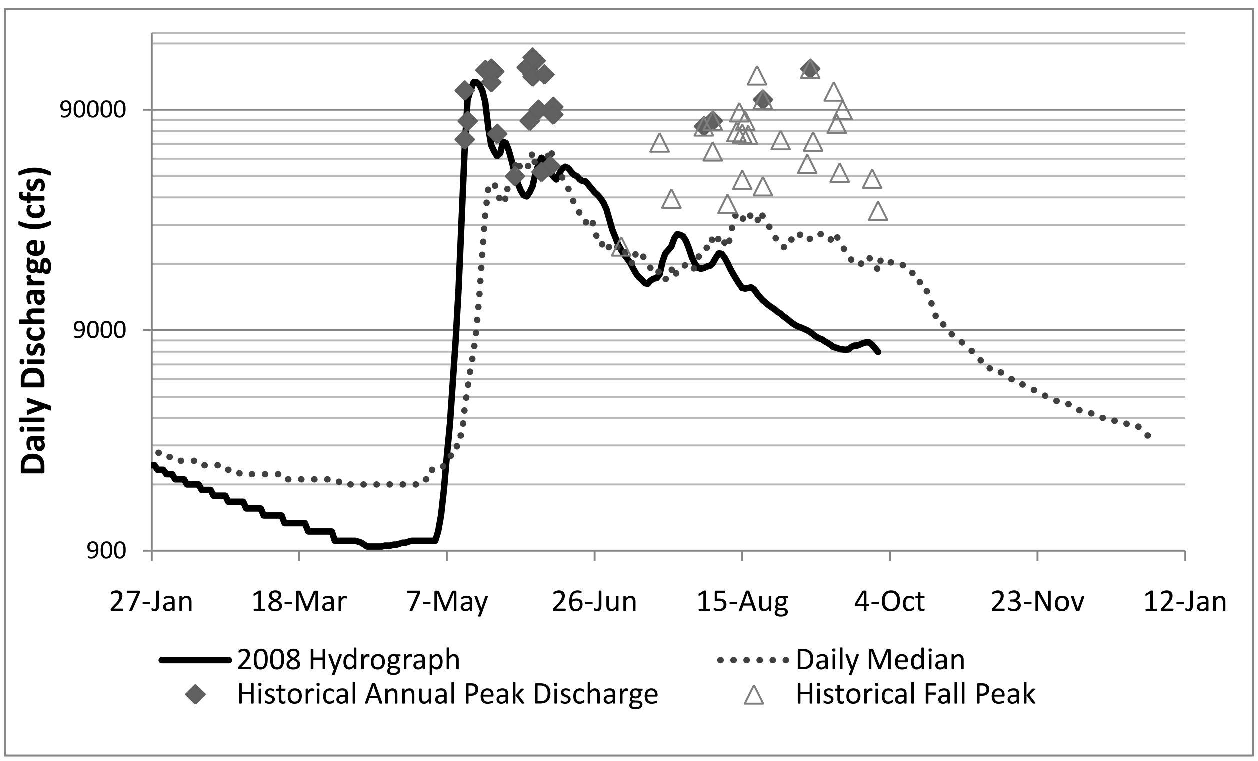


Figure 3. Kobuk River hydrograph near Kiana, AK for the 2008 season with mean daily statistics for the previous 27 years. Data courtesy of the USGS.

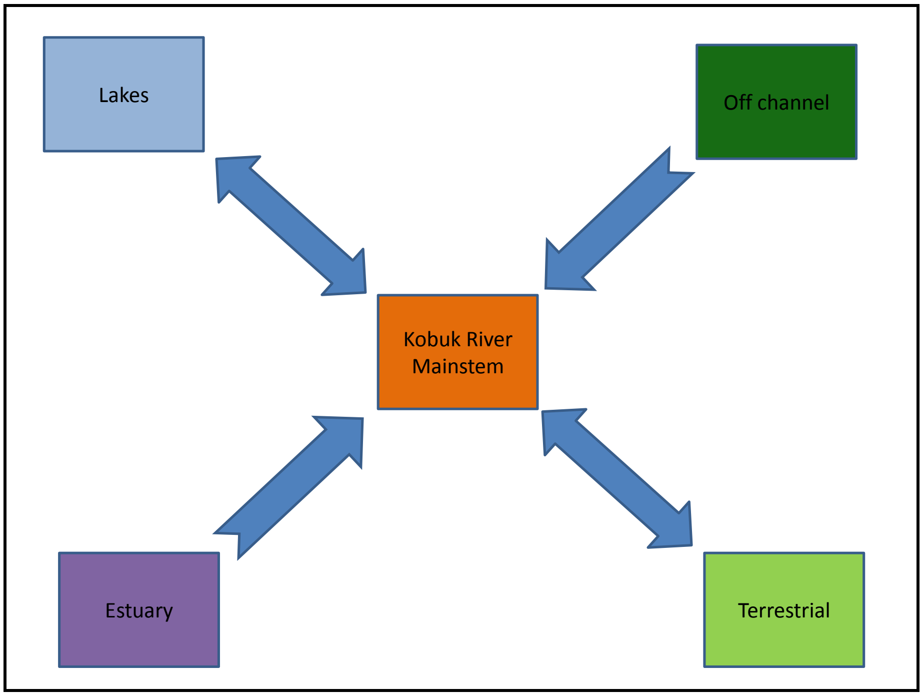


Figure 4. Connectivity between key components of the Kobuk River ecosystem, mediated by seasonal changes in flows.

In late autumn, falling temperatures cause a winter freeze that acts as an annual "reset" on Arctic rivers by stopping or slowing physical and biological activity. Organisms that persist must either tolerate freezing, or find ice-free habitat at the bottom of lakes or deep pools. Riverine inputs from baseflows, insulated by winter snow, may provide sources of unfrozen water that allow organisms to persist in ice-free areas at the river bottom (Woo, Kane et al. 2008). Biological activity moves from the periphery of the system to deep channels and lakes.

Arctic river channel morphology and habitat are influenced primarily by two physical drivers: 1) spring ice break-up and resultant peak flows; and 2) surrounding hillslope processes (mainly related to permafrost dynamics), which govern the supply of sediment and nutrients to the watershed (McNamara, Kane et al. 1999; Hinzman, Kane et al. 2003; Prowse and Culp 2003).

In late spring, the Kobuk undergoes a dynamic ice jam flood. Ice break-up is an important geomorphic driver on Arctic rivers, capable of generating rapid increases in stage and velocities. Successive failure and formation of ice jams force the river to forge alternate flow paths (Scrimgeour, Prowse et al. 1994). It is often associated with anabranch cycles on wandering rivers (Burge and Lapointe 2005) driving island formation, channel network complexity, and recruitment of large woody debris (Tockner, Pennetzdorfer et al. 1999). Scouring and erosion during break-up can produce sediment loads 2 to 5 times higher than that produced by equivalent open water flows (Beltaos and Burrell 2003; Beltaos and Prowse 2009). The winter freeze and spring break-up together create significant annual biological disturbance (Scrimgeour, Prowse et al. 1994) by (a) limiting the establishment of perennial aquatic vegetation and macroinvertebrate habitat (Gammon 1970; Ryder 1989; Ryan 1991); (b) defining the conclusion of the winter fish embryo incubation period; and (c) increasing mortality in most lifestages of fish (but especially small juveniles). Recolonization of peripheral habitat on a river such as the Kobuk occurs as break-up ends, concurrent with increasing air temperature, day length, and decline in river stage.

Permafrost likewise has a major influence on flows and geomorphology. The Kobuk watershed is underlain by discontinuous permafrost (Brabets 2001) which provides channel structure by reinforcing banks, slowing changes in channel migration and anabranching, and reducing erosion and other hillslope processes. It also creates a foundation for the active layer of soil, which in turn governs water, sediment, and nutrient supply to the watershed (White, Hinzman et al. 2007; Woo, Kane et al. 2008; Gooseff, Balser et al. 2009). The thickness of the active layer determines the rate of base flows into the mainstem. When summer precipitation surpasses the storage capacity of the active layer, water can also run off as surface flows, contributing to the summer peak in stage.

When permafrost melts, it does so unevenly, creating depressions (thermokarsting) in the ground surface from reduced support of overlying unfrozen layers (the active layer). Connected depressions form channels that quickly funnel precipitation runoff to the stream network as surface flows, causing a rapid and less prolonged response in the hydrograph. The resulting erosion and bank instability increases the amount of sediment to the river, which may accumulate locally until fall rain events or the year’s spring flood provides sufficient capacity to remove such deposits (Gooseff, Balser et al. 2009). As a consequence, thermokarsting may lead to major geomorphic and water quality changes affecting productivity and spawning habitat in both the mainstem and Kobuk tributaries.

RESULTS

Long Profile and River Segments.

Channel plan form, substrate, and complexity varied over the study area, and appeared closely related to five other physical features: (1) slope, (2) geological confinement, (3) ice scour, (4) sediment contribution from tributaries, and (5) dominant vegetation. Channel plan form varied between straight single channel, meandering single channel, and anabranching. Based on these physical features, channel plan forms, and substrate, we divided the 190-km study area into five river segments, summarized in Table 2 and Figure 2.

Segment 1 (Upper Kobuk River) is characterized by a single channel plan form, a gravel and cobble substrate, and a lack of off-channel habitat, as would be expected in a high-energy, steep gradient system with geologic constraints on meandering, heavy exposure to ice scour, and minimal input from tributaries. While black spruce (*Picea mariana*) dominates the riparian vegetation, there was little evidence of large woody debris (dead trees, etc.), which is likely removed from most of the Upper Kobuk during spring break-up.

Segment 2 (Canyon) resembles Segment 1, except that the channel is confined to two extremely narrow bedrock canyons (Upper and Lower Kobuk River Canyons), separated by the Nutuvukti Lake

Outlet, which deposits considerable sand into the intervening section, allowing the establishment of fast-growing willows, poplar, and birch.

In Segment 3 (Reed River), the Kobuk becomes much less confined and morphs into an anabranching system due to sediment influx from the Reed. The river decreases in gradient and becomes multi-channeled. A mature mix of birch and spruce trees appears, along with larger established islands, as the meander belt widens significantly. Two major bedrock-controlled tributaries enter from the North side of the river (the Reed and Beaver). Maps and samples were taken at both. There was an abundance of large woody debris at both tributary sites, and grain sizes on the point bars ranged from fine sand to cobble, with less than 10% silt. Vegetation on tributary point bars was a mix of shrubs, willows and poplars. The Reed River has a large effect on channel formation in the Kobuk, and probably dominates flow in high water events. The Kobuk River has blocked the eastern Beaver Creek outlet with sediment and forced it to migrate west toward the end of a large island complex. The confluence is characterized by fine-grained sand, mixed with gravel and cobbles.

Segment 4 (Sheefish) returns to a predominantly single-channel plan form with very wide meander bends and only occasional anabranching. Sand-gravel ripples dominate substrate patterns, and mid-channel gravel bars appear devoid of vegetation, signifying more recent sediment deposition. Backwater sloughs also begin to appear with significant lateral movement of the Kobuk's main channel. Several point bars show significant signs of ice scour, and cut banks become higher with visible

Channel Segment	1. Channel Planform	2. Dominant Substrate	3. Abundance of Backwaters and Oxbow Lakes	4. Mean % Gradient per River Kilometer	5. Range of Meander Belt Width (km)	6. Evidence of Ice Scour	7. Major Tributaries	8. Dominant Riparian Veg	Key Features
1. Upper Kobuk km 177 - 190	Single channel	Cobble and gravel	None	0.134%	1 - 2	High	None	black spruce	Minimal geomorphic complexity and uniform rectangular cross sections
2. Canyon Stretch km 139 - 177	Single channel	Boulders and gravel	None	0.126%	0.2 - 2	High	Nutuvukti Lake Outlet	willows, poplars, birch	Two confined, bedrock controlled canyons. No apparent barriers to fish migration. Middle of segment contains single-channel, sand-rich, semi-confined, reach.
3. Reed River km 119 - 139	Anabranching	Gravel	Low	0.064%	1 - 2.5	High	Reed, Beaver	mixed conifers, willows, poplars, shrubs	Large sediment contribution from Reed induces extensive anabranching with numerous large, well-vegetated, stable islands
4. Sheefish km 53-119	Single channel meandering w/ limited anabranching	Gravel and sand	Low	0.099%	1 - 3	Medium	Sulakpoatokvik, Akpelik, Selby, Kokumpat, Pah, Killak	mixed conifers, grasses, willows, poplars	Increased gradient, sand-gravel riffles, and large cut banks.
5. Valley & Tundra km 0-53	Anabranching	Sand and fines	High	0.061%	1.5 - 9	Low	Mauneluk	mixed conifers and tundra	Large stands of mature mixed conifer forest give way to mixed forest / tundra floodplain

Table 2. Kobuk long profile segment description.

disturbance to trees from recent floods. With the exception of the Pah, most tributaries in this section are small and very confined, with variable substrate and pool-riffle features just upstream of their confluence with the Kobuk.

The meander belt becomes much wider in Segment 5 (Valley and Tundra), and significant anabranching separates the Kobuk into multiple channels across a broad unconfined valley. Backwater sloughs are common, and well-established spruce forest gives way to tundra, with no bands of willow or alder adjacent to the river. Ice scour is no longer visible on most point bars. Fine sands and organic silts dominated the substrate at many of these study sites.

Water Quality

The Kobuk River and its tributaries are generally oligotrophic, a property held in common with most Arctic rivers (LaPerriere, Jones et al. 2003). The water chemistry of the Kobuk mainstem shows very low concentrations of N, P, Fe and tannins, and a neutral pH (~7) (Figs 5-10). High concentrations of base cations (Ca and Mg) in the mainstem indicate considerable buffering capacity.

The tributaries show diverse chemical signatures, although pH was generally lower than in the mainstem. Groundwater flows adjacent to the river generally had higher concentrations of nutrients and iron, accompanied by low pH. Walker Lake and surveyed tundra ponds were also low in pH and high in nutrients and iron. In general, variability in tributary water chemistry increases downriver. However, the variability from source inputs is largely buffered or diluted upon entering the mainstem of the Kobuk.

Water temperature on the mainstem of the Kobuk River averaged 12°C, with a range of 10.5 to 13.4°C (Fig 4). However, tributaries and springs varied from 5.8 to 13.5°C, suggesting that some inputs from baseflow are considerably cooler. In contrast, two ponds adjacent to the riparian corridor, but not directly connected to the mainstem, were measured at 13.1 and 16°C, suggesting that at least some ponds were warmer than the mainstem by late summer.

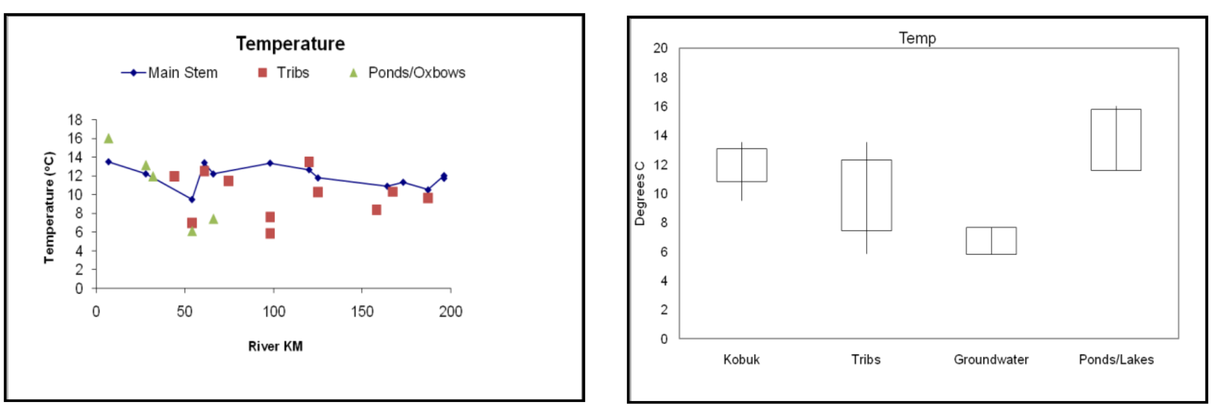


Figure 5. Water temperature in the Kobuk River and nearby tributaries, groundwater, ponds and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.

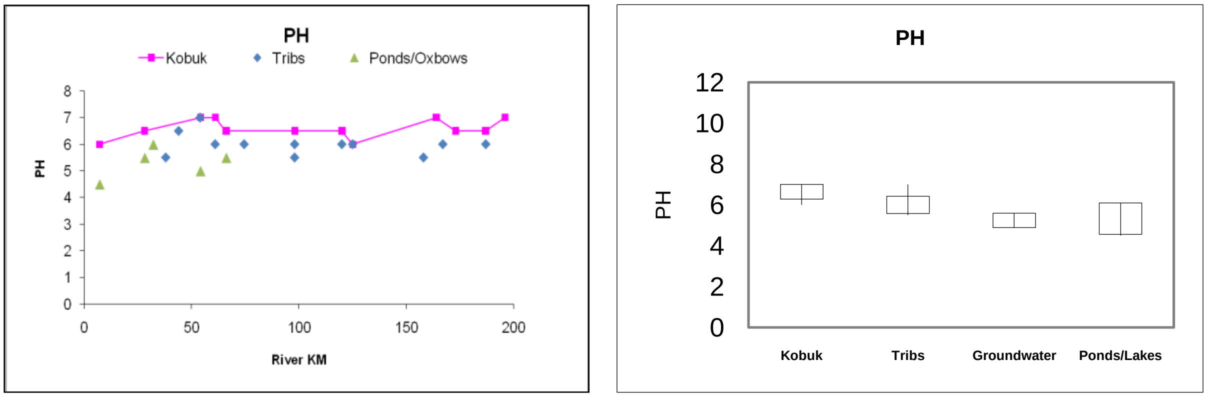


Figure 6. pH in the Kobuk River and nearby tributaries, groundwater, ponds, and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.

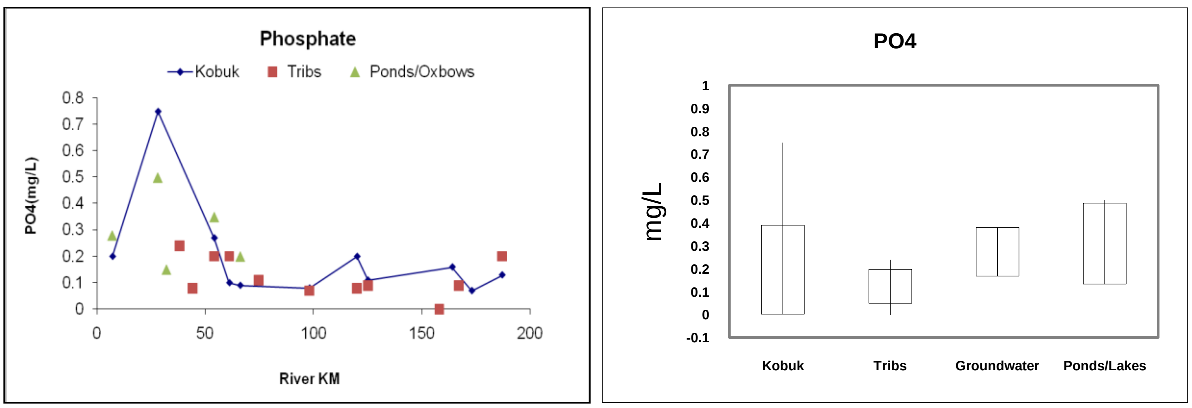


Figure 7. PO4 in the Kobuk River and nearby tributaries, groundwater, ponds and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.

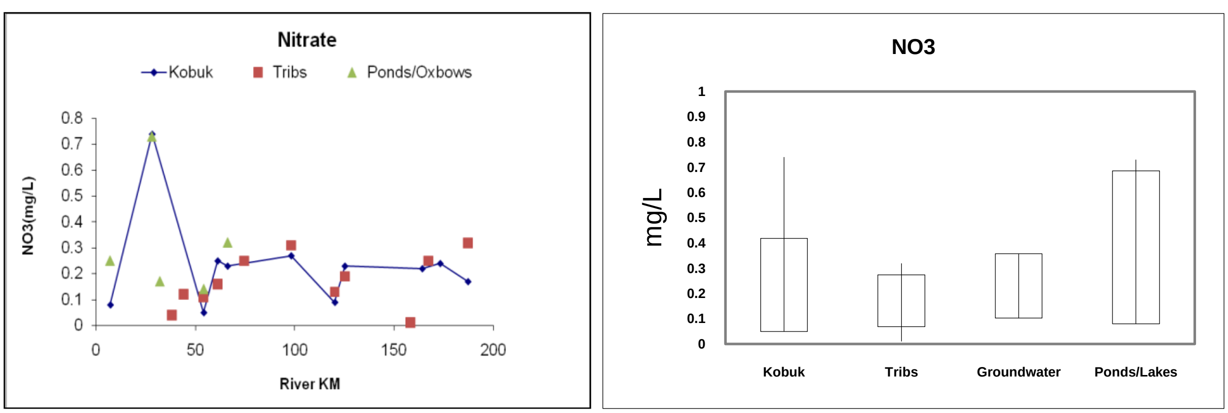
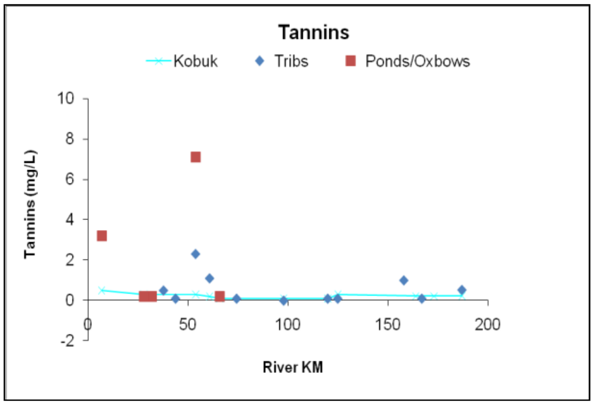


Figure 8. NO3 in the Kobuk River and nearby tributaries, groundwater, ponds, and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.



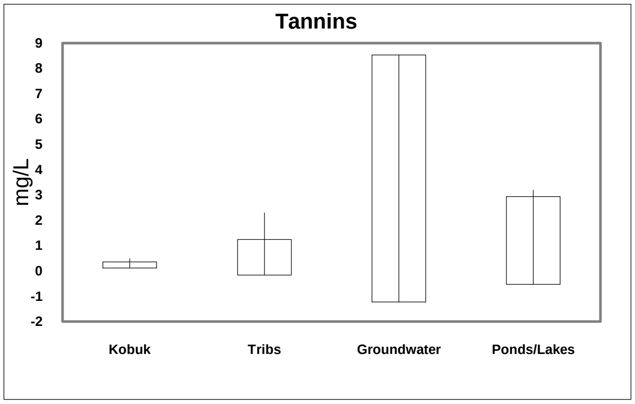
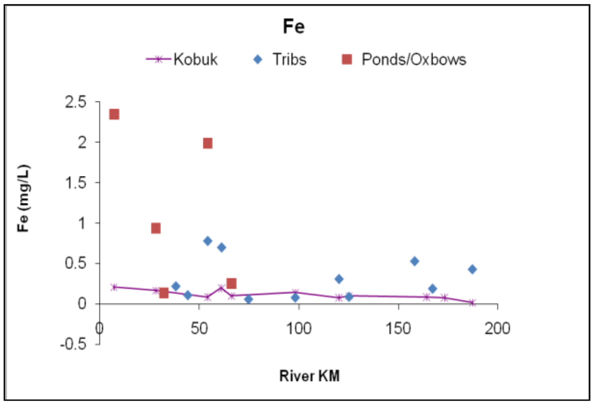


Figure 9. Tannins in the Kobuk River and nearby tributaries, groundwater, ponds and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.



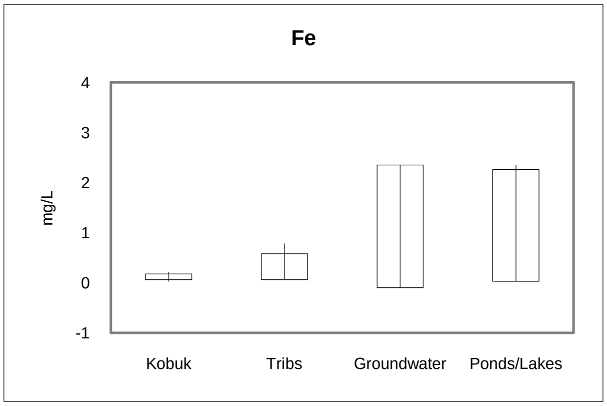


Figure 10. Fe in the Kobuk River and nearby tributaries, groundwater, ponds and oxbow lakes. Boxes are ±1 standard deviation from the mean and whiskers are high and low values.

Primary production

Primary production in the Kobuk River proper seems to be restricted to diatom films, filamentous algae and a few emergent vascular species of macrophytes (sedges, etc.). Perennial macrophytes with extensive root systems are rare due to the short growing season and the annual scouring of substrate due to break up (Mackay and Mackay 1977; Nichols, Schloesser et al. 1989; Scrimgeour, Prowse et al. 1994). In contrast with Arctic rivers dominated by glacial runoff, the Kobuk watershed lacks glaciers, resulting in exceptionally clear water, fueling seasonal algal growth (Jones, LaPerriere et al. 1990). However, primary production appears to be largely limited by low nitrogen and phosphorous availability, although inputs from adjacent tundra or riparian corridors may increase nutrients downriver and at the substrate-water interface (Roy 1989; Robinson, Tockner et al. 2002). Carbon is probably derived primarily from allochthonous terrestrial, wetland or estuarine inputs, rather than autochthonous plant growth (Scrimgeour, Prowse et al. 1994).

Nonetheless, benthic epilithic diatoms were surprisingly prevalent in cobbled, hard-bottomed segments of the mainstem Kobuk. Off channel habitat, with a fine substrate, was occasionally characterized by thick growth of filamentous green algae. Arctic tundra ponds are often characterized by abundant benthic algaes, forming a large reservoir of carbon production that may accumulate perennially, with seasonal connectivity being established during the spring flood (Alexander, McRoy et al. 1980; Arscott, Bowden et al. 1998).

Rooted aquatic plants are represented by sedges, grasses, and forbs such as *Ranunculus sp*, which are able to endure the short growing season and harsh conditions by living in protected areas and propagating rhizomally, re-directing energy from sexual reproduction into vegetative growth (Alexander, McRoy et al. 1980). Quite abundant in the slow-moving water of off-channel habitat, these plants provided refuge for many benthic and pelagic aquatic invertebrates.

<u>Benthic Invertebrates.</u>

Benthic macroinvertebrates were dominated by two orders of aquatic insects, Ephemeroptera (mayflies) and Diptera (true flies). Ephemeropterans accounted for approximately 40% of all identified macroinvertebrates over all sample sites, while dipterans constituted 35% of all sampled macroinvertebrates (Figure 11). Within the Ephemeroptera, Ephemerellidae was the most abundant mayfly family, followed by Heptageniidae and Baetidae. Diptera were primarily represented by Chironomidae (non-biting midges) and Simuliidae (black flies). Plecoptera (stoneflies) and Trichoptera (caddisflies) accounted for only 10% and 4%, respectively, of the entire sampled assemblage. The ubiquitous nature of ephemeropterans and dipterans suggest that these insects have adaptations that allow them to persist in the highly variable Kobuk River, presumably as the result of physiological or behavioral adaptations such as freeze tolerance or avoidance, dispersal and colonization ability, or rapid development times.

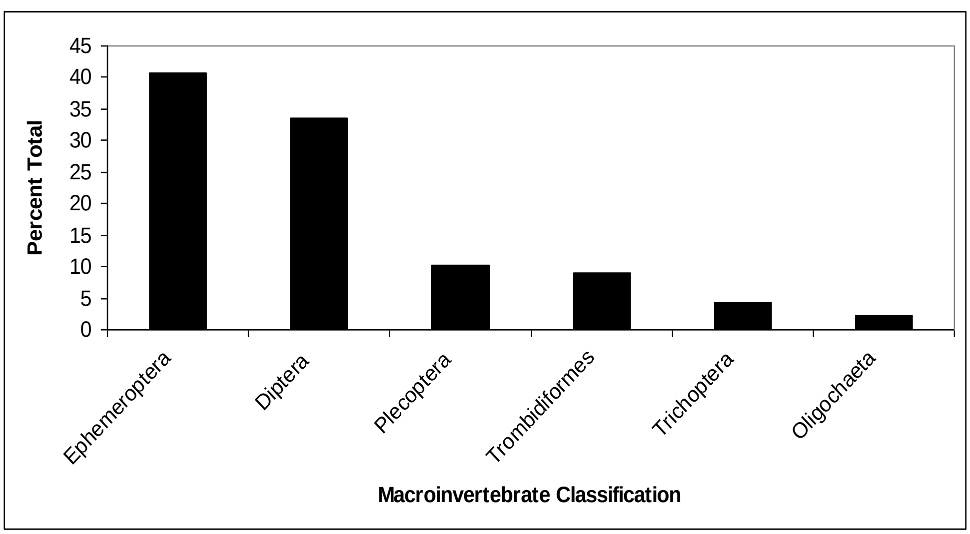


Figure 11. Percent total abundance of benthic macroinvertebrates for all sample sites.

In order to compare productivity and diversity between habitats, we calculated mean abundance (Fig 12), total family richness (Fig 13), and EPT (Ephemeroptera-Plecoptera-Trichoptera) richness (Fig 14) for the mainstem, tributaries, and off-channel habitat. The EPT index is regarded as a measure of water quality (Plafkin, Barbour et al. 1989; Lenat and Barbour 1994). For each characterization, the off-channel habitats showed greater overall productivity and diversity, followed by the tributaries. The mainstem of the Kobuk was depauperate, with low overall mean abundance (< 25% of the mean abundance of the side channels), and lower diversity by both measurements.

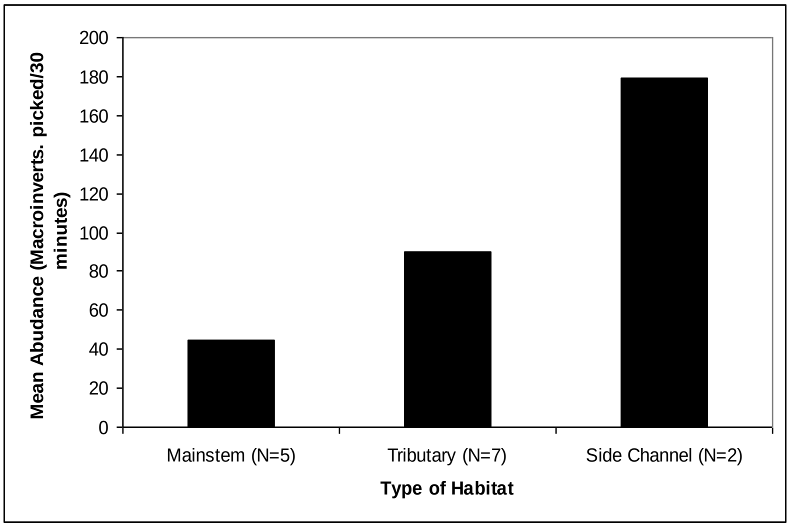


Figure 12. BMI abundance by habitat type.

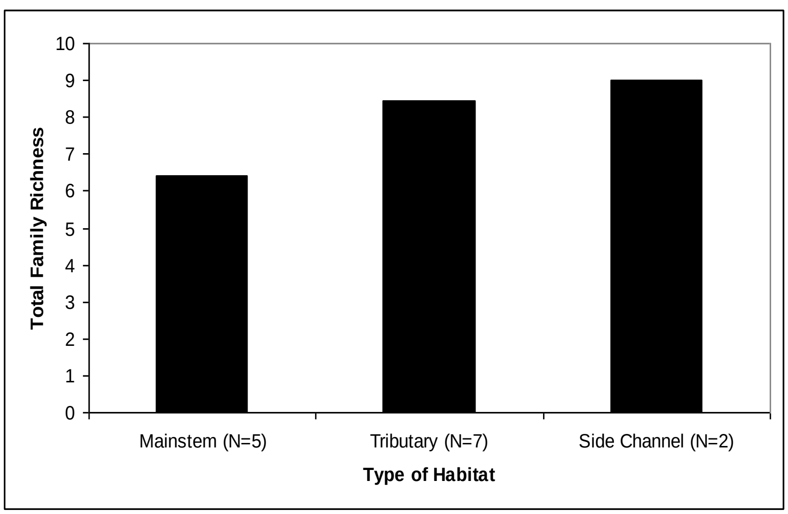


Figure 13. BMI total family richness by habitat type.

We further evaluated diversity by comparing functional feeding group composition (Merritt, Cummins et al. 2008). Overall, the benthic community was dominated by collector/filterer/gatherers, which accounted for approximately 60% of the entire assemblage over all sample sites. Predators were the next most dominant functional feeding group, accounting for approximately 20% of the entire assemblage, while scrapers and shredders constituted the remaining 17% and 1%, respectively. Functional feeding group structure remained similar between habitats, except for the increased presence of scrapers in side channels, where they replaced predators as the second most dominant group (Fig 15).

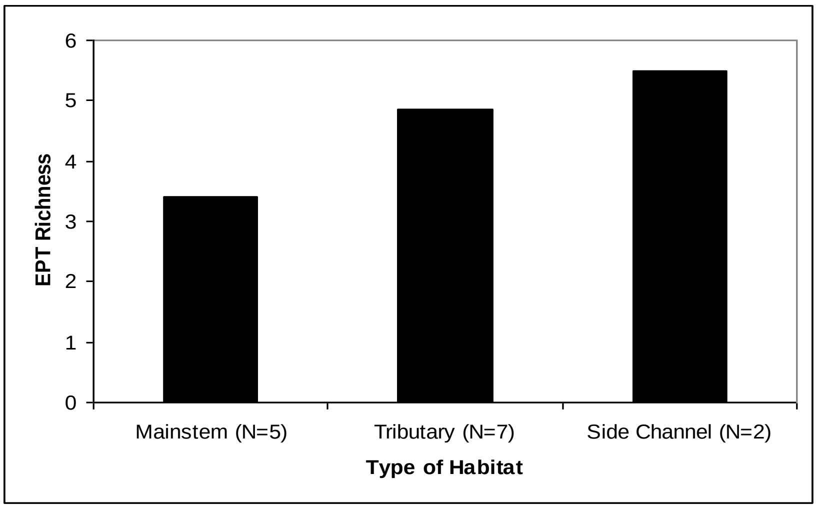


Figure 14. BMI EPT by habitat type.

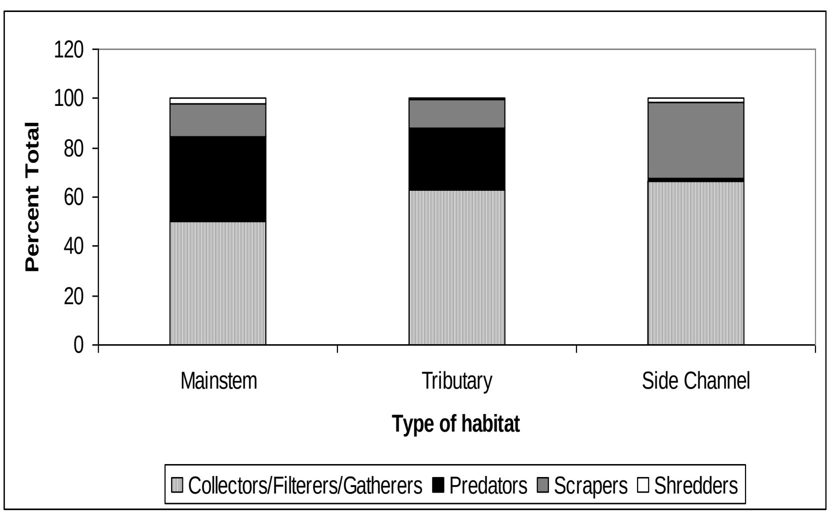


Figure 15. Percent total FFG by habitat type.

Overall, aquatic insects were more diverse than expected on the Kobuk River based upon the literature (Miller and Stout 1989; Oswood 1989; Hershey, Merritt et al. 1995), in part because of the diversity of habitat provided by off-channel sites and tributaries. Fine particulate organic matter apparently plays an integral role as a basal carbon resource to primary consumers (collectors), which act as the main conduit to higher trophic levels, including predatory insects and fish. However, the abundance of scrapers in side channels suggest that fine particulate organic matter may be supplemented by increased levels of epilithic algae in off-channel habitat.

Drift invertebrates.

Drift organisms in the mainstem of the Kobuk and its tributaries were relatively scarce. However, the diversity of drift organisms mirrored the diversity found in the benthic invertebrates. Dipteran pupae were the most common organism in drift samples, followed by fly and midge larvae, mayflies, and water mites (Hydracarinidae). Extremely scarce were copepods, stoneflies and caddisflies, in part because of dilution due to high water volume and flow rates in the mainstem (Fig 16). The highest abundance and species richness of drift organisms were found in three tributaries off of Segment 4 (Sites 6, 8 and 10), each of which drained upstream lakes or extensive tundra plain. In contrast, Sites 3 (in the Segment 2) and 9 (in Segment 4) had the lowest abundance of organisms and relatively low diversity. However, no clear pattern of drift abundance appeared in the data, except that drift was consistently low on the mainstem Kobuk.

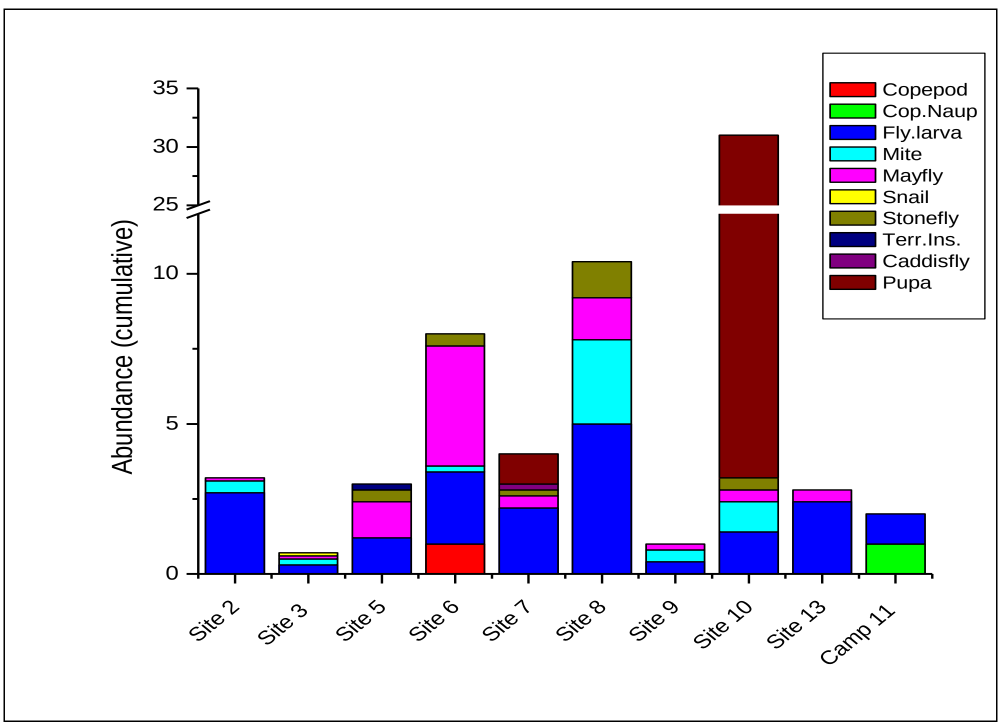


Figure 16. Cumulative abundance of drift from river and tributary sites.

Zooplankton were sampled from three off-channel sloughs in the Valley and Tundra Segment (Fig 17). The first site was a backwater of the Mauneluk River confluence (Site 12) and the other two sites were contiguous pools (Site 14a and 14b), formed through channel abandonment. All of these sites had low flow and presumably high residence time, but are subject to occasional high flows from rain-flood events. Each site showed considerably higher species abundance than the drift samples, and was distinct in having abundant copepods present. The lower pool (14a) showed physical signs of recent flooding, reflecting connection with the mainstem. Hydrograph data indicates that this took place approximately two weeks prior to sampling. The upper pool (14b) appears to have maintained disconnection from the mainstem during this event. The species composition and abundance in each pool reflected the relative age of their waters. Only copepod nauplii < ~2 weeks in age were found in the lower pool, while the upper pool was dominated by adults, including gravid females. The females in the upper pool appeared to be seeding the lower pool after it had been washed out by the pulse flow.

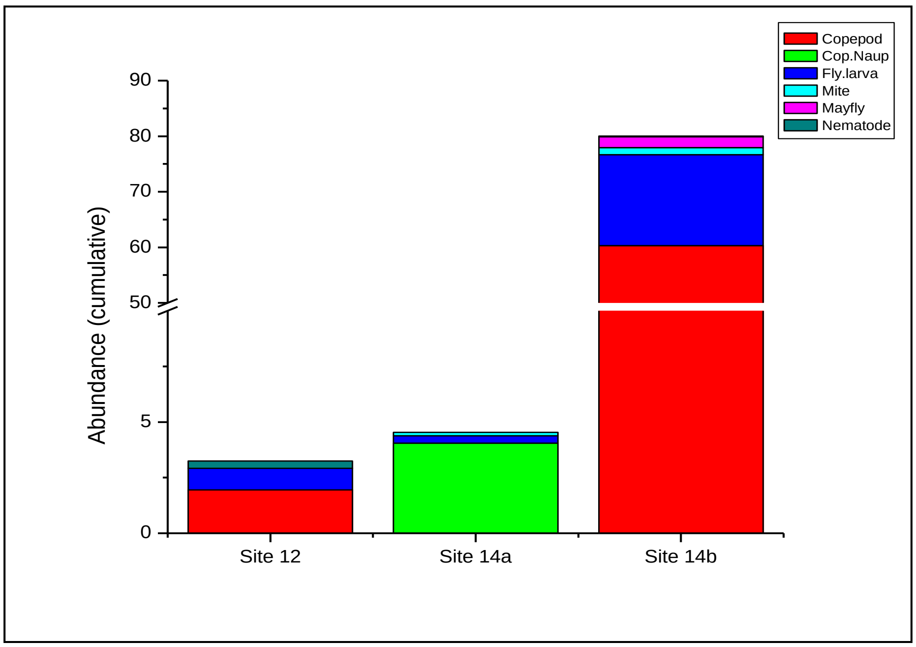


Figure 17. Cumulative abundance of zooplankton from off-channel sloughs.

Zooplankton were also sampled in several ponds, which had only limited connectivity with the mainstem, all of which were in the Valley and Tundra Segment (Fig 18). Ponds showed low diversity, but had the highest abundance out of all sites by 1 to 2 orders of magnitude. Most of this abundance was attributable to copepods and cladocerans. The two samples collected at an oxbow (Site 15) were dominated by copepods, with a few cladocerans present near emergent vegetation. In samples from the tundra ponds (Site 17) and a lower oxbow (Site 18), this pattern changed and the samples showed a very high abundance of almost exclusively cladocerans.

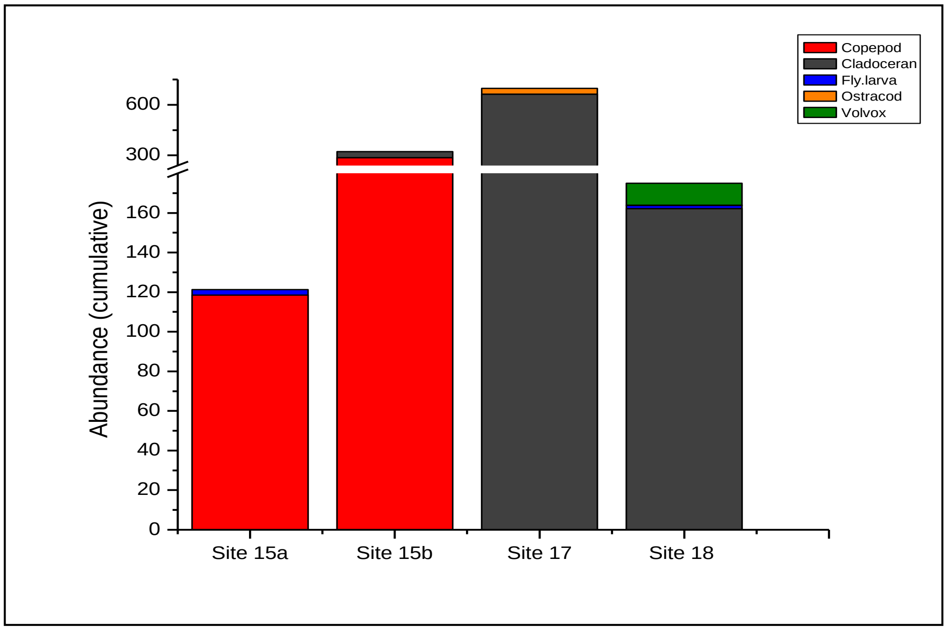


Figure 18. Cumulative abundance of zooplankton from pond samples.

Fish.

Ten species, totaling 2,170 fish, were captured at 24 sampling sites (Table 3). Seining accounted for 91% of captures with the remaining fish taken by angling. Adult specimens of six species were captured via hook and line: Arctic grayling (*Thymallus arcticus*), Arctic char (*Salvelinus alpinus*), lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), sheefish (*Stendous leucichthy*), and chum salmon (*Oncorhynchus keta*). Five species were captured via seine, ordered here by total catch abundance: Arctic grayling, longnose sucker (*Catostomous catostomus*), round whitefish (*Prosopium cylindraceum*), slimy sculpin (*Cottus cognatus*),northern pike and unidentified whitefish. Except for slimy sculpin, of which both adults and juveniles were captured, all fish captured by siene were juveniles. Fish known to be present in the river but not captured in our survey include the broad whitefish (*Coregonus nasus*), least cisco (*Coregonus sardinella*), Bering cisco (*Coregonus laurettae*), Dolly Varden (*Salvelinus malma*), burbot (*Lota lota*), Alaska blackfish (*Dallia pectoralis*) and ninespine stickleback (*Pungitius pungitius*) (USNPS 2008). Adults of most species were also observed visually in the river from our rafts.

The Arctic grayling was the most abundant and widely distributed species sampled (Fig 19). Juvenile grayling were caught at 14 of 18 (78%) seine samples sites, while adults were captured by hook-and-line on each day of the survey and were the most common fish sighted. Round whitefish were caught at 66% of seine sites. Large schools of unidentified adult whitefish were observed at several sites, most often in slow-moving water at the mouths of tributaries or in other off-channel habitat. Shoals of large longnose suckers were also commonly observed in the moderately deep (1-2 m), slower moving sections of river. Chum salmon, were seen spawning in side channels and river margins downstream of RKM 137 (Reed River Segment) and were particularly abundant near the confluences of major tributaries. One of the largest spawning aggregations observed was at Site 7 (Segment 4), in a series of pools on the delta fan at the mouth of Akpelik Creek. Redds had been constructed in areas of where extremely cold (10˚C) spring water entered the pools. Schools of shee (some estimated to contain over 200 individuals) were readily visible and available to hook-and-line sampling beginning at RKM 83 (Segment 4).

Common name	Scientific name	Seining	Angling	Total
Arctic grayling	*Thymallus arcticus*	989	82	1071
Longnose sucker	*Catostomous catostomus*	653	0	653
Round whitefish	*Prosopium cylindraceum*	250	0	250
Sheefish	*Stendous leucichthys*	0	83	83
Slimy sculpin	*Cottus cognatus*	61	0	61
Chum salmon	*Oncorhynchus keta*	0	10	10
Northern pike	*Esox lucius*	6	8	14
Lake trout	*Salvelinus namaycush*	0	8	8
Humpback whitefish	*Coregonus pidschian*	0	2	2
Arctic char	*Salvelinus alpinus*	0	1	1
Total		1976	194	2170

Table 3. Number of fish by species captured by seining or angling.

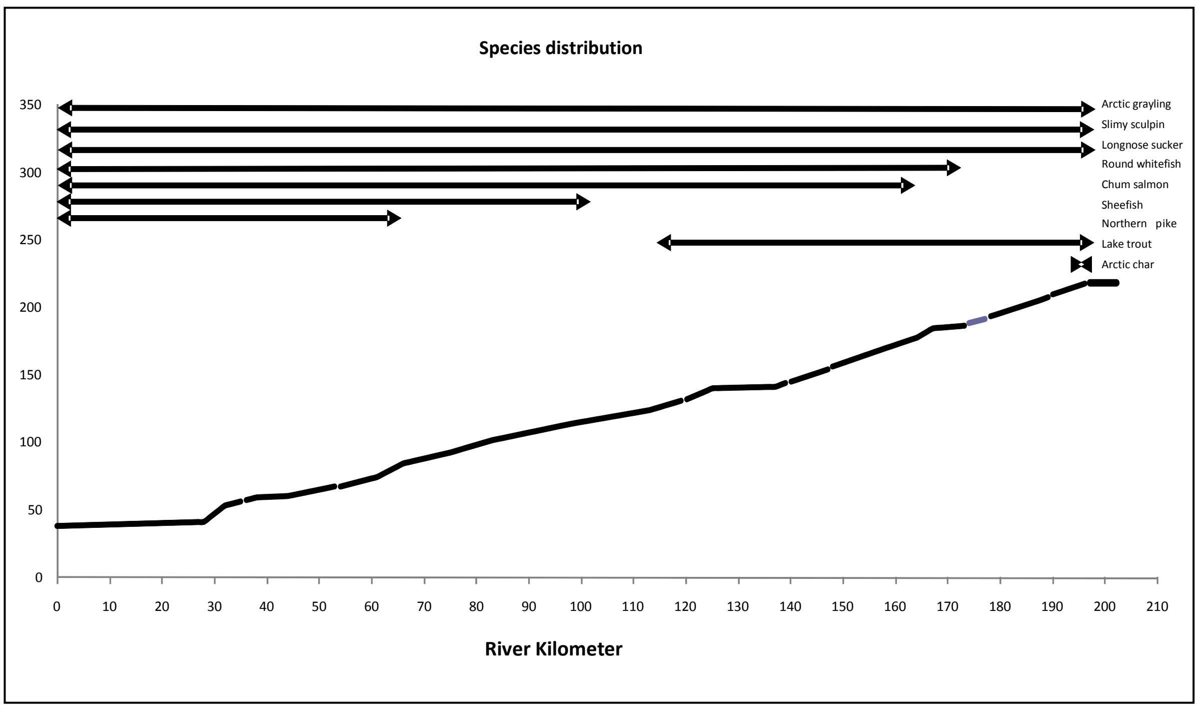


Figure 19. Fish species distribution along the Kobuk River.

Catch per unit of effort (CPUE, measured as number of fish captured per seine haul) was calculated by habitat type. CPUE was much lower in the mainstem Kobuk (15 fish per seine haul) than in off-channel habitats (24 fish per seine haul). Abundance and diversity of fish species per seine haul increased as we moved downstream. Diversity increased from 2 species at the first sampling site to 6 species at the final site (Fig. 20).

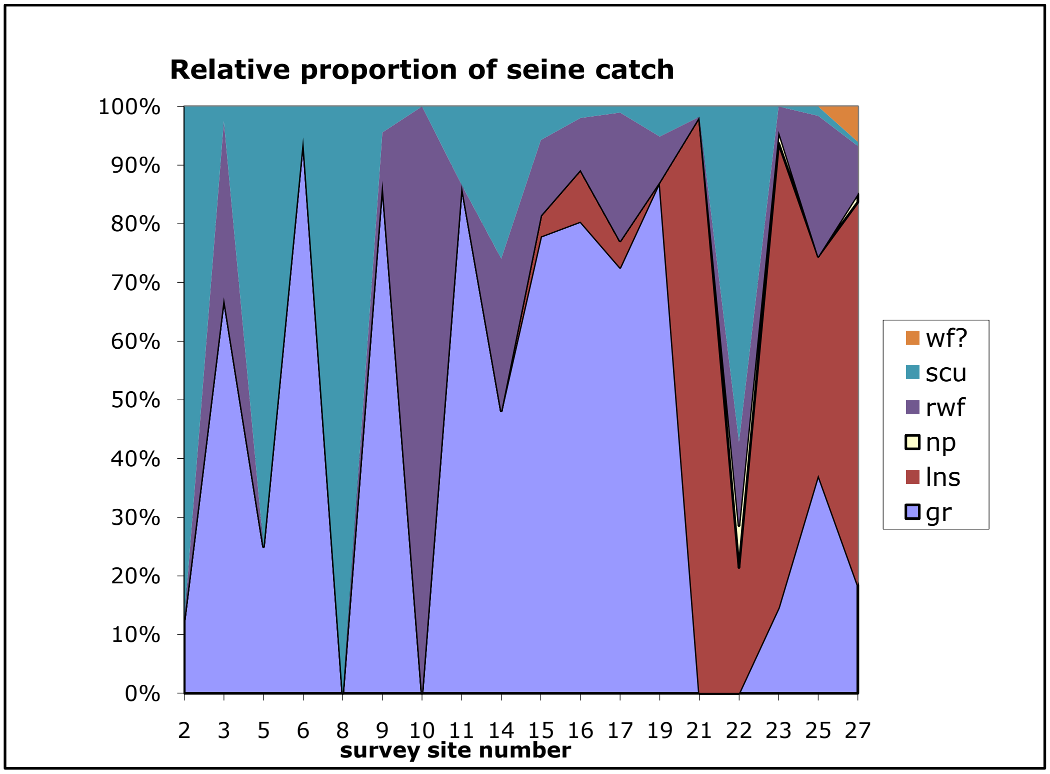


Figure 20. Relative proportion of seine catch, showing increasing species diversity at downriver sites. wf? is unidentified whitefish; scu is slimy sculpin; rwf is round whitefish; np is northern pike; lns is longnose sucker; gr is Arctic grayling.

Food Web and Connectivity.

Geomorphic geological processes create habitat heterogeneity which is typically positively associated with taxonomic and functional diversity in river systems (Ward, Tockner et al. 1999; Robinson, Tockner et al. 2002). Figure 21 displays a simplified schematic depicting the dominant biotic interactions on the upper Kobuk River. An essential component of this model addresses the importance of the different types of habitat that occur within the Kobuk River watershed. On the Kobuk, we defined aquatic habitat types as mainstem, side channel or tributary. Often side channel and tributary habitats are grouped and referred to as off-channel habitats. The mainstem is of critical importance to overall ecosystem structure and function because it is the primary connection between habitats (Fig 4). The extent to which individual habitats are spatially and temporally connected may ultimately determine the future structure of this ecosystem.

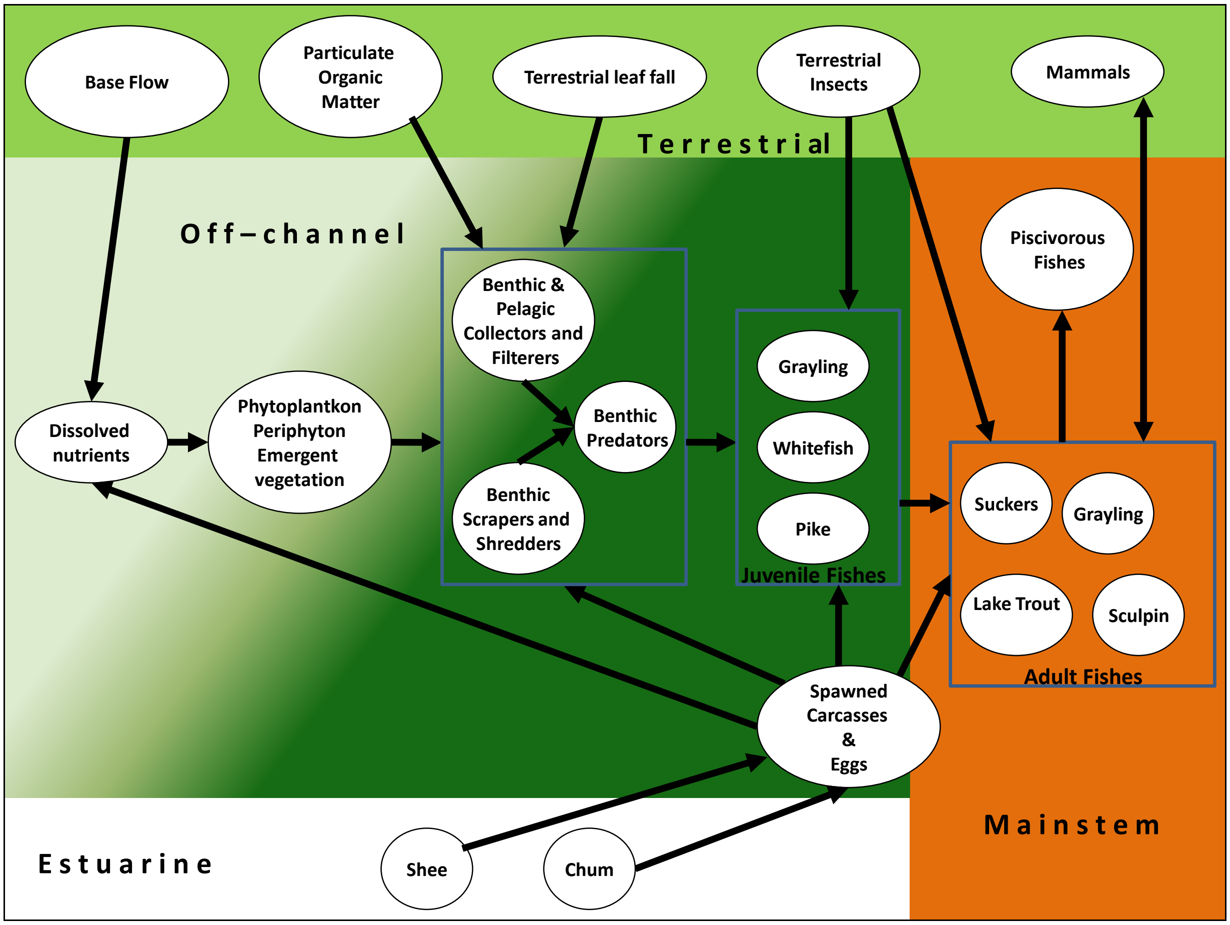


Figure 21. Schematic of simplified Kobuk River foodweb, showing habitat connectivity and trophic relationships.

Our data and analysis indicate that off-channel habitat of the Kobuk River contributes most of the biological production to this ecosystem. Primary productivity in off-channel habitat is largely composed of autotrophic producers and particulate organic matter (both peat and terrestrial leaf litter) that are consumed by functionally distinct invertebrate guilds. These primary consumers, in turn, support populations of juvenile fish including Arctic grayling, several species of whitefish, and northern pike (*Esox lucius*). Off-channel habitat productivity is additionally supported by allochthonous inputs of marine-derived nutrients from chum salmon eggs and post-spawned carcasses, while riparian corridors provide terrestrial insects during the growing season. Finally, off-channel habitat may provide periodic subsidies to a biologically depauperate mainstem.

Conversely, mainstem habitats are predominately occupied by adult fishes including lake trout, slimy sculpin, Arctic grayling, and longnose sucker. Juvenile fish densities appear to be low, implying that off-channel habitats also serve as the most important rearing grounds for young of the year fish. Low mainstem benthic macroinvertebrate densities also suggest a reason for the limited mainstem rearing capacity for juvenile fishes. The adult fishes are supported largely by allochthonous food resources. Grayling, for example, were found to feed on a wide variety of terrestrial insects, while lake trout were piscivorous, while occasionally feeding on small mammals from adjacent terrestrial habitat. Because shee and chum do not feed on their upriver migration, eggs and carcasses deposited upstream provide a source of allochthonous carbon from the estuary and ocean. Overall, each habitat type plays an integral role in sustaining this system's biological integrity.

Fish Life History Strategies.

The Kobuk River fish assemblage can be categorized roughly according to spawning season and winter refuge areas, which appear linked to the timing of the annual hydrograph. Figure 22 shows the relationship of life history stages to the historical hydrograph, which is drawn in black. Spring spawners include Arctic grayling, longnose sucker, northern pike, and slimy sculpin all of which overwinter in the upper river below ice in deep pools or lakes. These spring spawners are able to access off-channel habitat during the spring runoff peak, and larvae incubate and emerge during summer, taking advantage of high productivity before entering the mainstem during the fall peak, presumably to seek winter refuge (Georgette and Shiedt 2005).

In contrast, most adult coregonids and all the salmonids overwinter in the estuary or ocean, and spend the summer migrating up river to suitable habitat before spawning in the late summer or early fall. Some of these fall spawners (such as chum salmon) may rely upon the late summer hydrograph peak to access off-channel habitat, but most utilize tributaries for spawning. Embryos and larvae incubate under ice and move toward the estuary in spring, timed with the spring break up and hydrograph peak. This delivers them to the estuary in time to utilize high spring and summer productivity (Morrow 1980).

In winter, flows in the Upper Kobuk are at their lowest and the river and its tributaries freeze to the bottom over much of their length. Winter refuge habitat is known to limit Arctic grayling and Dolly Varden populations in Arctic Alaska (Craig 1989) but other species that over-winter in upper basin lotic habitats, such as broad and round whitefish, long-nose sucker, northern pike, slimy sculpin and burbot, also depend on the unfrozen habitat created by deep pools and/ or groundwater flow. Such species are also likely affected by the quantity, quality and availability of winter refuge habitat. During this period, oxygen limitation may be a source of physiological stress for fish because of insulation of unfrozen water from the air, even though biological oxygen demand is greatly reduced due to low water temperature (Reist, Wrona et al. 2006).

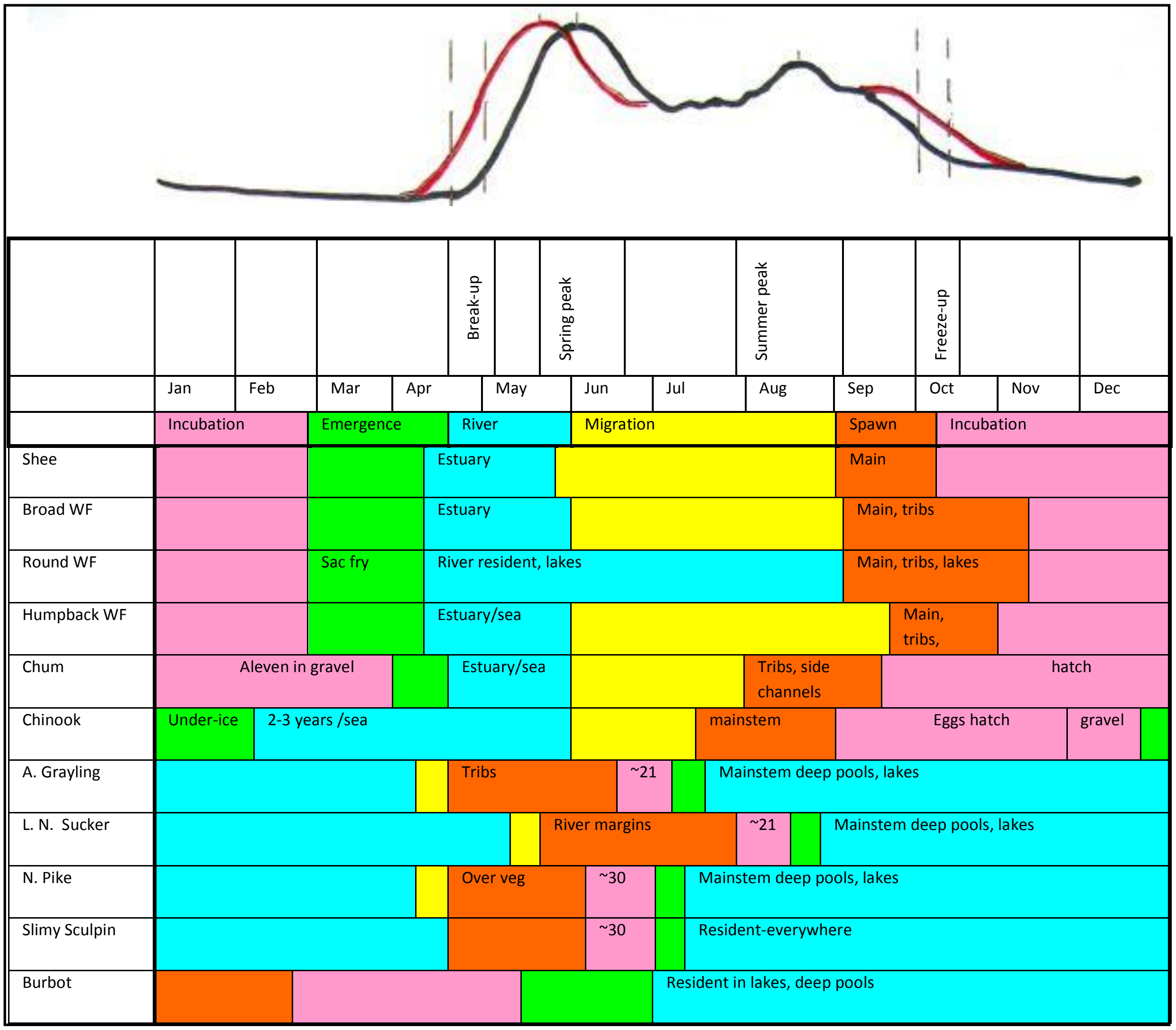


Figure 22. The effects of timing shifts in key seasonal hydrographic and geomorphic events on a sub-Arctic freshwater fish assemblage. The black line shows the current average hydrograph. The red hydrograph shows predicted shifts that are expected in the next century.

EFFECTS OF CLIMATE CHANGE

Changes in climate over the next 100 years will produce shifts in the geomorphology, hydrograph, nutrient load and biological functioning of the Kobuk River, as it will throughout the Arctic (2000). Physical changes will indirectly determine biological outcomes through habitat modification and phenological shifts, rather than by direct impacts on physiological functioning. While uncertainty remains about the physical response of the system to climate change, we outline the range of potential geomorphic and hydrologic responses and interactions, and use our current understanding of ecosystem functioning to predict resultant changes to biota. This analysis presents four potential system responses to climate change onto the ecosystem model (Table 4). We believe that a cascade of predictable changes to the biological community will result from the range of possible geomorphic and hydrologic processes that will occur on the Kobuk River in response to climate change (Figure 23).

		Spring Ice Break-up Conditions	
		Large Spring Discharge; Ice Strength Maintained	Reduction in Ice Strength; Increased Thermal Decay
Dominant Hillslope Changes	Increased Active Layer	1. More severe ice breakup, attenuated summer flows and an increase in nutrients in low-gradient tributaries.	3. Less severe ice breakup, attenuated summer flows, and an increase in nutrients in low-gradient tributaries.
	Thermo-karsting	2. More severe ice breakup, flashy summer flow peaks, major increase in sediment to tributaries in summer.	4. Less severe ice breakup, flashy summer peaks, major increase in sediment to tributaries in summer.

Table 4. Climate change scenarios for main physical drivers.

Three key assumptions about future climate conditions are made based upon regional climate trends (Summarized in column 1 of Figure 23).

First, climate change projections predict a shift in spring thaw for the region of about 12 days, for the 2090-2099 period (Beltaos and Burrell 2003; Pohl, Marsh et al. 2007; SNAP 2008; Beltaos and Prowse 2009). Fall freeze-up dates are also expected to shift later by an average of 9 days. Using these projected changes in thaw and freeze-up dates, we assume a significant increase in length of the growing season and open water period. In the North American Arctic, there has already been an increase in the duration of snow-free days at the rate of 5-6 per decade (Anisimov 2007).

Secondly, observations of precipitation in the Arctic indicate an increase by about 8% over the last 100 years (ACIA 2004). Much of the increased precipitation has fallen as rain, mostly in the winter months. We assume a continuation of this trend.

Finally, air temperatures from 1961-90 show a warming trend of about 0.68 C per decade (Brabets 2001), leading to a concurrent increase in the percentage of annual precipitation that falls as rain (rather than snow), mostly in the winter months. The increase in warming is more pronounced in the winter months relative to summer (Anisimov 2007).

If these trends continue, winters may become markedly warmer, while summer maxima change only slightly. Because of this, we hypothesize that changes to fish and invertebrate populations will result not from physiological limitations to temperature (but see Reist, Wrona et al. (2006)). Rather, biological shifts will be mediated by two physical drivers: 1) the spring ice break-up and resultant peak flows, and 2) surrounding permafrost processes, which govern the supply of nutrients and/or sediment

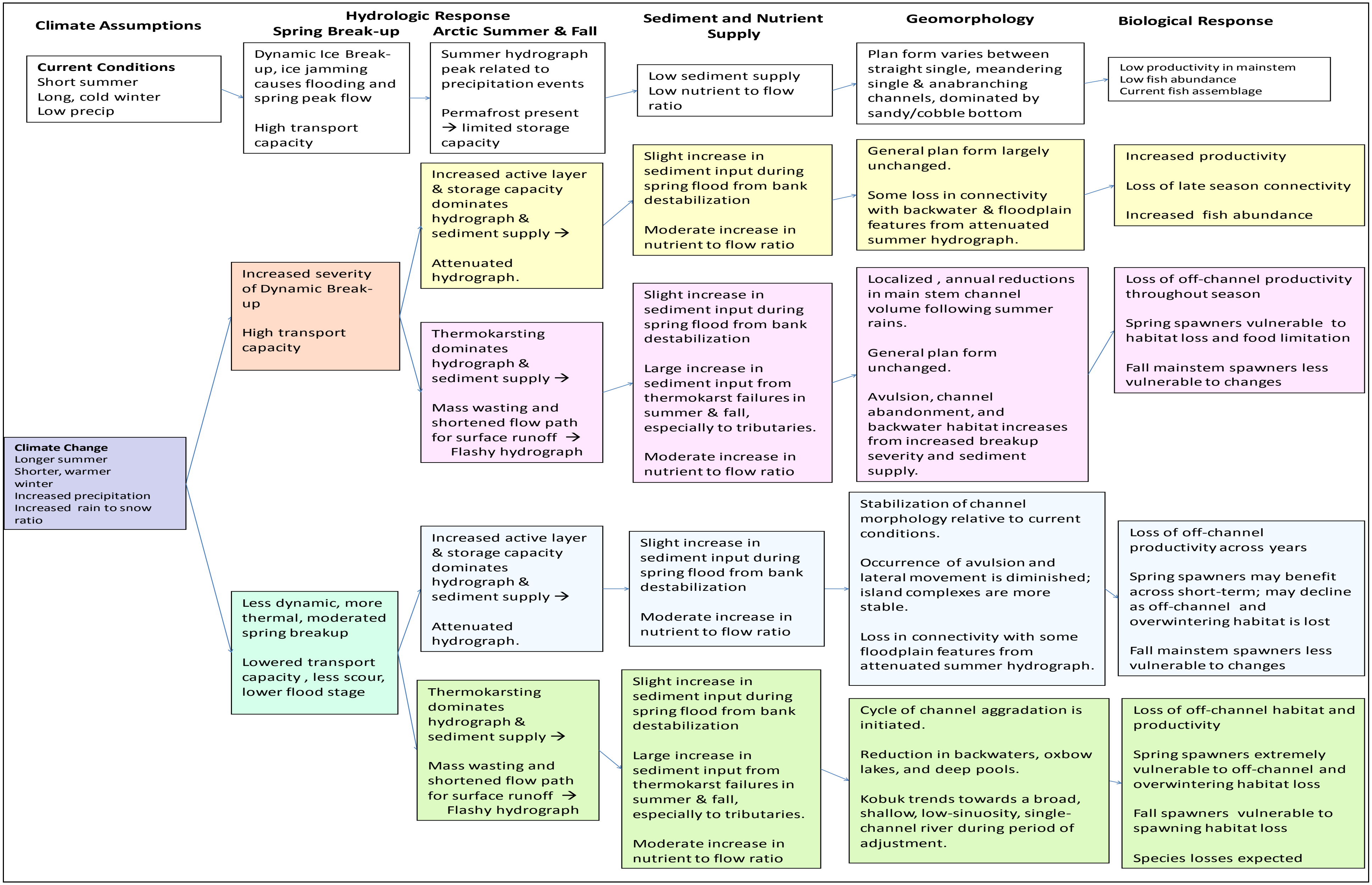


Figure 23. Climate assumptions, physical and geomorphic drivers and the predicted biological outcomes of climate change models.

to the watershed (Table 4). Both of these drivers are expected to undergo significant changes with climate change, which will interact in novel ways with the expected increase in precipitation.

Potential Hydrologic and Geomorphic Responses to Climate Change

Spring ice break-up.

Spring break-up is characterized by its timing and intensity. The timing of spring thaw affects break-up intensity and the length of the growing season. While our climate change assumptions predict an earlier annual spring thaw, we are less certain about the effect of climate change on spring break-up intensity. Ice break-up severity is partly a function of ice thickness at time of break-up and the volume of spring runoff. The thicker the ice, the larger the volume of flow required to initiate a mechanical break-up. If flows are not large enough to mechanically break and move the ice downstream, thermal decay of the ice will occur reducing the severity of ice jamming and flooding (Beltaos and Prowse 2001)

One strong possibility for the Kobuk River under climate change is an increase in the severity of the effects of ice break-up. According to Beltaos and Burrell (2003), in cold regions, ice thickness will unlikely change significantly due to the insulation provided by the ice sheet and snow cover. Therefore, volume of spring runoff could be the primary factor influencing future severity relative to current conditions. The composite GCM from the SNAP project (SNAP 2008) and the Arctic Climate Impact Assessment (ACIA 2004) predict more precipitation, possibly exceeding a 30% increase in the winter and autumn. Therefore, it is reasonable to predict a scenario in which spring thaw flows exceed current flows. If larger and earlier discharge applies pressure on river ice before significant thermal decay, break-up will occur while more of the river is still frozen, translating to an increase in spring flood severity relative to current conditions.

Alternatively, combined conditions could cause ice break-up to become less severe. It is possible that ice strength and thickness will be significantly reduced by increasing air temperature and winter baseflows (Pohl, Marsh et al. 2007). In contrast to our first scenario, this alternative requires more dramatic changes in air temperature for extended time periods in late winter and early spring. Earlier spring thaw implies melting during a time of less intense solar radiation, causing a more protracted and less intense melt (Prowse, Wrona et al. 2006). This would result in a less severe ice break-up and less flooding relative to current conditions.

Permafrost melting.

With projected increases in temperatures, the spatial extent of permafrost in the sub-Arctic is expected to decrease and the active soil layer thickness is likely to increase (Anisimov 2007). Decreasing permafrost will allow additional infiltration and groundwater flow and translate to increased winter baseflow (Woo, Kane et al. 2008). Consequently, changes in the spatial and temporal extent of nutrient influx are also predicted within the Kobuk River watershed. While increased active layer thickness from permafrost melt should result in a less "flashy" (ie, a more attenuated) response to summer rainfall (McNamara, Kane et al. 1997; Hinzman, Bettez et al. 2005; Pohl, Marsh et al. 2007; Walvoord and Striegl 2007), melting permafrost also leads to the co-occurring and countervailing effects of thermokarsting.

In contrast to active layer thickening and consequent shifts from overland to groundwater flows, thermokarsting can shorten flow pathways to the river and reinforce peaks in the summer hydrograph (Gooseff, Balser et al. 2009).

Both active layer thickening and thermokarsting are likely to occur under warming scenarios. The spatio-temporal distribution of these effects is unpredictable and the relative extent of one or the other is unknown. High gradient tributaries draining high elevation basins underlain primarily by bedrock will likely be unaffected by permafrost melt. However, lower gradient tributaries surrounded by discontinuous permafrost near stream-banks and continuous permafrost beyond will see increasing inputs of fine sediments and nutrients from decaying organic material and increased base flows concurrent with increases in the active surface layer, causing a shift from relatively clean (nutrient and solute poor) overland flow, to baseflows rich in nutrients (N, P and C), organic acids, and dissolved humic material (Prowse, Wrona et al. 2006).

Most of these liberated nutrients and sediments will be diluted quickly once mixed with the main-stem Kobuk. Similarly, while highly tannic material containing large quantities of carbon and very low pH will increasingly drain into the Kobuk, the enormous dilution and buffering capacities of the river will make acidification negligible over the next 100 years. Many of the dramatic water quality changes in the Kobuk will likely occur not in the main-stem, but in the tributaries, side channels, and back waters.

The net effect on the main river will depend on the relative importance of active layer thickening or thermokarsting. Thickening of the active layer may not significantly affect the Kobuk mainstem, because its large size can effectively dilute groundwater derived solute inputs. However, thermokarsting has the potential to introduce enormous inputs of sediments and nutrients in small spaces and short times to the mainstem. Depending on volume and timing, this could have important and possibly deleterious consequences for fish and other organisms.

Conceptual Model: Predicting Physical and Biological Responses to Climate Change

Using our climate change assumptions and understanding of current ecological conditions, we present four different scenarios that depend upon the stochastic interaction of two key physical mechanisms— changes in breakup intensity and permafrost condition—with a third physical driver, the predicted increase in precipitation. The resulting scenarios bracket the range of likely responses in hydrology and morphology, allowing us to project changes in the system’s biological condition, including productivity, biomass, and species assemblage (Fig 23). Future observations of physical change in the system will provide increased accuracy of predicted biological outcomes with time.

Scenarios

Scenario 1

*Increased magnitude of spring breakup

*Attenuated summer flows

*Increased nutrients

Under this scenario, the spring break-up is more severe than current conditions. An increase in active layer thickness leads to attenuated summer peaks in the hydrograph and increased baseflow. As a result, there is an increase in warm water input to the river during winter months, and a higher nutrient influx during the spring and summer. Changes in nutrient inputs will be especially significant for low-gradient tributaries and side channels that are largely disconnected from the river during summer months. Nutrient inputs to the mainstem will likely be diluted. A larger sediment flux in springtime to downstream valley reaches and oxbow lakes will result from increased scour, bank erosion, and transport capacity that accompany a more severe ice break-up. General channel form will be largely unchanged, wandering between straight and meandering, single and anabranching channels.

Increases in allochthonous nutrients from a more severe break-up and permafrost degradation are projected to stimulate primary production, including the establishment of aquatic macrophytes (Benstead, Deegan et al. 2005), in tributary and side channel habitats where a low flow to nutrient ratio exists. The increase in aquatic and terrestrial primary production and an influx of organic carbon (such as peat) from melting permafrost may increase available food resources for aquatic invertebrates. In conjunction with the extended growing season, the abundance, diversity, and biomass of invertebrates in all Kobuk River habitats, including the mainstem, is expected to increase. This should in turn benefit spring spawning fish and round whitefish that rely upon local food sources throughout the year.

The more forceful break-up may also benefit fish by maintaining connectivity between off-channel habitats and the mainstem (especially important for spring spawners and round whitefish), increasing velocity refuge, exposing gravel substrate for spawning, and promoting the accumulation of large woody debris (Junk 2005). However, by late summer, the benefit may be largely lost because of the attenuation of the late summer hydrograph, reducing the availability of off-channel and side channel habitat.

An increase in ice scour during break-up may increase mortality in the embryos and alevin of fall spawners (which emerge before breakup) and resident adult fish. The success of spring spawning fish (non-salmonid and Arctic grayling) may be less affected by more severe spring flows since spawning occurs just after the spring break up. Fish that spawn in mainstem are most likely to be affected by increases in the magnitude of break up. These fish include the broad whitefish, humpback whitefish and especially shee, which require very particular main channel spawning habitat of mixed gravel and sand, with little silt (Alt 1969).

Scenario 2

*Increased magnitude of spring breakup

*Increased flashiness of hydrograph

*Increased nutrients and sedimentation

Thermokarsting replaces active layer depth as the dominant driver of the summer hydrograph and sediment supply rate. Flow is more rapid and less prolonged (not attenuated), and hillslope erosion increases. This results in increased sediment accumulation post-break-up and throughout the summer, until transported by the high flows of late summer rain events or the following spring break-up. Tributaries experience high local inputs of fine and coarse-grained sediment that may exceed their transport capacity during the spring and summer, possibly leading to poor water quality and benthic smothering. During heavy summer rain events, this store of sediment will be partially transported into the mainstem Kobuk, where some of it may settle and fill pools and other refuges for fish before the winter freeze and cause local, annual reductions in channel volume. In spring, the ice break-up will scour and transport the sediment downstream, depositing it on lower-reach floodplains and in the estuary. General channel structure in the main stem Kobuk will be largely unchanged, although there will likely be an increase in avulsion, channel abandonment, and backwater habitat resulting from intensified break-up and larger sediment supply.

As in the first scenario, a more severe spring ice break-up is expected to produce an increase in available allochthonous material and nutrients supporting primary and secondary production due to a larger flood event and a predicted increase in terrestrial primary productivity. A longer growing season may encourage the establishment of primary and secondary producer communities that were historically unable to persist in this environment. However, thermokarsting may initiate a cycle of erosion and sediment influx during late season rain events that may suppress primary and secondary producers. Suspended sediments can reduce primary productivity through light attenuation associated with increased turbidity (Scrimgeour, Prowse et al. 1994) and sudden influxes of sediment can deplete oxygen levels, cover food supplies, increase macroinvertebrate drift rates, and clog filter feeding structures (such as labral fans), leading to an overall decline in habitat quality and quantity (Ryan 1991). The effect of sedimentation on these communities largely depends on the spatial arrangement and frequency of thermokarsting in the Kobuk River Valley, making low gradient tributaries and off-channel habitat particularly vulnerable. However, the spring ice break-up is projected to scour previously accumulated sediment each year, creating an annual cycle of high productivity in the spring and early summer, with declining productivity and species abundance in the late growing season as sedimentation reduces habitat quality.

Spring spawners become vulnerable to thermokarsting because of increased egg and larval mortality due to smothering, habitat loss, or expulsion into the main channel where food resources and refuge are limited. Mainstem fall spawners may be largely unaffected by sedimentation because of the high sediment transport capacity of the Kobuk. Rather, fall spawner eggs, fry and alevin may be vulnerable to earlier and more intense scouring as break-up occurs earlier and more forcefully. Because whitefish spawning is triggered by decreasing water temperatures, they may be subject to both a delay in spawning and an earlier spring break up (Fig. 22, red line shows a predicted hydrograph). Late season flashiness due to storms may interfere with fall spawners. Chum may be vulnerable to changes in the benthos of tributaries from heavy scouring in spring and high sediment deposition in fall.

Scenario 3

*Decreased magnitude of spring breakup

* Attenuated summer flows

* Increased in nutrients

Ice break-up becomes less, rather than more, severe. Instigation of the spring thaw is earlier with less intense solar input allowing for a more prolonged, thermal melt. While spring floods are still likely, they will be less severe than under current conditions, with reduced bank erosion and scour. Much like scenario 1, active layer depth dominates the summer hydrograph, nutrient, and sediment supply: baseflow increases and summer peaks are attenuated due to increased active layer thickness. Similar increases in nutrient flux are expected. However, a decrease in stream competence and capacity in spring, combined with the loss of a summer peak event, causes stabilization of channel morphology relative to current conditions. The occurrence of channel abandonment, avulsion, and lateral movement is diminished: point bars, gravel islands, and anabranching occur much less frequently and island complexes become more stable. Some sediment that would otherwise be transported downstream is deposited in backwater sloughs and oxbows. Also, the attenuation of summer flows translates to a loss in connectivity with some backwater and floodplain features.

A less severe spring ice break-up may decrease allochthonous inputs to the Kobuk River, while sedimentation increases due to hydrograph attenuation. Reduced break-up intensity will allow for the persistence of particular autotrophic communities due to a longer growing season and a decrease in scour potential (e.g., the perennating organs of aquatic macrophytes may persist in the bed substrate after ice break-up). In the short term, nutrient enrichment from permafrost degradation may promote the growth of autotrophic communities in tributaries, side channels, and oxbow habitats. Secondary producers are expected to capitalize on these additional carbon sources, including the release of peat associated with permafrost melt. However, a moderated ice break-up may lead to a decline in backwater sloughs and oxbow habitats over an unknown time period. In addition, an attenuated summer hydrograph could lead to abrupt late season disconnect between these habitats and the mainstem Kobuk River. A combination of these events would negatively affect primary and secondary production, likely reducing overall abundance, diversity and biomass with subsequent impacts on higher trophic levels. Because low gradient tributaries are typically one of the dominant sources of ecosystem productivity on the Kobuk, the positive effect of an extended growing season may be limited through a loss of these productive habitats.

The loss of habitat complexity resulting from the decline in anabranching, scour pools and large woody debris may negatively impact fishes as well. The loss of off-channel habitat may be particularly detrimental to northern pike, which rely upon it for reproduction, rearing and adult foraging. While pike spawning may benefit in the short term from an increase in macrophytic vegetation, over the long term, much of this habitat is expected to become successional wetland, poorly suited for most fishes. Other spring spawners will be subjected to a decrease in both suitable spawning and foraging habitat, exacerbated by the attenuation of the late summer hydrograph. Aggradation of scour pools may lead to a decrease in winter refuge. Fall spawners may be less subject to loss of foraging, refuge, and spawning habitat in the main channel, but populations that use off-channel habitat (for instance, chum, or possibly some of the whitefish) remain vulnerable.

Scenario 4

*Decreased magnitude of spring breakup

*Increased flashiness of hydrograph

*Increased nutrients and sedimentation

The spring break-up becomes less severe (as in scenario 3), leading to reduced bank erosion and sediment scour during ice break-up. Thermokarsting (rather than active layer depth) dominates the summer hydrograph, nutrients, and sediment supply: the response in flow to summer rain events is more rapid and less prolonged (not attenuated), and hillslope erosion significantly increases sediment supply to the entire watershed. As in scenario 2, some of this sediment is transported into the mainstem during storm events during the late summer, filling in some pools and causing local reductions in channel volume. However, the river loses much of its spring transport capacity and ability to annually entrain and move sediment downstream. A combined increase in coarse-grained sediment from thermokarsting and reduction in the spring flood from warmer temperatures leads to a decrease in channel avulsion and anabranching, and initiates a cycle of channel aggradation and simplification. This reduces the number and size of backwaters and oxbow lakes and fills in deep pools. Over time, the Kobuk adjusts and straightens itself in order to cope with its increased sediment supply and loss of stream power, trending towards a broad, shallow, low-sinuosity, single-channel river.

Similar to scenario 3, a less severe ice break-up suggests an overall decline in the size of the early season allochthonous load and nutrient inflow associated with this event. While a longer growing season and less severe ice break-up might promote an increase in primary and secondary production, thermokarsting works antagonistically by delivering a major influx of sediment to the system, resulting in benthic smothering, depleted oxygen levels, and overall habitat loss. These declines in habitat complexity are expected to amplify across years, because of the reduction in flow transport capacity associated with the less severe ice break-up. A combination of sedimentation in tributaries and loss of critical habitat such as incipient oxbows and side channels should strongly affect both primary and secondary producers with overall declines in abundance, diversity, and biomass. Backwater habitat would tend to be transformed into successional wetland habitat, with an associated loss of food support for the Kobuk. If tributary transport capacity is sufficient to flush sediments out during the spring melt, then low gradient tributaries may continue to provide suitable resource subsidies to biota early in the growing season. However, where thermokarsting frequently occurs or sedimentation exceeds early season transport capacity, tributaries may show an overall decline in productivity throughout the growing season. This latter situation may prove to be deleterious for overall ecosystem structure and function, suggesting that biotic communities may become dependent on a depauperate mainstem for resources.

Spring spawners may be subject to declines in spawning, rearing and foraging habitat due to the loss of structural complexity. Overwintering habitat may be severely affected by the loss of scour pools, which provide under ice refuge. A decrease in winter baseflows due to a decline in upslope conditions may further impact winter refugia.

Fall spawners may be most subject to a loss of spawning habitat if mainstem transport capacity is reduced. Shee may be particularly vulnerable because of their specific (and apparently narrow) habitat requirements, and limited global distribution. A thermokarst event along the prime shee spawning habitat of the Kobuk could significantly impair the population. Fall spawner larvae may be susceptible to any changes in post-emergent conditions under ice, and any reduction in river transport capacity may have unknown effects on downstream larval migration.

CONCLUSIONS

Although uncertainty exists in both our understanding of the Kobuk River's sub-Arctic riverine ecosystem and in future climatic conditions, our models of ecosystem function and climate change give resource managers a basis upon which to monitor and understand future change in the Kobuk River watershed. Off-channel productivity, permafrost processes, and the magnitude and timing of spring and summer flows are of critical importance to local species (especially fish) and food web structure.

In particular, we believe that the effects of air temperature on the spring melt and on permafrost degradation are the most critical elements to monitor in the Kobuk ecosystem. Climate models suggest that while winter temperatures may be higher than normal, summer temperatures will change only slightly. Physiological and phenological responses to temperature may be neither as critical nor as predictable as geomorphic changes to habitat in Arctic and sub-Arctic river ecosystems. In contrast, the interaction between the nature of the spring ice break-up and the rate of sediment inputs as suggested by our Scenarios suggest a progression of ecosystem disturbance and unpredictability (Fig. 23).

Increased sedimentation from permafrost degradation may be mediated to some extent by the annual break-up. In Scenario 1, the increase in active layer erosion and deposition, combined with a severe break up, may have a positive effect on primary and secondary productivity in the early season, benefitting fish somewhat. However, the effect of thermokarsting in Scenario 2 is that critical habitat for fish foraging is lost throughout the season, heavily impacting spring spawning fish larvae during a critical time in development. Fall spawners may be less vulnerable, unless the break up is advanced before emergence, which could result in considerable embryo or larval mortality. Expected population-level effects to monitor would be increased variability in spawning success of key fishes.

The alternative possibility, the attenuation of spring break up severity, increases the deleterious effects of sedimentation. In Scenario 3, the result is a loss of off-channel habitat, affecting the most productive foraging components of the river system, that accrues over time. This would again have the largest impact on spring spawning fish, while fall spawners may be less vulnerable (particularly if the spring break up produces less mortality) if spawning habitat remains available. However, an increase in thermokarsting without annual scouring from break up, as in Scenario 4, may have enormous and irreversible effects on fish species due to the loss of foraging, refuge and spawning habitat. Under both of these scenarios, the loss of break up severity will lead to long-term, irreversible declines in fish populations. Shee in particular appear to be quite vulnerable to rapid declines and extinction, and are therefore a good choice for monitoring climate change effects.

Managers trying to monitor an entire ecosystem are faced with broad challenges in deciding where to direct money and energy. We suggest that early responses to climate change will be manifest in the loss of off-channel habitat and productivity, with immediate effects on spring spawning fish, indicating minor system changes. In contrast, declines in fall spawners may suggest more dramatic effects of thermokarsting or changes in ice break-up that result in both off-channel and mainstem habitat changes, and presage basin-wide extinctions of some species. We suggest the use of satellite imagery and local knowledge for information about permafrost degradation, and a monitoring program to track changes to select areas that show evidence of intact permafrost, a deep active layer, and recent thermokarsting. In addition, we suggest that key fish populations (shee, chum, grayling) be monitored as indicators of undetected but inevitable geomorphic change on the Kobuk River.

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