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Environmental heterogeneity and community structure of the Kobuk River, Alaska, in response to climate change

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Abstract. The Kobuk River runs west along the southern Brooks Range from Gates of the Arctic National Park in Alaska, USA, to the Chukchi Sea. It is highly vulnerable to changes in climate due to its sub-Arctic location, unique geography, and permafrost foundation. Combined with its pristine condition, these qualities make the Kobuk an ideal system upon which to build a conceptual model for predicting ecosystem effects of climate change. We constructed a conceptual ecosystem model for the Kobuk River synthesizing surveyed baseline hydrologic, geomorphic and biotic conditions with literature on Arctic rivers. While the mainstem Kobuk has limited 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 dependent largely on intermittent pulse flows that connect riverine habitats, allowing periods of late summer high productivity in off-channel habitat. Spring break-up and hill slope processes are critically important for maintaining habitat complexity and inter-connectivity. Climate change models predict the region will experience a disproportionate increase in average winter air temperature relative to summer temperatures, in the number of ice-free days, and in annual rainfall. Our conceptual model predicts that changes to fish and invertebrate populations on the Kobuk River will result not from physiological responses to increased temperatures, but rather to shifts in two main physical drivers: 1) spring break-up intensity, resulting in changes to scour rate and sediment deposition; and 2) discontinuous permafrost melt, resulting in widespread heterogeneous zones of active layer thickening and thermokarsting. The interaction of these two drivers offers four potential scenarios of geomorphic change in the system and four dramatically different biological outcomes. This model should help managers and scientists evaluate the magnitude and direction of ecosystem changes as they occur within the Kobuk system and potentially other sub-Arctic river systems.

Key words: Alaska; climate change; ecosystem function; fish biology; flow-pulse; food webs; hydro-geomorphology; permafrost; sub-Arctic; thermokarst.

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Introduction

Arctic climates have warmed at approximately twice the global rate over the last several decades, making Arctic ecosystems more sensitive to climate change than those in temperate regions (Anisimov et al. 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 et al. 2005, Prowse et al. 2006, Pohl et al. 2007), but none have developed an integrated ecosystem conceptual model to form the basis for predicting outcomes. We present the results of an interdisciplinary study on the sub-Arctic Kobuk River as an example of such a model. The Kobuk River is well suited to climate change study because of its relatively pristine condition, which allows isolation of climate effects from other anthropogenic drivers.

In August 2008, an interdisciplinary team of 12 researchers surveyed the upper river from near the headwaters (in Gates of the Arctic National Park) to Kobuk Village (Fig. 1), characterizing physical habitat, water quality, invertebrate and fish assemblages, and the natural history of the region. The results of this survey were combined with a literature review to create a conceptual model detailing the biological effects 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 the effects of climate change on two physical drivers: 1) timing and magnitude of the spring break-up, and 2) degradation of permafrost.

Spring ice break-up is an important geomorphic driver on Arctic rivers, capable of generating rapid increases in stage and velocity. Successive formation and failure of ice jams force the river to forge alternate flow paths (Scrimgeour et al. 1994), causing cycles of anabranching (Burge and Lapointe 2005) which in turn drive recruitment of large woody debris, island formation, and channel network complexity (Tockner et al. 1999). Cycles of scour and erosion during break-up can produce sediment loads two to five times higher than that produced by equivalent open water flows (Beltaos and Burrell 2003, Beltaos and Prowse 2009).

Permafrost likewise has a major influence on flows and geomorphology. The Kobuk River basin is largely underlain by continuous permafrost (about 83%) which provides channel structure by reinforcing banks, slowing changes in channel migration and anabranching, and reducing erosion and other hillslope processes. Most soils are classified as gelisols where permafrost dominates; about 21% of the basin area is classified as rugged mountain, presumably dominated by bedrock (Brabets 2001). Soils that freeze and thaw seasonally define the active layer, which governs water, sediment and nutrient supply to the watershed (White et al. 2007, Woo et al. 2008, Gooseff et al. 2009). In the Kobuk watershed, active layer thickness ranges from 40–80 inches depending on soil types and vegetation cover (Brabets 2001). The thickness of the active layer affects the rate of baseflows 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 in the ground surface from reduced support of overlying unfrozen layers (i.e., thermokarsting). Connected depressions can form channels that quickly funnel precipitation runoff to the stream network as surface flows, causing a rapid response in the hydrograph (Gooseff et al. 2009). The resulting erosion and bank instability can increase the amount of sediment in the river, which may accumulate locally until fall rain events or the spring flood provide sufficient capacity to remove such deposits (Gooseff et al. 2009). As a consequence, thermokarsting and associated hillslope erosion may lead to major geomorphic and water quality changes affecting productivity and spawning habitat in both the mainstem and Kobuk tributaries.

The geomorphic consequences of warming have biological implications that can be understood ecologically as loss of habitat, food supply, and connectivity. These disturbances, rather than attainment of physiologically limiting conditions for organisms, will drive future changes on the Kobuk River. Under the current climate change predictions for the region, most warming will occur in winter (Anisimov et al. 2007), when it is unlikely to reach physiologically limiting temperatures. Instead, the pattern and timing of

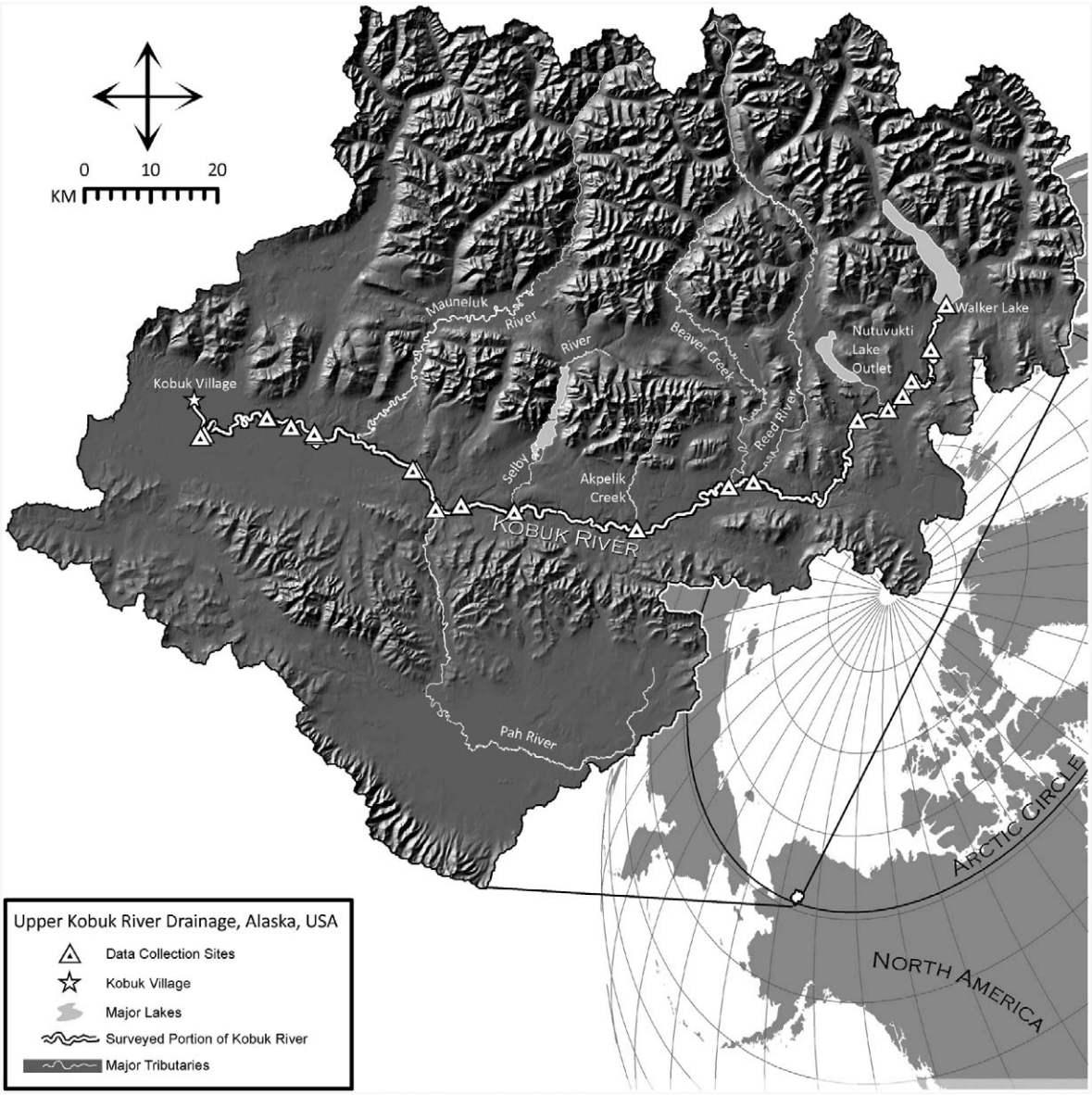

Fig. 1. Study area and data collection sites along 190 km of the Upper Kobuk River, Alaska.

warming may have large impacts on stream hydrodynamics and morphology, resulting in ecological disturbance. While uncertainty surrounds the interaction of the physical drivers, four different scenarios logically emerge which bracket the range of potential riverine morphological, hydrological and biotic responses across the next century. Because each scenario leads to a distinct biological outcome, our model provides a framework for understanding the implications of observed changes in the system, which can be used to drive hypothesis-driven science and management on the Kobuk.

Materials and Methods

Field survey, climate data and literature review

Using standard methods, we collected and quantified water chemistry, invertebrates, and fishes at 17 sites along 190 km of river (hereafter referred to as river kilometer, RKM) (see Durand et al. 2009 for a full treatment). Primary producer

categories, such as filamentous algae, diatom films and emergent vegetation were visually identified. Physical and biological data were collected from 11–22 August, 2008 during a rafting expedition that began at the Walker Lake outlet (RKM 190) and ended at Kobuk Village (RKM 0). Data collection sites were selected to cover a variety of "off-channel" habitats in addition to the Kobuk mainstem, including tributary confluences, backwaters, oxbow lakes, and tundra ponds. A core group of seventeen sites were fully characterized (Fig. 2), while additional water quality, invertebrate and fish samples were taken sporadically at additional sites in order to broadly characterize habitats of interest. Collectively, these data were used to describe current (baseline) river conditions.

Physical site characteristics were recorded on maps geo-referenced using a Trimble Nomad Global Positioning System (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 geolocating off-channel habitats. In conjunction with US Geologic Survey topographical maps (US Geologic Survey 2009*a*) these data were used to measure sinuosity and meander belt width.

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 and dissertations. This synthesis 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 the Discussion. The scenarios for future climate change are based on predictions from the IPCC Fourth Assessment Report: Polar Regions (Anisimov et al. 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 area weighted average composite predictions of the five best performing Global Climate Models (GCMs) applied to the Kobuk River watershed (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, and dates of freeze up and of thaw which have been broken down into decadal averages.

Results

Survey results

Geomorphology and hydrology.—The Kobuk River is a gravel and sand-bedded wandering river, located just north of the Arctic Circle running from east to west, 67° N and between 161°45′ and 154°03′ W (Fig. 1). The term "wandering river" is used here and elsewhere to describe a fluvial channel comprising alternate stable single-channel reaches and unstable multi-channel sedimentation zones (Brierley and Fryirs 2005). The Kobuk has these features and several of the reaches are clearly migrating over time. The lack of headwater glaciers leaves the water exceptionally clear. 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 six river segments, depicted in Fig. 2, and related it to the longitudinal distributions of key fish species.

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 three km long. The gradient is consistent, with no major knick points or bed steps. There are relatively straight stretches with striking channel uniformity. These stretches are wide and shallow, with gravel substrate. After the Reed River enters the Kobuk, the gradient decreases and river character changes significantly. Anabranching begins directly downstream of the Reed confluence, and island

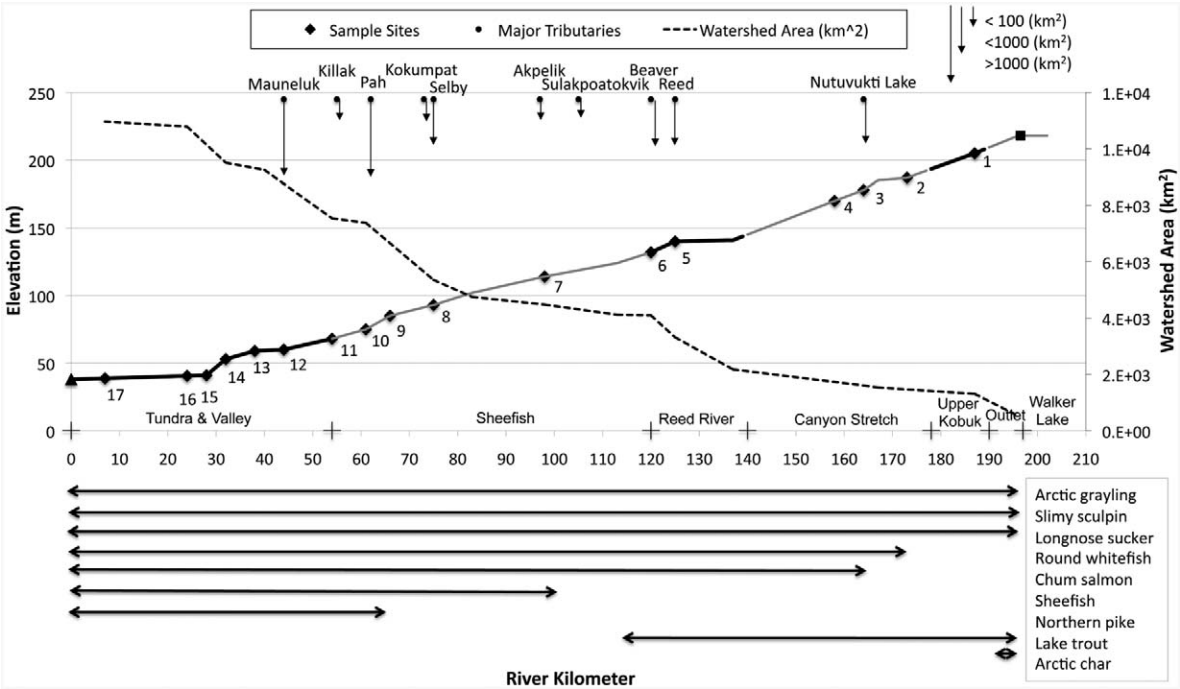

Fig. 2. Longitudinal profile of Upper Kobuk River with segment descriptions and fish species distributions.

complexes reappear several times for the remainder of the river's course down to Kobuk Village. After RKM 119, sand-gravel ripples appear, 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, about 250 km downriver.

Because the Kobuk is a sub-Arctic river, the region through which it flows 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 et al. 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, measured at Ambler and Kiana (Brabets 2001), with a range of 40–100 cm. Precipitation is greater in the upper reaches of the river basin. The Brooks Range shields the river basin from polar storms, distinguishing it from more studied rivers of the north slope of the Brooks Range, such as the Colville, the Porcupine and the Kuparuk (Hamilton and Porter 1975). Although the rain shadow effect makes the Kobuk River basin comparatively arid throughout the year (Cooper 1986), the basin is exposed to late summer storms that move inland from the Chukchi Sea (Mann et al. 2002). As a result, the Kobuk's annual average hydrograph (Fig. 3)

Table 1. Decadal averages of five GCM predictions for the A1B scenario. Predictions are given as the area weighted average of the modeled values (SNAP 2008) for the upper Kobuk River watershed.

Decade	Average air temperature (°C)		Precipitation (mm)		Length of growing season (days)	Date of freeze up (ordinal date)	Date of thaw (ordinal date)
	Summer	Winter	Summer	Winter			
2000–2009	12.5	−22.2	77.7	26.4	146.4	270	123.5
2030–2039	12.8	−21	83	29.3	149.8	272.5	122.6
2060–2069	13.9	−17.4	89.7	32.2	160	277.8	117.9
2090–2099	15	−14.6	86.5	37.6	167.9	282.2	114.4

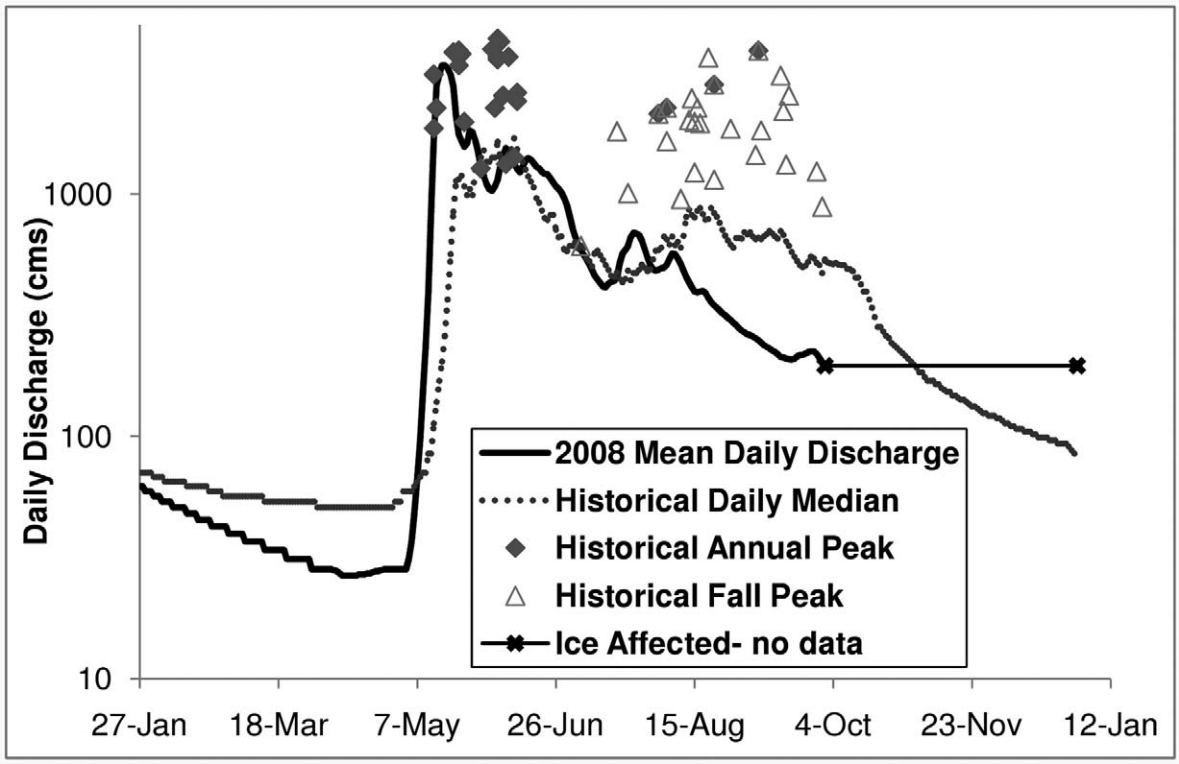

Fig. 3. Kobuk River hydrograph near Kiana, AK for the 2008 season with mean daily statistics for the previous 27 years. Data: US Geologic Survey (2009*b*).

shows one peak during the spring flood, and another in late summer, with concomitant flow variability throughout the late summer (Brabets 2001, US Geologic Survey 2009*b*).

In general, the basin experienced a drier than average year in 2008 (mean annual discharge was 370 m^3s^{-1}, placing it in the 35th percentile of water years (US Geologic Survey 2009*b*). A small summer peak occurred earlier than usual (in July), but by August the river stage had declined to below average, with a small rise observed during the sampling period associated with characteristic afternoon thundershowers.

Water quality.—Like most Arctic rivers, the Kobuk River and its tributaries are generally oligotrophic (LaPerriere et al. 2003). The Kobuk mainstem showed very low concentrations of N, P, Fe and tannins, and a neutral pH (~7) in samples taken in August 2008. High concentrations of base cations (Ca and Mg) indicated considerable buffering capacity. Groundwater flows adjacent to the river generally had higher concentrations of nutrients and iron, accompanied by low pH. Surveyed tundra ponds were also high in nutrients and iron and low in pH. Water temperature on the mainstem of the Kobuk River varied between 10.5 to 13.4°C; however, some measurements of baseflow were considerably cooler (down to 5.8°C), while ponds not directly connected to the river had somewhat warmer temperatures (up to 16°C).

Primary production.—Primary production in the Kobuk River mainstem seems to be restricted to diatom films, filamentous algae and a few emergent species of macrophytes (sedges etc.). Perennial macrophytes are rare due to the short growing season and the annual scouring of substrate due to break-up (Mackay and Mackay 1977, Nichols et al. 1989, Scrimgeour et al. 1994). Seasonal algal growth appears to be limited by low phosphorus and nitrogen availability, rather than by turbidity (Roy 1989, Robinson et al. 2002). Benthic epilithic diatoms were prevalent in cobbled, hard-bottomed segments of the mainstem Kobuk in August 2008. Fine sediment dominated off channel habitat, which was

occasionally characterized by thick growth of filamentous algae.

Secondary production.—We quantified invertebrate abundance (number of organisms sorted per unit time) and diversity (taxa richness) in order to characterize differences in production among off-channel and mainstream sites. Benthic invertebrates were dominated by two orders of aquatic insects, Ephemeroptera (mayflies) and Diptera (true flies) during the 2008 survey (Durand et al. 2009). Off-channel habitats consistently showed the highest overall abundance and diversity, followed by the tributaries. The Kobuk mainstem was depauperate, with low overall mean abundance (<25% of the mean abundance of side channel habitat) and lower diversity. Overall, aquatic insects were more diverse than expected for an Arctic River (Miller and Stout 1989, Oswood 1989, Hershey et al. 1995), in part because of the diversity of habitat provided by off-channel sites and tributaries.

Invertebrate drift was consistently low on the mainstem Kobuk, but somewhat higher in tributaries which drained upstream lakes or extensive tundra plain. High densities of pelagic zooplankton were found in off-channel sloughs and ponds with high residence time and only episodic connectivity to the mainstem (ranging from <5 to >600 individuals/m^3).

Fish.—Ten fish species, totaling 2,170 individuals, were captured at 24 sampling sites (Table 2) during the survey. Arctic grayling (*Thymallus arcticus*) was the most abundant and widely distributed species sampled. Juvenile grayling were caught at 14 of 18 (78%) seine sample sites, while adults were captured by hook-and-line on each day of the survey and were the most common fish sighted. Round whitefish (*Prosopium cylindraceum*) 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 (*Catostomus catostomus*) were also commonly observed in the moderately deep (1–2 m), slower moving sections of river. Chum salmon (*Oncorhynchus keta*) were seen spawning in side channels and river margins downstream of river RKM 137 (Reed River Segment) and were particularly abundant near the confluences of major tributaries. Redds had been constructed in areas where extremely cold (10°C) spring water entered the pools. Schools of sheefish, or inconnu (*Stenodus leucichthys*), some estimated to contain over 200 individuals, were readily visible and available to hook-and-line sampling beginning at RKM 83 (Segment 4). Catch per unit of effort (CPUE, measured as number of fish captured per seine haul) was much lower in the mainstem Kobuk (15 fish per seine haul) than in off-channel habitats (24 fish per seine haul). Overall, abundance and diversity of fish increased in downstream hauls.

Ecosystem Synthesis Model I: Current processes

The above results from August 2008 were synthesized into the following ecosystem model of current baseline function on the Kobuk River. This synthesis in turn informs the predictive climate change model found in the Discussion.

Baseline function.—The winter freeze and spring break-up together create significant annual biological disturbance (Scrimgeour et al. 1994) through both direct mortality and by limiting the establishment of perennial habitat (Gammon 1970, Ryder 1989, Ryan 1991). Annual re-colonization of off-channel habitat occurs as break-up ends, concurrent with increasing air temperature, day length, and decline in river stage. However, high flows and low nutrients limit the development of a complex food web on the mainstem. Thus the main channel acts as a corridor that provides connectivity among more highly productive habitats adjacent to the Kobuk, used by some species of fish (such as whitefish and longnose suckers) for transportation to various feeding sites, usually backwater tributaries or intermittently connected oxbow lakes and sloughs. Migrating fish (sheefish, chum salmon) use the Kobuk River corridor to travel from the highly productive ocean/estuary system to upstream spawning grounds that provide appropriate substrate largely free from fouling by sediment, algae, or bacteria.

Changes in river stage are important in controlling connectivity between off-channel habitats and the mainstem Kobuk by regulating the exchange of nutrients and biota. For example, spring floods dramatically increase the lateral extent of the river, allowing inputs of allochthonous nutrients and carbon that initiate seasonal biological production. As spring flows decline,

Table 2. Number of fish by species captured by seining or angling, Kobuk River, August 2008.

Common name	Scientific name	Seining	Angling	Total
Arctic grayling	*Thymallus arcticus*	989	82	1071
Longnose sucker	*Catostomus catostomus*	653	0	653
Round whitefish	*Prosopium cylindraceum*	250	0	250
Sheefish	*Stenodus 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
Total		1976	193	2169

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 et al. 2006). Productivity in these off-channel habitats largely derives from autotrophic producers and particulate organic matter (both peat and terrestrial leaf litter) that are consumed by functionally distinct invertebrate guilds. Secondary producers, in turn, support populations of juvenile fish including Arctic grayling, and several species of whitefish, and northern pike. Episodic high summer flows re-establish connectivity with the mainstem, allowing transfer of nutrients and food for foraging fish.

Fig. 4 shows a simplified schematic depicting the dominant biotic interactions on the upper Kobuk River. Terrestrial, estuarine, and off-channel (including tributaries, side channels, and backwaters) habitats all contribute to the greater mainstem ecosystem in ways that vary by mechanism and time of year. For instance, off-channel habitat contributes carbon primarily during the summer and fall through pulse flows (Tockner et al. 1999, Malard et al. 2006), predation by adult fish, and ontogenetic development of juvenile fish. The estuary contributes to upstream habitats through the annual summer-fall migrations of chum salmon, sheefish and some whitefish, which deposit eggs and post-spawned carcasses. Terrestrial habitat contributes to the river system during punctuated annual events typified by ice break-up (Scrimgeour et al. 1994), but may also occasionally contribute large amounts of both carbon and nutrients through thermokarsting (Bowden et al. 2008, Frey and McClelland 2009). The extent to which individual habitats are spatially and temporally connected in the face of climate change will ultimately have a profound impact on the future structure and function of the system.

Fish life history strategies.—Kobuk River fish life histories can be organized around overwintering and spawning strategies, and are linked to the timing of the annual hydrograph as shown in Fig. 5. Spring spawners (such as Arctic grayling, longnose sucker, northern pike, and slimy sculpin) overwinter below ice in deep pools or lakes, allowing them to easily access off-channel foraging and spawning habitat during the spring runoff peak, although availability of winter refuge habitat may be limiting to at least some fish populations (Craig 1989, Reist et al. 2006). Embryos incubate and larvae emerge during summer, capitalizing on high off-channel productivity, then enter the mainstem during the late summer flow peak to seek winter refuge (Georgette and Shiedt 2005).

In contrast, most adult anadromous coregonids (primarily broad and humpback whitefish and sheefish) and chum salmon in the Kobuk basin overwinter in the highly productive estuary or ocean, and spend the summer migrating upstream before spawning in the late summer or early fall (Alt 1988, Georgette and Loon 1990, Menard 2003). 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 and Dalen 1980).

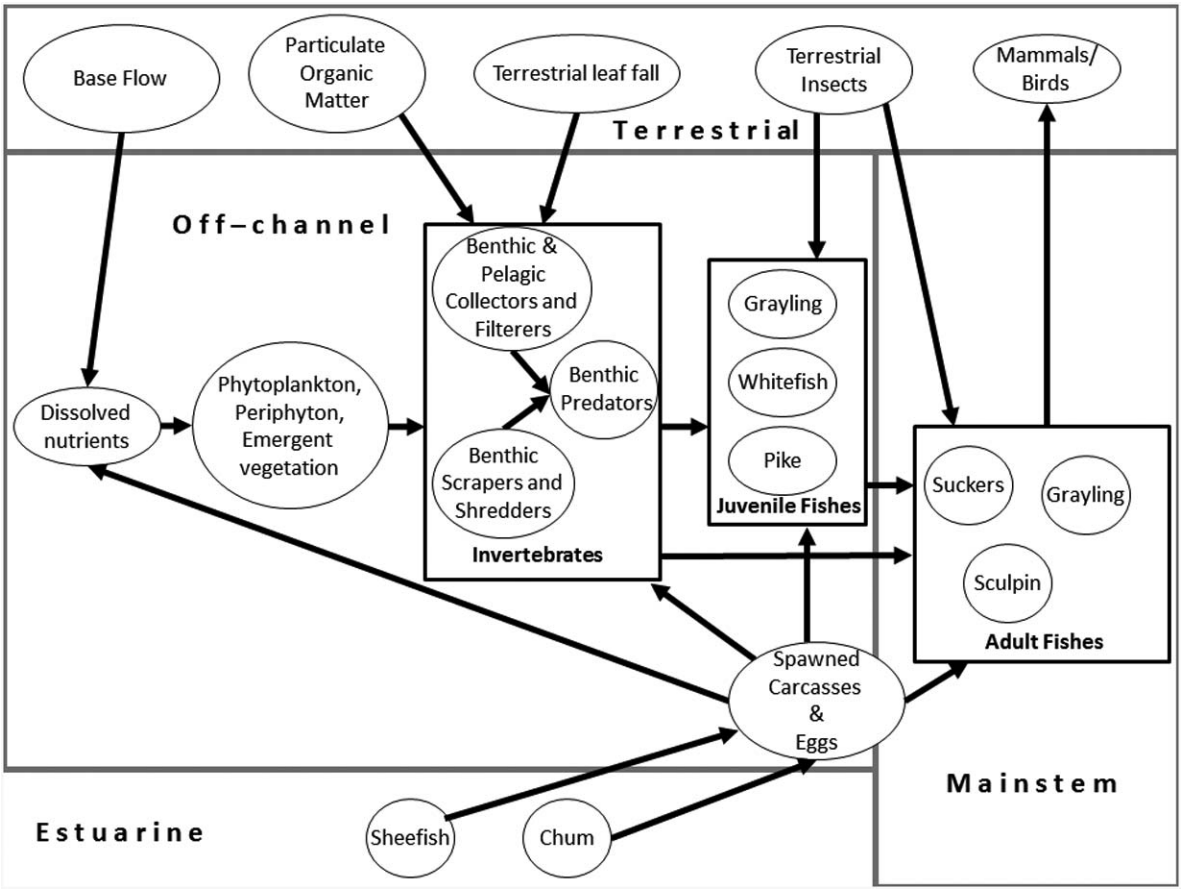

Fig. 4. Schematic of simplified Kobuk River food web showing habitat connectivity and trophic relationships.

Discussion

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 (as presented above) to predict changes to biota (Fig. 6). This analysis layers four potential hydrogeormophic responses to climate change onto the Ecosystem Synthesis Model I (which describes current conditions) to produce a second synthesis below.

Hydrogeomorphic responses to climate change

Key assumptions about future climate conditions are made based upon regional climate trends (summarized in column 1 of Fig. 6). Regional climate change projections for the Kobuk River basin in the 2090–2099 period predict spring thaws will occur about 12 days earlier than present (Beltaos and Burrell 2003, Pohl et al. 2007, SNAP 2008, Beltaos and Prowse 2009). Fall freeze-up dates are also expected to shift later by an average of nine 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 et al. 2007). 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 during the winter months. We assume a continuation of this trend in the early and late parts of winter. 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

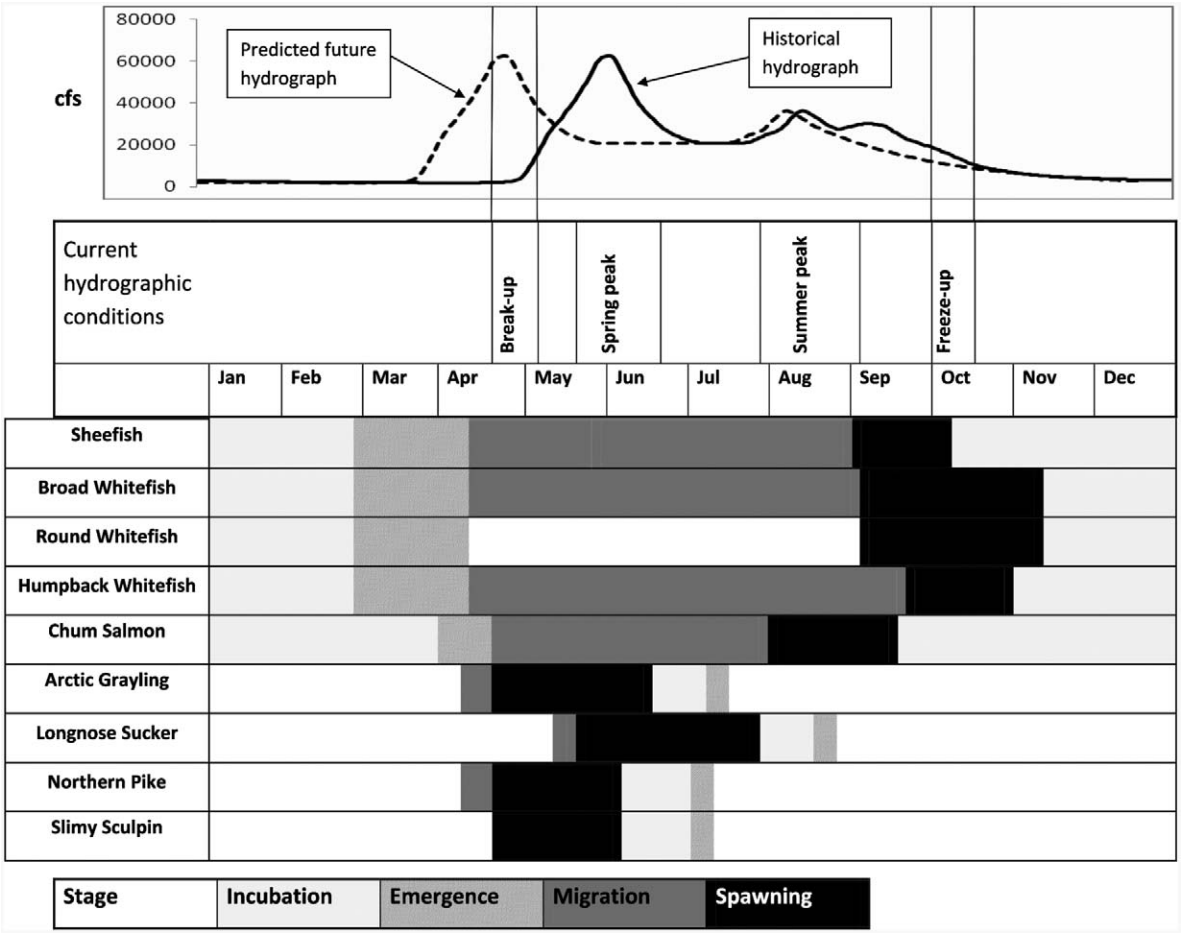

Fig. 5. Effects of timing shifts in key seasonal hydrographic and geomorphic events on an Arctic freshwater fish assemblage. Solid black line shows the average historical hydrograph and the broken line shows predicted shifts expected in the next century.

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 et al. 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. 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 to the watershed (Fig. 7). 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.

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 intensity is a function of degree-days of thaw, 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

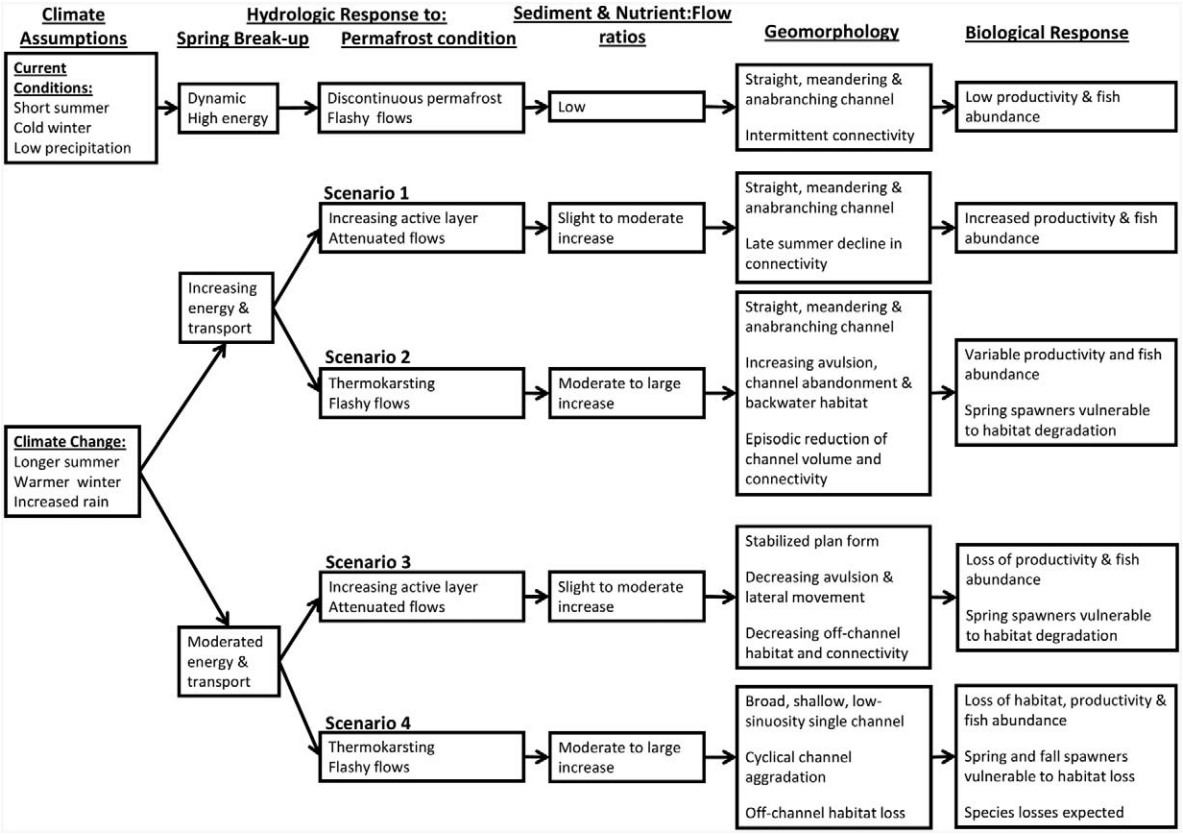

Fig. 6. Climate assumptions, physical and geomorphic drivers and the predicted biological outcomes of climate change models.

large enough to mechanically break and move the ice downstream, thermal decay of the ice may reduce the severity of ice jamming and flooding (Beltaos and Prowse 2001).

If ice thickness remains unchanged by temperature increases (Beltaos and Burrell 2003), the volume of spring runoff would be the main influence on future break-up severity. 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. 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 and prone to ice jams, translating to an increase in spring flood intensity relative to current conditions.

Alternatively, ice strength and thickness may be significantly reduced by increasing air temperature and winter baseflows in late winter and early spring (Pohl et al. 2007). Earlier spring thaw implies melting during a time of less intense solar radiation, causing a more protracted and less intense melt (Prowse et al. 2006), resulting 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 et al. 2007). Decreasing permafrost will allow additional infiltration and groundwater flow and translate to increased winter baseflow (Woo 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" response to summer rainfall (McNamara

		Spring Ice Break-up Conditions	
		Large and Rapid Spring Discharge; Ice Strength Maintained; Mechanical Break-up	**Low and Gradual Spring Discharge; Reduction in Ice Strength; Increased Thermal Decay**
Dominant Hillslope Processes	**Increased Active Layer**	Scenario 1. *More severe ice break-up, attenuated summer flows, increase in nutrients in low-gradient tributaries*	Scenario 3. *Less severe ice break-up, attenuated summer flows, increase in nutrients in low-gradient tributaries*
	Thermokarsting	Scenario 2. *More severe ice break-up, flashy summer flow peaks, major increase in sediment to tributaries in summer*	Scenario 4. *Less severe ice break-up, flashy summer peaks, major increase in sediment to tributaries in summer*

Fig. 7. Climate change scenarios for main physical drivers.

et al. 1997, Hinzman et al. 2005, Pohl et al. 2007, Walvoord and Striegl 2007), melting permafrost also leads to the co-occurring and potentially countervailing effects of thermokarsting. In contrast to active layer thickening and consequent shifts from overland to groundwater flows, thermokarsting may shorten flow pathways to the river and reinforce peaks in the summer hydrograph (Gooseff 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 and beyond the scope of this analysis. 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 baseflows concurrent with increases in the active layer. This will cause 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 et al. 2006).

Most of these liberated nutrients and sediments will be diluted quickly once mixed with the mainstem 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 mainstem, but in the tributaries, side channels, and backwaters.

The net effect on the mainstem Kobuk will depend on the relative importance of active layer thickening and 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, resultant thermokarsting has the potential to occur on a frequent and large enough scale to initiate widespread hillslope erosion and solifluction, introducing 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.

Ecosystem Synthesis Model II: Predicting the biotic response 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 break-up 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 geomorphology, allowing us to project changes in the system's biological condition, including productivity, biomass, and species assemblage (Fig. 6). The following four potential scenarios are listed in order of increasingly dramatic changes from what we have chosen to call current (or baseline) conditions (Fig. 7).

Scenario 1.—Under this scenario, spring break-up becomes more severe than current conditions because earlier spring run-off occurs before ice melt, causing increased ice jamming, scour, and flood intensity. 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 baseflow to the river during the late fall and winter months and in 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 may result from increased scour, bank erosion, and transport capacity that accompany a more severe ice break-up. However, an increase in vegetation cover resulting from longer growing seasons will promote bank stability (Huisink et al. 2000). General plan form will be largely unchanged, varying 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 autotrophic production, including the establishment of aquatic macrophytes (Benstead 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 refuge, exposing prime gravel substrate for spawning, and promoting the accumulation of large woody debris (Junk et al. 1989). 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 may have both direct and indirect effects on the reproductive success of spawning fish. Increased scour may increase mortality in the eggs and alevin of fall spawning fish that are still present in the substrate at break-up. Spring spawning fish (longnose sucker and Arctic grayling) may be less affected by more severe spring flows because spawning occurs just after the spring break-up. Indirect effects may result from changes to gravel substrate due to spring scour, affecting spawning success and egg or alevin survival (Alt 1969).

Scenario 2.—Thermokarsting promotes extensive thermal erosion and mass wasting events in the Kobuk watershed, and becomes the dominant driver in the summer hydrograph and sediment supply. Flow becomes rapid and less prolonged, 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 (Syvitski 2002, Bowden et al. 2008). 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 refugia before the winter freeze, causing 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 plan form in the main stem Kobuk is largely unchanged, although an increase in avulsion, channel abandonment, and backwater habitat are likely to result from intensified spring ice jamming and a larger sediment supply, both of which have previously been linked to avulsion in other systems (Ettema 2002, Ashworth et al. 2004).

As in Scenario 1, a more severe spring ice break-up is expected to produce an increase in available nutrients and allochthonous material due to widespread flooding and an increase in terrestrial 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 et al. 1994) and sudden influxes of sediment can deplete oxygen levels, cover food supplies, increase invertebrate 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, spring scouring will remove accumulated sediment, creating an annual cycle of high productivity in the spring and early summer, with declining productivity (and species diversity) in the late growing season as sedimentation reduces habitat quality.

Spring spawners become vulnerable to thermokarst-driven erosion because of increased embryo 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 transport capacity of the Kobuk. Rather, fall spawner embryos, 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. 5). Late season flashiness due to storms may interfere with fall spawners. Chum salmon may be vulnerable to changes to the substrate of tributaries from heavy scouring in spring and high sediment deposition in fall.

Scenario 3.—Ice break-up becomes less, rather than more, severe. Instigation of 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. As in Scenario 1, thermokarsting and associated erosion is minimal; changes in active layer depth dominate changes to 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 in flow, causes stabilization of channel morphology relative to current conditions (Knighton 1998, Mann et al. 2002). 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 some autotrophic communities to persist, due to a longer growing season and a decrease in scour potential (causing retention of the perennating organs of aquatic macrophytes in the bed substrate after break-up). In the short term, nutrient enrichment from permafrost degradation may promote the growth of autotrophs 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. These events could negatively affect primary and secondary production, reducing the overall abundance, diversity and biomass of food available to 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 macrophytes, 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 salmon, or possibly some of the whitefish) remain vulnerable.

Scenario 4.—Spring break-up becomes less severe (as in Scenario 3), leading to reduced bank erosion and sediment scour during ice break-up. Thermokarsting promotes extensive thermal erosion and mass wasting events in the Kobuk watershed, and becomes the dominant driver in the summer hydrograph and sediment supply. 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 and reduction in the spring flood leads to a decrease in channel avulsion and anabranching, and initiates a cycle of channel aggradation and simplification, as is thought to have occurred on Arctic rivers under similar conditions during early Holocene climatic changes (Mann et al. 2002). This reduces the number and size of backwaters and oxbow lakes, fills in deep pools, and causes an overall reduction in habitat heterogeneity. 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 (Knighton 1998).

Similar to Scenario 3, a less severe ice break-up suggests a decline in early season allochthonous inputs. 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 reduction in flow transport capacity associated with less severe ice break-up. A combination of sedimentation in tributaries and loss of critical habitat such as incipient oxbows and side channels will strongly affect both primary and secondary producers with overall declines in abundance, diversity, and biomass. Backwater habitat will transform 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 devastating for overall ecosystem structure and function as biotic communities become increasingly dependent on a depauperate mainstem for resources.

Spring spawners may be subject to losses 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. Sheefish may be particularly vulnerable because of their narrow habitat requirements and limited global distribution. In particular, a thermokarst event near sheefish spawning habitat could significantly impair the population. Fall spawner larvae may be susceptible to changes in post-emergent conditions under ice, and reductions in river transport capacity may have unknown effects on downstream larval migration.

Conclusions

Changes in climate over the next 100 years will produce shifts in the geomorphology, annual hydrograph, nutrient load and biological functioning of the Kobuk River, as they will throughout the Arctic (National Assessment Synthesis Team, 2001). Physical changes will indirectly determine biological outcomes through habitat modification and phenological shifts, rather than by direct impacts on physiological functioning. Although uncertainty exists in both our understanding of the Kobuk River's sub-Arctic riverine ecosystem and in future climatic conditions, our synthesis of ecosystem function and climate change provides resource managers and scientists 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 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 like the Kobuk. In contrast, the interaction between the nature of the spring ice break-up and the rate of sediment inputs as indicated by our scenarios suggest a progression of increasingly serious consequences (Fig. 6).

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 to some extent. However, by adding the effect of intense thermokarsting in Scenario 2, it seems that critical habitat for fish foraging will be lost seasonally, 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, combined with poor returns.

If, however, ice break-up intensity is attenuated by thermal decay, increased sedimentation will not be mediated by spring scouring. In Scenario 3, the loss of off-channel habitat effects the most productive foraging components of the river system. This would again have the largest impact on spring spawning fish, while fall spawners may be less vulnerable if spawning habitat remains available. However, an increase in thermokarsting without annual scouring from

break-up (Scenario 4), may have enormous and irreversible effects on fish abundance due to the loss of foraging, refuge and spawning habitat. Under both of these scenarios, the loss of break-up intensity will lead to long-term, irreversible declines in fish populations. Sheefish 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 ecosystem responses to climate change will be manifested in loss of off-channel habitat and productivity, with immediate effects on spring spawning fish, but relatively 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 degradation, and presage basin-wide extinctions of some species. We suggest the use of satellite imagery and local knowledge for determination of permafrost degradation and a monitoring program to track changes to select areas that show evidence of intact permafrost, a deep active surface layer, and recent thermokarsting. Areas of interest should also include those deemed important for fish spawning, development and foraging. These regions should be monitored for permafrost extent and condition at the beginning and end of each summer season. In these same areas, off-channel flows and baseflows should be monitored for sediment input and water quality. The intensity of break-up should be evaluated as a function of scour evidence, geomorphic condition and macrophyte establishment in these same key areas. Additionally, off-channel habitat should be monitored for evidence of sedimentation and connectivity to the mainstem. The data from Durand et al. 2009 provide a baseline for each of these metrics. The response of macrophytes, invertebrates and fish to geomorphic change can be deduced from these measurements over time by using hierarchical modeling methods. Therefore we suggest that key fish populations (sheefish, chum salmon, and grayling) be monitored as indicators of undetected but inevitable geomorphic change on the Kobuk River. Such a model may be useful for other regions and habitats in the temperate zone that may be vulnerable to climate changes at a longer timescale than that currently being experienced in the Arctic.

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