SURFACE WATER CONNECTIVITY OF ARCTIC LAKES DRIVES PATTERNS OF FISH SPECIES RICHNESS AND COMPOSITION, AND FOOD WEB STRUCTURE

By

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ABSTRACT

Hydrological processes regulate fish habitat, largely controlling availability and suitability of habitat for freshwater fishes. Seasonal fluctuations in surface water distribution and abundance on the Arctic Coastal Plain, Alaska, influence individual fish species occupancy in lentic habitats. On low-relief tundra, permafrost processes and climate are chiefly responsible for lake formation and surface water dynamics, such as the timing, duration, and availability of water that affects fish species distributions. However, it is unclear how these relationships scale up to influence fish community richness and composition, or food web structure. Further, each of these processes is also likely to change with rapid climate warming occurring in the Arctic. By observing patterns of fish species occupancy, we examined how fish species richness and composition in Arctic lakes varied with surface water connectivity at coarse and spatial fine scales. Through experiments and observation, we determined the structure of food webs as they related to surface water connectivity and foraging habits of associated fish species. We found surface water connectivity was a driver of fish species richness and assemblage patterns. Permanently connected lakes contained nearly twice as many species as disconnected lakes; and the most strongly connected lakes contained an average of four additional species compared to isolated lakes. Functional traits of fishes, like life history or body morphology, likely dictate their ability to colonize habitats. Given reduced colonization potential, isolated lakes either never supported or could not retain larger predatory fishes. In isolated systems only one fish predator occurred consistently, and this species showed strong top-down control of invertebrate prey in experimental systems. Yet, in natural environments single-predator systems have fewer trophic links than multi-predator systems, and therefore, less trophic redundancy across species. The loss

of species due to isolation reduced the total number of trophic links and shortened food chains. However, I argue that the complexity and addition of top-predators in surface water connected lakes adds trophic redundancy, stabilizes energy flow, and potentially enhances persistence within in food webs and across the meta-community of food webs. Changes to fish species richness, composition, or food web structure from climate warming may be dampened by the resilience of food webs locally, but across the broader landscape it is likely that some food webs will be restructured due to changes in colonization potential regulated by surface water connectivity.

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GENERAL INTRODUCTION

Arctic ecosystems are experiencing dramatic changes due to the rapid rate of climate warming occurring at high latitudes (White et al. 2007). At a rate twice the global average, warming in the Arctic has already facilitated landscape changes including permafrost thawing, erosion, and increased shrub growth (Martin et al. 2009). Typically, Arctic freshwater system productivity tends to be low due to prolonged periods of ice cover, short growing seasons, low temperatures, and low nutrient levels. However, changes to climatic factors like temperature and precipitation may directly affect physical, chemical, and biological processes in freshwater habitats (Prowse et al. 2006). Rising temperatures may stimulate aquatic productivity through mobilization of nutrients and organic matter and lengthening of the growing season (Rautio et al. 2011). Yet, simultaneously, some thermally limited species (e.g., Lake Trout *Salvelinus namaycush*) will likely experience limited or declining habitats and ability to forage (McDonald et al. 1996). Changes in the timing, duration, and magnitude of precipitation events will alter surface water hydrology and influence aquatic species' abilities to access habitats or persist in them (Bowling et al. 2003; Prowse et al. 2006). The richness of fish species in lakes is influenced by surface water connectivity of lake habitats to a stream network (Hershey et al. 2006), and certain species may respond directly to water flow rates (i.e., stream discharge) as a cue for migration timing (Heim et al. 2016b). With changing climate, the anticipated changes in water temperatures and surface water availability/connectivity (Martin et al. 2009; Arp et al. 2012) will affect fish species distribution and habitat use or access (Reist et al. 2006).

Organisms adapted to the harsh, seasonally extreme environment of the Arctic use strategies that enable them to either tolerate conditions or migrate to preferable habitats (Prowse et al. 2006; Haynes et al. 2014). Flexibility and opportunistic behaviors found in Arctic species

may provide them with the ability to respond to variability in their environment (e.g., Crawford 1974; Heim et al. 2016a; Eloranta et al. 2015), but it is unknown whether the limits of a species' plasticity will be exceeded under new climate patterns. Further, relatively little is known with respect to fish community composition and assemblage or food web structure in Arctic Alaska. Certain species are more well studied than others (e.g., Arctic Grayling *Thymallus arcticus*), yet those studies tend to focus on individual species or population level questions (e.g., Golden and Deegan 1998; Buzby and Deegan 2000; Heim et al. 2016b). Little information has been gathered on whole fish community assembly or food web structure in Arctic lakes (e.g., Hershey et al. 1999), and scarce information exists for fishes in the lake-dense Arctic Coastal Plain.

The low relief tundra of the Arctic Coastal Plain is a unique environment, where > 20% of the landscape is covered in lakes and streams (Martin et al. 2009). Permafrost processes are chiefly responsible for the creation of thermokarst water bodies on the landscape and provide an impenetrable barrier that contributes to surface flow of water during the spring freshet and summer months (Prowse et al. 2006; Martin et al. 2009). At the beginning of summer, snow melts and runs overland and through ephemeral channels, connecting permanent and temporary water bodies for a limited span of time. During this event, fish may colonize new or previously depopulated habitats (Haynes et al. 2014). Among fish species, certain functional traits (e.g., life history or body morphology) will foster opportunities for colonization of new habitats; for example, small body size may allow some fishes to move into new areas through shallow, marginal habitat. Other intolerant species or those with poor swimming abilities may not adapt readily to or have access to new habitats and may require relatively stable environments afforded by nearby refuge habitat (Hershey et al 2006, Haynes et al. 2014). However, disruptions to

current hydrological dynamics and climate regimes will likely have profound effects on species abilities to access and persist in lake habitats.

The response from wildlife (fish, birds, and mammals) to a 30 year warming trend on the Arctic Coastal Plain remains largely unknown, but serves as the impetus for this work. The studies presented here were conducted as part of the U.S. Geological Survey's Changing Arctic Ecosystems Initiative (for more information see: alaska.usgs.gov/science/interdisciplinary_ science/cae/index.php. Accessed: March 6, 2017), which aims to quantify wildlife and habitat response to ecosystem change in the Arctic. The focus of my dissertation was to understand the current dynamics between aquatic species, with particular focus on fish, and the physical environment while the Arctic warms. I focused on two primary areas – community and food web structure in lentic (i.e. lake or pond) habitats – because the fish community influences the flow of energy between aquatic and terrestrial habitats. Furthermore, fish and invertebrate prey are directly relevant to the potential success of an apex freshwater predator, the Yellow-billed Loon *Gavia adamsii*. At the outset of this study in 2011, Yellow-billed Loons were part of agency conservation efforts aimed at understanding the abundance and distribution of the species (USFWS 2014); and ongoing research that examines aquatic resource use (e.g., fish prey) by Yellow-billed Loons would assist in their assessment and conservation efforts (Uher-Koch et al. 2014).

Lakes on the Arctic Coastal Plain contain summer foraging habitats for loons and resident or migratory fish species (Haynes et al. 2015; Heim et al. 2016b). A complete picture of aquatic food web function depends on the interaction of fish species' colonization potential and feeding strategies (Beckerman et al. 2006; Pillai et al. 2011). In four chapters, I examined the importance of physical drivers on fish species composition and richness (Chapter 1) and the

foraging roles of fishes (Chapters 2 and 3) – fishes that ultimately lead to the formation and structure of aquatic food webs (Chapter 4). Considering the importance of surface water connectivity to individual species occupancy (Hershey et al. 1999; Hershey et al. 2006; Haynes et al. 2014), I was interested in examining its role, both locally and regionally, in driving patterns of species richness, assemblage composition, and food web patterns. Moving beyond single-species responses allowed me to explore relationships in metacommunities (collections of communities that are linked by migration between spatially subdivided habitats) and explore the role of colonization potential in local patch function. In lakes that are well connected to stream networks, colonization should occur readily and compensate for any extinction events (Hershey et al. 2006). In an environment as harsh as the Arctic Coastal Plain, where the average annual air temperature is −12°C, and winter occurs from October through May with aquatic habitats existing under >1.8 m of ice, the ability of fish species to access foraging habitat for the short summer growing season is critical.

CHAPTER 1

SURFACE WATER CONNECTIVITY DRIVES RICHNESS AND COMPOSITION OF ARCTIC LAKE FISH ASSEMBLAGES[1]

ABSTRACT

1. Surface water connectivity can influence the richness and composition of fish assemblages, particularly in harsh environments where colonisation factors and access to seasonal refugia are required for species persistence.

2. Studies regarding influence of connectivity on Arctic fish distributions are limited and are rarely applied to whole assemblage patterns. To increase our understanding of how surface water connectivity and related hydrologic variables influence fish assemblage patterns, we investigated species richness and composition of Arctic lake fishes over a large region, 8500 km^2, of the central Arctic Coastal Plain, Alaska.

3. We collected fish presence/non-detection data from 102 lakes and used a hierarchical multispecies occupancy framework to derive species richness and inform species composition patterns. Our mean estimate of regional richness was 12.3 (SD 0.5) species. Presence of a permanent channel connection was an overriding factor affecting species richness (mean 3.6, 95% CI 3.1–4.9), presumably driving lake colonisation potential. In lakes without a permanent channel connection, data suggest richness (mean 2.0, 95% CI 1.7–3.3) increased with the availability of in-lake winter refugia and with the potential of ephemeral connections during spring floods.

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[1] Laske, S. M., T. B. Haynes, A. E. Rosenberger, J. C. Koch, M. S. Wipfli, M. Whitman, and C. E. Zimmerman. 2016. Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology 61:1090–1104. doi:10.1111/fwb.12769

4. Fish species functional traits and environmental faunal filters contributed to patterns of richness and assemblage composition. Composition corresponded with richness in a coherent manner, where each successive level of richness contained several discrete assemblages that showed similar responses to the environment. Lakes with permanent channel connections contained both widespread and restricted species, while the species-poor lakes that lacked a connection contained mainly widespread species.

5. This work provides useful baseline information on the processes that drive the relations between patch connectivity and fish species richness and assemblage composition. The environmental processes that organise fish assemblages in Arctic lakes are likely to change in a warming climate.

INTRODUCTION

An understanding of habitat patch connectivity is central to the field of landscape ecology. Connection among patches of suitable habitat facilitates movement of individuals and species across landscapes, and movement among patches depends on the arrangement, permeability and context of available patches and corridors (Wiens, 2002; Thomaz, Bini & Bozelli, 2007; Mehner, Emmrich & Hartwig, 2014). In freshwater ecosystems, fish distributions are controlled by surface water availability, with surface water connections facilitating fish movement and colonisation of unoccupied patches (e.g. Tonn & Magnuson, 1982; Jackson, Peres-Neto & Olden, 2001; Henriques-Silva, Lindo & Peres-Neto, 2013). When a patch is well connected, colonisation is rapid or continuous, compensating for local extinction events (Hershey et al., 2006). In particularly harsh environments, extinction rates may exceed colonisation permitted by ephemeral or permanent movement corridors (Schleuter et al., 2012); however, adaptation to these local conditions, or the presence of within-habitat refugia, may

allow persistence in a given patch (Lesack & Marsh, 2010; Haynes et al., 2014). Thus, the interaction of surface water connectivity and patch characteristics contributes to landscape patterns of fish species richness and assemblage composition (Rathert et al., 1999; Sharma et al., 2011; Miyazono & Taylor, 2013).

Further, environmental factors, such as surface water connectivity, act as a faunal filter (Tonn, 1990; Poff, 1997) and operate on fish assemblages differently depending on the life history of each species (Angermeier & Winston, 1998; Hershey et al., 2006; De Bie et al., 2012). Depending on its life-history characteristics (Winemiller & Rose, 1992), a species may or may not have the ability to pass through a series of multi-scale environmental filters to colonise a patch of aquatic habitat (Tonn, 1990; Poff, 1997; Jackson et al., 2001). At the regional scale, features of climate, geology and hydrology influence patterns of species richness or composition along environmental gradients, while at the local scale, physical isolation and patch-specific features (e.g. lake or stream size) influence species richness and composition within an individual patch (Tonn et al., 1990; Schleuter et al., 2012). Across broader landscapes, this creates a mosaic of local species pools, where species assemblage patterns arise from regional processes and local features, and the fish species response to them (Legendre, Borcard & Peres-Neto, 2005; Hershey et al., 2006).

Low-gradient Arctic landscapes are composed of a complex array of landforms largely shaped by permafrost dynamics (Bowling et al., 2003; Grosse, Jones & Arp, 2013). Repeated freezing and thawing of the active layer results in creation of hydrologic complexes of lakes, ponds, streams and wetlands that provide fish habitat. Arctic fish have adapted to extreme seasonal fluctuations in water availability, light and temperature through evolved strategies of avoidance or tolerance of extreme cold and seasonal loss of aquatic habitat (West et al., 1992).

To avoid negative effects of winter, some species migrate to suitable overwintering refugia like deep lakes, springs or estuaries (Craig, 1984; West et al., 1992; Heim et al., 2016), while others stay in place and tolerate harsh local conditions (e.g. Ostdiek & Nardone, 1959; Lewis, Walkey & Dartnall, 1972). At the end of the Arctic winter, the spring freshet inundates the landscape with water, maximising surface water connectivity in the hydrologic network of lakes, ponds and wetlands (Bowling et al., 2003). These floods allow fish to move through ephemeral channels and redistribute themselves in otherwise unconnected systems as the growing season begins (Haynes et al., 2014). Species capable of passing through the same faunal filters may gain access to the same local patch, thereby comprising the local fish assemblage.

A limited number of studies have examined the influence of regional and local scales on Arctic fish distributions (Hershey et al., 1999, 2006; Haynes et al., 2014), and rarely have they focused on whole assemblage patterns (e.g. Hershey et al., 1999). This paucity of knowledge limits our understanding regarding the processes that influence fish species richness and assemblage composition in the Arctic. Extreme seasonality and flow regimes, and the array of fish species morphological and life-history adaptations for coping with harsh winters and short growing seasons, result in species-specific responses to variation in environmental conditions (Haynes et al., 2014). Hydrologic connectivity plays a primary role in determining individual fish species occupancy in lakes (Haynes et al. 2014). Recognizing this, we took the next step to examine how connectivity affects fish species richness and composition patterns, yielding a more comprehensive view of fish ecology for management of communities across landscapes rather than for individual species. This information will help elucidate current patterns of richness and assemblages in anticipation of the physical and biological changes that will arise from rapid climate warming (Prowse et al., 2006). Because of the strong response of Arctic freshwater

ecosystems to climate-induced change in hydro-ecological processes, it is crucial to understand how lake fish assemblages change along a gradient of surface water connectivity.

We expected that surface water connectivity would be a primary driver of species richness in Arctic lakes, anticipating that lake connections would provide greater accessibility and colonisation potential for more species (Tonn & Magnuson, 1982; Olden, Jackson & Peres-Neto, 2001; Haynes et al., 2014). Further, we investigated the importance of hydrologically related landscape characteristics on fish species richness and assemblage composition (Table 1.1). We predicted that variables that increased the amount of, or accessibility to, habitat (connection, surface area, maximum depth, total stream length, and total pond and lake area) would have positive effects on species richness and that variables that decreased the amount of or accessibility to habitat (bedfast ice, distance to nearest lake, distance between lakes and distance from coast) would have negative effects. Additionally, variables with the potential to support different species pools (catchment or ecological landscape) would maintain differences in richness. We aimed to determine whether the processes that organise species richness also operate on assemblages in a predictable fashion. We anticipated that the responses of individual species to variables of lake connectivity lead to an association among species such that species richness corresponds to a distinctive fish assemblage.

METHODS

Study area

We sampled fish from freshwater lakes (surface area 0.13–14.89 km^2; National Hydrography Dataset, U.S. Geological Survey, 2013) in an 8500-km^2 section of the central Arctic Coastal Plain (ACP) within three catchments: Meade River, Admiralty Bay and Ikpikpuk River (Fig. 1.1). Lakes are an important feature in this region, covering over 40% of the

landscape, and permafrost processes are chiefly responsible for both lake formation and distribution (Grosse et al., 2013). Permanent streams originate in the foothills of the Brooks Range and flow generally south to north until they reach the Beaufort Sea (Martin et al., 2009). Climate and permafrost dynamics regulate hydrology and the natural flow regime across the ACP, where surface water is available only for a short time, typically from mid-May to September. Flooding is common during the spring freshet in June, when high volumes of water from ice and snowmelt move over the landscape, temporarily increasing waterbody volume and connectivity. The numerous ephemeral connections created by this flooding may temporarily connect otherwise isolated lakes, ponds and wetlands to the hydrologic network.

Field methods

In summer 2009–10, we visited 86 lakes once each for 2–3 days (for lake selection information, see Haynes et al., 2013). We set two fyke nets constructed from 6-mm stretched mesh with 15.2 m × 1.2 m wings, a 30.5 m × 1.2 m centreline and a 1.1 m square opening (for additional details, see Haynes et al., 2014). We checked fyke nets every 12 h over a 24-h time period (2 spatial replicates + 2 temporal replicates = 4 replicates). We deployed two multifilament gill nets measuring 38 m × 1.8 m, with five panels ranging in mesh size from 13 to 65 mm. Each gill net was checked for fish three times with 3 h of soak time between checks (2 spatial replicates + 3 temporal replicates = 6 replicates). In summer 2011–13, we selected 23 lakes for sampling at two locations in the Admiralty Bay catchment based on their sub-basin location and surface water characteristics (connected versus not connected). We used fyke nets with a 1 m diameter opening, wings 9 m × 1 m, with 6-mm stretched mesh. Fyke nets in 2009–10 and 2011–13 differed only slightly in design, were deployed using similar methods and captured fish of the same size (based on mesh size). We found agreement in fish species detections and

preliminary analysis of detection probabilities for six lakes sampled with both fyke net designs. For those six lakes that we sampled on more than one occasion (2009–10 and 2011–13), only data from the first sampling event were included in the analysis. In 2011, we sampled each lake for two consecutive days using two fyke nets that were soaked overnight for 12 h (2 spatial replicates + 2 temporal replicates = 4 replicates). In 2012 and 2013, we deployed three fyke nets and soaked them for 4 h over four nights (total soak time of 12 h for three spatial replicates, over 4 nights = 4 replicates). We deployed two multifilament gill nets (North American standard; Lester, Bailey & Hubert, 2009) measuring 24.8 m × 1.8 m, with eight panels ranging in mesh size from 19 to 64 mm over 2–3 days and soaked gill nets for 3 h, checking for fish every hour (sum of two spatial locations over two to three nights = 4–6 replicates).

Data analysis

We estimated species richness using a hierarchical multi-species occupancy model that joins single-species occupancy models (MacKenzie et al., 2006) at the community level (Dorazio et al., 2006; Zipkin et al., 2010; Zipkin et al., 2012). This modelling framework allowed us to produce richness estimates for the entire study region and for individual freshwater lakes while accounting for imperfect detection of both observed and unobserved species (Dorazio et al., 2006; Zipkin et al., 2010). Without accounting for species-specific detection, estimates of both species richness and composition would be biased (Zipkin et al., 2010). Given the paucity of fish species in the Alaskan Arctic, it is critical to account for imperfect detection – missing one elusive species could have a dramatic effect on richness and on the inferences made regarding community patterns (MacKenzie et al., 2006; Zipkin et al., 2010).

For all lakes sampled, we assumed that each lake was closed to changes in fish species occupancy during the sampling period (MacKenzie, 2005). We constructed a matrix of species

occurrence for observed species (i = 12 species), at each location (j = 102 lakes; one brackish lake was excluded from analysis) and sampling event (k = 10 replicates; 4 fyke net + 6 gill net). We allowed missing occupancy data to remain in the matrix for the subset of lakes with fewer than 10 replicate nets sets. We then augmented the model with potential but unobserved species by creating a matrix of non-detection encounter histories (Dorazio et al., 2006; Zipkin et al., 2010) limited to three additional species known to occur on the ACP (Alaska Department of Fish and Game, Fish Resource Monitor, accessed Sept. 2014). This addition of unobserved species was meant to improve our estimates of richness in the region by accounting for those species that are exceptionally rare or not detected at any sample locations.

We accounted for differences in detection among species by including a covariate for gear type and for lake surface area, both of which strongly influence detection (Haynes et al., 2013). We did not include time of net set as a covariate; Haynes et al. (2013) found no difference in fish species detection probabilities for nets set at different time periods (morning–evening and evening–morning), likely because diel signals are muted in the Arctic summer that receives 24 h of sunlight (Kahilainen et al., 2004). The use of two gear types, fyke and gill nets, improved overall detection of species at the assemblage level, given differences in capture likelihood of small- and large-bodied species to each gear type (for more information on method-based detection probabilities, see Haynes et al., 2013). Including lake size as a covariate for detection was important, given that larger lakes require more effort to adequately sample, and as time and number of nets were limiting, we accounted for size differences by including surface area as a covariate of detection.

To account for the uneven distribution of species across the range of environmental conditions, we examined covariates for species occurrence. For each potential covariate, we

determined the range of values at each sample lake (Table 1.2). We classified surface water connectivity of a lake as either permanently connected or disconnected based on whether we detected a channel joining the lake to the hydrologic network during field sampling, or from digital maps (National Hydrography Dataset, NHD) or aerial photographs. Along an east to west gradient, lakes belonged to one of three catchments at the eighth-level Hydrologic Unit Code, which we determined from the NHD. Lakes existed within one of three ecological landscapes that differed in climate, physiography and geology: Arctic sandy lowland, Arctic peaty (silty or sandy) lowland and Arctic sandy riverine (Jorgenson & Grunblatt, 2013). We obtained lake surface area from the NHD. The proportion of bedfast ice was calculated from the proportion of the lake area that did not freeze to the bottom based on Synthetic Aperture Radar data (from Grunblatt & Atwood, 2014). Maximum depth was determined in the field in 78 of the 102 lakes by sounding the lake bottom with either an integrated GPS depth sounder (GPSmap 430s; Garmin International Inc., Olathe) or a portable depth sounder (SM-5; Speedtech Instruments, Great Falls).

We determined the distance to coast by manually measuring the shortest distance from a lake's surface water outlet to the coast via the hydrologic network on an orthophotograph in Geographic Information Systems (ArcGIS Version 10.1; Esri, Redlands). If the lake was disconnected and possessed no surface water outlet, we measured from the lake's edge overland to the nearest connected surface water before measuring along the network. We calculated distance to the nearest lake, average distance between lakes, total stream length, and total pond and lake area for each sample lake through analysis of the NHD in GIS, and we classified the spatial scale of all variables as either local or regional based on their extent (based on Tonn, 1990; local 10^{-2}–10^{2} km; regional, 10^{3}–10^{5} km). We measured the distance to the nearest lake as

the overland Euclidian distance from the edge of the sample lake to nearest edge of an adjacent lake and calculated average distance between lakes as the mean of the distance to nearest lake within a 5-km radius (local scale). We calculated total stream length and total pond and lake area by summing the area or length within a 5-km radius (local scale) and within 50-km radius (regional scale), with the sample lake at the centre.

Given the 13 variables of interest, we selected five covariates for our model based on the findings of Haynes et al. (2014): presence/absence of a permanent surface water connection (*Connect*), the distance to nearest lake (*Nearlake*), average distance between lakes (*Avedist*), distance to the coast (*Distcoast*) and the proportion of lake area covered with bedfast ice in winter (*Ice*). We modelled occupancy probability $\Psi_{i,j}$ for species *i* in lake *j* with the logit function, where the intercept term depended on whether the lake was connected:

$$\text{logit}\,(\Psi_{i,j}) = \alpha 1_{i,Connect_j} + \alpha 2_i Nearlake_j + \alpha 3_i Avedist_j + \alpha 4_i Distcoast_j + \alpha 5_i Ice_j\,.$$

We assumed that all species-specific parameters came from a normal community-level uninformed, diffuse, prior distribution [Normal (0, 1000), Uniform (0,1); Zipkin et al., 2010], and estimated parameters through a Bayesian approach using Markov chain Monte Carlo simulation in R package R2WinBUGS (Sturtz, Ligges & Gelman, 2005) and WinBUGS (Lunn et al., 2000). We ran three chains of 60,000 iterations with a burn-in of 30,000 and thinned posterior chains by 10. We evaluated model convergence using the Gelman–Rubin diagnostic (Brooks & Gelman, 1998) and visually by examining the Markov chains to ensure adequate mixing (Gelman & Hill, 2007).

Estimates of species richness come from the posterior distribution and can be used to examine relations between species richness estimates and the covariates included in the

hierarchical model. We reported the mean as the estimate of richness (scaled up to account for unsampled species) for both the region and individual lakes and compared model estimates to naïve richness (observed number of species). We determined the proportion of lakes where estimates of richness were greater than naïve richness. Further, we summarised richness estimates for connected and disconnected lakes independently because of the strong influence of surface water connectivity on fish life history and lake access (Tonn & Magnuson, 1982; Olden et al., 2001; Haynes et al., 2014). For lakes where estimated richness was greater than naïve richness, we determined the proportion of connected and disconnected lakes where richness estimates exceeded richness observations. We also determined the number of lakes at each level of richness, S, in terms of estimated richness, naïve richness and the number of lakes where estimated richness equalled naïve richness.

For each lake where estimated richness matched naïve richness, we examined the composition of fish assemblages. This conservative approach allowed us to assess patterns of composition without assuming species identities for those lakes where detection of species was imperfect. At each richness level, we examined the composition of species to determine whether richness corresponded to a distinctive fish assemblage. We calculated elements of metacommunity structure to describe patterns of species distributions among lakes using R package metacom (Leibold & Mikkelson, 2002; Dallas, 2014). We considered the three metrics of coherence, turnover and boundary clumping. Coherence relates to the level that species respond to the same environmental gradient, turnover relates to changes in species composition across local patches, and boundary clumping measures the distinctiveness of assemblages (Henriques-Silva et al., 2013). Each of these elements provides clarity to the organisational patterns of known assemblages across the ACP landscape. We also discussed the potential

relationship between known assemblages and surface water connectivity and environmental variables not included in the hierarchical model. We limited the examination to environmental variables that showed potential to influence naïve richness in a *post hoc* analysis.

We performed a *post hoc* analysis to explore the relationship between naïve species richness and covariates not included in the hierarchical model and assess covariates' potential influences on fish assemblages in Arctic ecosystems. We examined scatterplots of naïve richness across the range of conditions for each environmental variable separately for connected and disconnected lakes and considered variables to be potentially influential if they showed a positive or negative trend when viewing the raw data. The examination of these data was not intended to be conclusive, but to act as a guide in hypothesis development for future studies on the drivers of Arctic fish distributions or assemblages.

RESULTS

Multispecies occupancy model – richness estimation

Our final model contained only the presence or absence of permanent channel connection term, suggesting the importance of this variable in determining species richness in ACP lakes. Our results showed little support for models containing covariates in addition to connectivity. Lack of convergence of models, which included *Nearlake*, *Avedist*, *Distcoast* and *Ice*, indicated the lack of signal in the data for those variables to inform richness. Put simply, of the variables we investigated and across our sample of lakes, surface water connectivity was the primary factor influencing species richness. Relationships between richness and other variables were too weak (see section on *post hoc* analysis for more details) given our sample size and the depauperate ACP fish fauna. This was due, in part, to low numbers of detections of most observed species (Table 1.3), with the exception of ninespine stickleback *Pungitius pungitius* and

least cisco *Coregonus sardinella* that we encountered more frequently.

We estimated a regional richness of 12 species (mean 12.3, SD 0.5), corresponding with our observation over the course of the study. Our augmentation of the model with three unobserved species did not elevate the mean richness estimates, but capped the 95% posterior distribution at a maximum of 14 species. The naïve mean richness across all lakes was 2.6 species (range 0–9), while the estimated mean richness across all lakes was 3.0 species (95% CI 2.6–4.3). Of all lakes, 30% had an estimated mean richness greater than naïve richness by one fish, and in 1% of lakes, the mean richness estimate was greater than naïve richness by two fish. For a richness level of zero, S = 0, we observed seven lakes, but estimated only four fishless lakes. For all other richness categories, we found the following: $S = 1$, 20 observed, 14 estimated; $S = 2$, 30 observed, 29 estimated; $S = 3$, 14 observed, 15 estimated; $S = 4$, 20 observed, 28 estimated; and $S \geq 5$, 11 observed, 12 estimated. When we compared estimated versus observed richness in connected and disconnected lakes, estimates of richness were higher than observed for 48% of connected lakes and for 3% of disconnected lakes. Our estimated mean richness in connected lakes was 3.6 species (95% CI 3.1–4.9) com- pared with estimated mean richness in disconnected lakes at 2.0 species (95% CI 1.7–3.3; Fig. 1.2).

Species composition – patterns between richness, assemblages and the environment

We examined the composition of species only in lakes where naïve richness matched mean richness estimates (i.e. no evidence of imperfect detection; 70 of the 102 lakes, for $S = 0$, 4 lakes; for $S = 1$,11 lakes; for $S = 2$, 20 lakes; for $S = 3$, 6 lakes; for $S = 4$,18 lakes and for $S \geq 5$, 11 lakes; Table 1.4). Our examination of metacommunity structure revealed that these Arctic lake assemblages (excluding fishless lakes) fit a Clementsian gradient, where metacommunities have multiple assemblages at the same richness level. Coherence was significantly positive (z =

3.06, $P = 0.002$) and contained fewer species absences in ordinated matrices than expected. Turnover, or the number of species replacements, was non-significant ($z = 0.56$, $P = 0.57$), indicating that there were no more or less replacements of species than expected, and boundaries were clumped (Morisita's index = 3.23, $P < 0.001$), forming discrete assemblages, which respond similarly along environmental gradients and replace each other as a group.

Each of the four fishless lakes lacked a channel connection and were, on average, farther from the coast compared to lakes with fish (Table 1.4). All single-species lakes likely contained only ninespine stickleback; we saw no evidence for other species occurring alone (Fig. 1.3). The environmental characteristic common among most single-species lakes was the lack of a surface water connection (12 of the 14 lakes). In two-species lakes, ninespine stickleback generally co-occurred with Alaska blackfish *Dallia pectoralis* or least cisco (Table 1.4, $S = 2$). The ninespine stickleback-Alaska blackfish assemblage was the dominant assemblage type out of all species combinations (16 of 70 lakes, 23%) and dominant among two-species assemblages (16 of 20 known assemblages, 80%). This assemblage occurred in five connected and 11 disconnected lakes. However, all lakes that contained the ninespine stickleback-least cisco assemblage lacked a permanent surface water connection, which suggests that these lakes likely provided adequate overwintering habitat for the large-bodied species, although we have no depth information for these three lakes (Table 1.4; $S = 2$).

The greatest number of three-species lakes contained an assemblage of ninespine stickleback, Alaska blackfish, and least cisco (50% of three-species lakes; Table 1.4). Two of the three lakes where this assemblage occurred were connected, as were the lakes containing ninespine stickleback, Alaska blackfish and Arctic grayling *Thymallus arcticus*. The addition of a fourth species was either broad whitefish *Coregonus nasus* or char (either *Salvelinus malma* or

S. alpinus; Fig. 1.3). Ninespine stickleback, Alaska blackfish, least cisco and broad whitefish dominated the four-species assemblage type (Table 1.4, $S = 4$), and this was the second most abundant assemblage type in the study area (72% of four-species lakes and 19% of all known assemblages). All but two lakes with this assemblage had a permanent surface water connection. Among the four-species assemblages, lakes that contained slimy sculpin *Cottus cognatus* were, on average, closer to the coast and deeper than lakes with four-species assemblages without slimy sculpin (Table 1.4; $S = 4$). Lakes with five or more species contained the common species found in lakes with four or less species, but also sporadically contained some rare species: pike *Esox lucius*, rainbow smelt *Osmerus mordax*, burbot *Lota lota*, humpback whitefish *Coregonus pidschian* and threespine stickleback *Gasterosteus aculeatus* (Fig. 1.3). Because the majority of assemblages with five or more species occurred only once in our study, we can say little with respect to specific environmental patterns between them (Table 1.4; $S \geq 5$). However, for all lakes with five or more species, a permanent channel connection was always present (Fig. 1.3).

Post hoc analysis – trends between environmental variables and naïve richness

We could not assess relations between estimated species richness and variables not included in the hierarchical model; therefore, we examined each variable though a post hoc analysis of naïve richness. Post hoc trends of the four proposed variables (*Nearlake*, *Avedist*, *Distcoast* and *Ice*) and the remaining eight variables for which we hypothesised relationships (Table 1) showed five local and regional variables with potential to influence species richness (Fig. 1.4). We found positive trends for two variables that increased the availability or accessibility of habitat: maximum depth (Fig. 1.4a) and total local stream length (Fig.1.4b). The number of observed species increased with maximum depth in connected and disconnected lakes. Four additional metres of maximum depth (from 2 to 6 m) resulted in an increase of 1.5

species in connected lakes and 2.0 species in disconnected lakes. The number of observed species also increased with increasing total local stream length. An increase of 50 stream kilometres (from 25 to 75 km) was accompanied by an increase in naïve richness of 1.5 species in connected lakes and 0.5 species in disconnected lakes.

Two variables were negatively related to availability or accessibility of habitat: proportion of bedfast ice (Fig. 1.4c) and distance from coast (Fig. 1.4d). Proportion of bedfast ice in winter showed no trend with naïve species richness in connected lakes but a negative trend in disconnected lakes. In disconnected lakes, where the availability of *in situ* overwintering habitat is likely of greater importance, naïve richness approached zero when bedfast ice cover approached 100%. The response of naïve species richness to distance from coast was similar for lakes connected and disconnected to the hydrologic network. At a distance of 200 km from the coast, naïve richness was reduced *ca.* 1.5 species compared with naïve richness at 50 km from the coast. We also found that the arrangement of catchment was influential to naïve richness, suggesting possible differences in the species pool (Fig. 1.4e). The most western catchment, Meade River, averaged two or less species observed per lake, and naïve richness did not exceed three species. In lakes of the Admiralty Bay and Ikpikpuk catchments, we observed more species, with an average of two or more species per lake and naïve richness as high as nine species.

DISCUSSION

Presence of a permanent channel connection was an influential variable affecting species richness in lakes across the ACP region. In addition to its known effect on individual species distributions (Hershey et al., 2006; Haynes et al., 2014), we found surface water connectivity also influenced fish assemblage composition. Connected lakes contained both spatially

widespread (e.g. ninespine stickleback) and restricted (e.g. humpback whitefish) species, while isolated, species-poor lakes contained mainly widespread species (Snodgrass et al., 1996; Henriques-Silva et al., 2013). With increasing richness, species were generally added to assemblages in a sequential manner, a pattern common to harsh and homogenous environments (Kodric-Brown & Brown, 1993; Henriques-Silva et al., 2013). Yet, these additions are not perfectly predictable given species richness. The Clementsian gradient of assemblages describes metacommunities that have multiple assemblages at the same richness level, and that those assemblages may replace one another along a similar environmental gradient (Henriques-Silva et al., 2013). We see this in comparisons of assemblages at each richness level >1 ($S = 2$); the wide variation in environmental variables contributed little to distinctions between assemblages, even though each environmental variable we examined was potentially influential to richness. Likely, fish species occupancy in any lake patch resulted, in part, from particular species functional traits (e.g. life history and body morphology; Poff, 1997; Haynes et al., 2014).

By examining the common assemblages, we see patterns that support the interaction between faunal filters and species functional traits (Tonn, 1990; Winemiller & Rose, 1992; Poff, 1997). Organisation of assemblage composition began with one of the most tolerant and the most widespread species, ninespine stickleback (Lewis et al., 1972; Haynes et al., 2014). This fish was consistently found in connected and disconnected lakes and was the sole fish resident in single-species lakes. This species showed little dispersal limitation, which allowed it to gain access even to isolated lakes (Henriques-Silva et al., 2013). Alaska blackfish was the next species to appear. Also highly tolerant, this species was widely distributed but does not have the same dispersal behaviours as the ninespine stickleback and may not access the same ephemerally connected waterbodies (Ostdiek & Nardone, 1959; Cameron, Kostoris & Penhale, 1973; Haynes

et al., 2014). Next, least cisco appeared in lakes with and without permanent channel connections. However, unlike its tolerant counterparts, least cisco may require more in-lake overwintering habitat and, when no channel connection is present, are better suited to deeper lakes that provide ample winter refugia compared to shallow lakes with limited refuge (Henriques-Silva et al., 2013; Haynes et al., 2014). Broad whitefish were found most often in connected systems, likely due to the migratory nature of this species (Craig, 1984) that necessitates the availability of nearby stream networks and coastal areas that provide habitat and lake access (Haynes et al., 2014). This agrees with our post hoc findings of increased richness nearer to the coastline and with increasing local stream length (Olden et al., 2001). At richness of five or more species, we were unable to discern compositional patterns, but expect that the patchy presence of these rare species arose from a combination of extinction and colonisation events taking place within a specific local habitat patch (Olden et al., 2001; Hershey et al., 2006).

As we anticipated, surface water connectivity was the primary driver of fish species richness and associated assemblages in Arctic lakes. Fish species partitioned themselves along a connectivity gradient or filter (Tonn, 1990). With nearly half of all species occupying only connected lakes, we can speculate that their dispersal was limited to permanent migratory pathways and that these species are less opportunistic than others (De Bie et al., 2012). Other species, like Arctic grayling, may use surface water flows as a cue to move among habitats (Heim et al., 2015) and often show fidelity to summer feeding sites, which reduces the risks associated with foraging in risky or ephemerally connected habitats (Buzby & Deegan, 2000; Heim et al., 2016). Further, species may occupy both connected and disconnected lakes, but be constrained by factors such as water depth. Slimy sculpin, for example, occur in deep lakes (Hershey et al., 2006; Haynes et al., 2014). Their limited dispersal abilities and potential need for

large amounts of overwintering habitat may ultimately restrict their distribution (Haynes et al., 2014). In contrast, ubiquitous species, like ninespine stickleback, exhibit few specific environmental requirements and are tolerant to extreme thermal and dissolved oxygen regimes (Lewis et al., 1972; Cameron et al., 1973). Not only can they persist in disconnected lakes but their ability to move through shallow, temporary corridors gives this species a colonising advantage for ephemerally connected habitats (Cameron et al., 1973). Given differences in species ecology, assemblages in connected lakes are likely structured primarily by species dispersal abilities and colonisation factors, while assemblages in disconnected lakes are likely structured by local extinction factors (Taylor, 1997).

We found that colonising factors – primarily a permanent channel connection – increased access to wetted habitats and provided migratory corridors important for increasing richness and adding new species. Proximity to coastal habitats also plays a role in colonisation of lakes because of the importance of sources such as refuge habitats – deep lakes, stream channels and estuaries (Olden et al., 2001; Beisner et al., 2006; Haynes et al., 2014). For example, downstream locations tend to support greater species richness, because they are closer to colonising sources than upstream habitats (Olden et al., 2001). On the ACP, downstream locations are nearer to the coastline and may be more environmentally stable and have greater refuge potential than inland locations (Miyazono & Taylor, 2013). Additionally, coastal areas are stream dense. The vast network of connected channels and lakes potentially operates as a metacommunity that promotes colonisation of species (Mehner et al., 2014) and stabilises richness or saturates local assemblages (Schleuter et al., 2012).

Increased species richness near the coast may be driven, in part, by migratory species, which are confined to habitats made available via permanent migratory pathways. For example,

whitefish use the narrow band of brackish water along the Beaufort Sea coast as a dispersal corridor (Craig, 1984). This band of water allows fish to move parallel to the coast from species pools in large rivers of Canada and eastern Alaska towards Admiralty Bay and into the Ikpikpuk, Admiralty Bay and Meade catchments (Craig, 1984). Following this pathway, we observed a reduction in species richness further west, particularly for disconnected lakes of the Meade River catchment. Reduced richness in lakes of the Meade River catchment should be accompanied by reduction in the pool of available species, because five of the 12 known species only occur in lakes with local richness greater than five.

Extinction factors, which limit local habitat availability and local persistence of vulnerable species, are also likely important for species richness and composition (Hershey et al., 2006; Haynes et al., 2014). Compared with shallow lakes, deep lakes supply more habitat and stable environments for pelagic and benthic species (e.g. char or burbot; Hershey et al., 2006; Dembkowski & Miranda, 2014). Deep lakes also act as refuge habitat in the winter, because they contain adequate volumes of oxygenated water for overwintering fish (Hershey et al., 2006). Adequate deep-water habitat in disconnected lakes supports the overwintering populations of large-bodied salmonids like least cisco, Arctic grayling, broad whitefish and char. Reduced richness in disconnected lakes was likely tied to effects of isolation and harsh, hypoxic winter conditions (Tonn, 1990; Schleuter et al., 2012). Ice-rich, disconnected lakes likely experience frequent winterkill events and were, therefore, dominated by small-bodied, tolerant species like ninespine stickleback and Alaska blackfish (Danylchuk & Tonn, 2003; Haynes et al., 2014).

Permanent and ephemeral connections provided environmental stability to assemblages in connected and disconnected lakes. For example, after local extirpation from a harsh winter, fish species can return to lakes from refuge habitats as conditions improve. In permanently

connected lakes, where colonisation potential is high, richness readily returns to its former level (Tonn & Magnuson, 1982; Hershey et al., 2006), and, in disconnected lakes, the spring freshet may provide a brief opportunity for fish to colonise otherwise isolated lake ecosystems (Heim et al., 2015). With greater flood frequency or duration comes greater colonisation opportunity (Baber et al., 2002; Haynes et al., 2014). Without an ephemeral pulse of water, colonisation to disconnected lakes is unlikely. Our work suggests that these ephemeral connections may be particularly important to otherwise disconnected lakes and to opportunistic dispersers that overwinter locally and readily seek out vacant habitats.

Implications of future climate change

Our study on the relation between surface water connectivity and fish species richness and assemblage composition provides an informative baseline, as the environmental processes that organise fish assemblages in Arctic lakes are likely to shift with warming climate (Wrona et al., 2006). In this region, rates of warming are approximately twice the global average, exposing tundra ecosystems to immediate consequences (Prowse et al., 2006). Apart from increasing water temperatures, new climate patterns are predicted to lengthen the ice-free season, degrade permafrost and increase evapotranspiration, processes that structure surface water hydrology (Prowse et al., 2006; Reist et al., 2006; White et al., 2007). To predict future changes in the Arctic, it is crucial to understand mechanisms that give rise to the distribution of Arctic species and how the physical and biotic processes important to species will change. The empirical data we present provide insights into the potential for future changes in Arctic fish communities.

Our results support the notion that alterations to surface water hydrology and dynamics could lead to profound changes in lake fish assemblages across the landscape (Reist et al., 2006). The projected change to surface water connectivity of habitats may reduce colonisation

opportunities for fish (Thomaz et al., 2007). Species that rely on permanent channel corridors or have specific requirements under the current flow regime may shift in distribution and dominance in the landscape, leading to changes in local species richness or assemblage composition (Hershey et al., 2006; Haynes et al., 2014). Alterations to lake water budgets through increased evapotranspiration may dry ponds, lakes and formerly permanent channel connections (Tejerina-Garro, Fortin & Rodríguez, 1998; Bowling et al., 2003). Drying would effectively isolate lakes from the hydrologic network, preventing access or trapping fish in a system at the end of the ice-free season (Prowse et al., 2006; Haynes et al., 2014) or limit dispersal pathways on which fish rely for movement between habitats (Beisner et al., 2006; Sharma et al., 2011). Given that fish are important ecosystem components – playing key roles in energy flows as predators of aquatic invertebrates and as prey of top avian predators – an understanding of natural patterns and processes will help to manage these landscapes for ecosystem resilience in a changing climate.

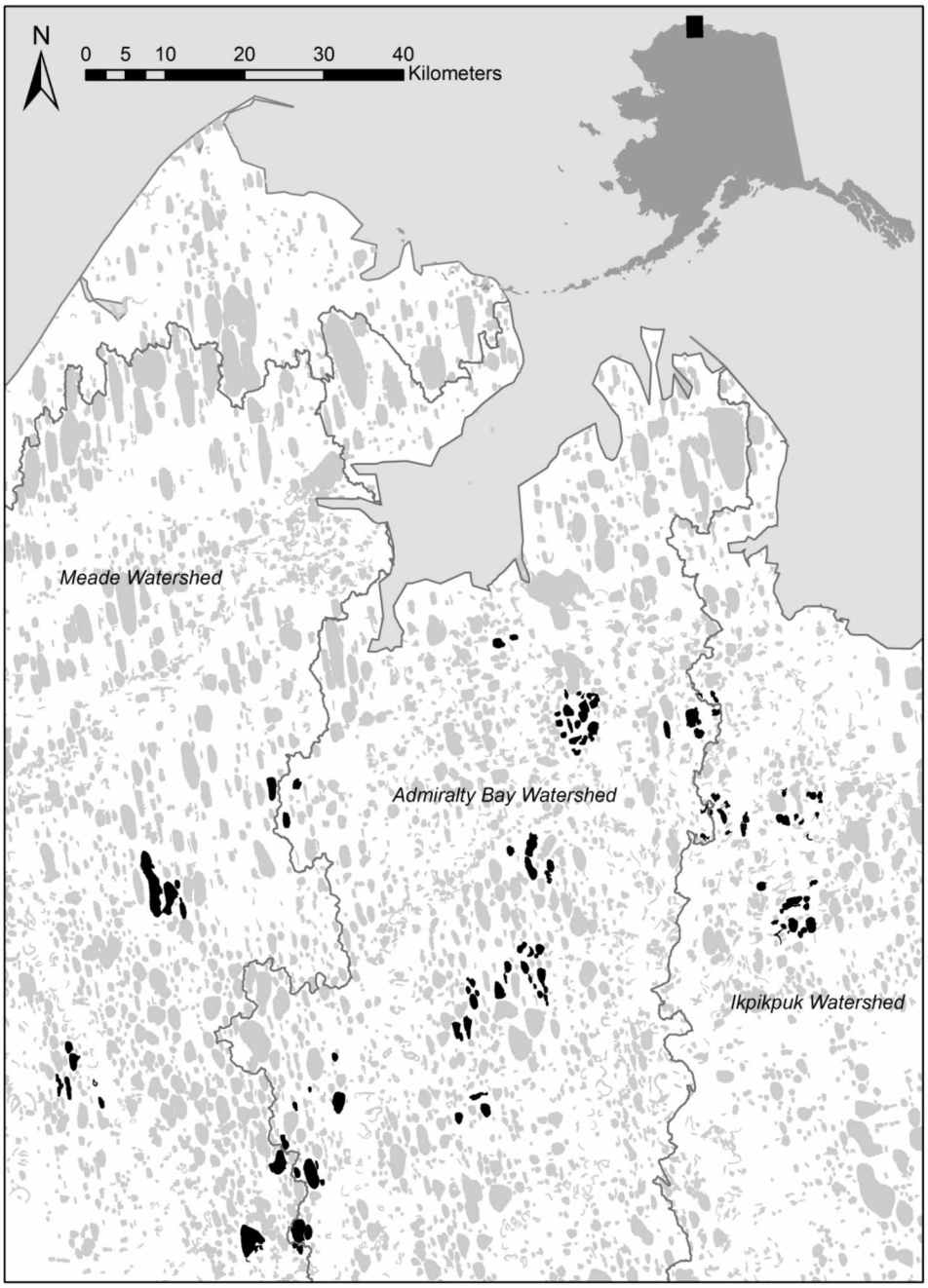

Figure 1.1. Study area on the Arctic Coastal Plain of Alaska within three major catchments. Standing surface water is shaded grey, whereas lakes sampled for fish are shaded black.

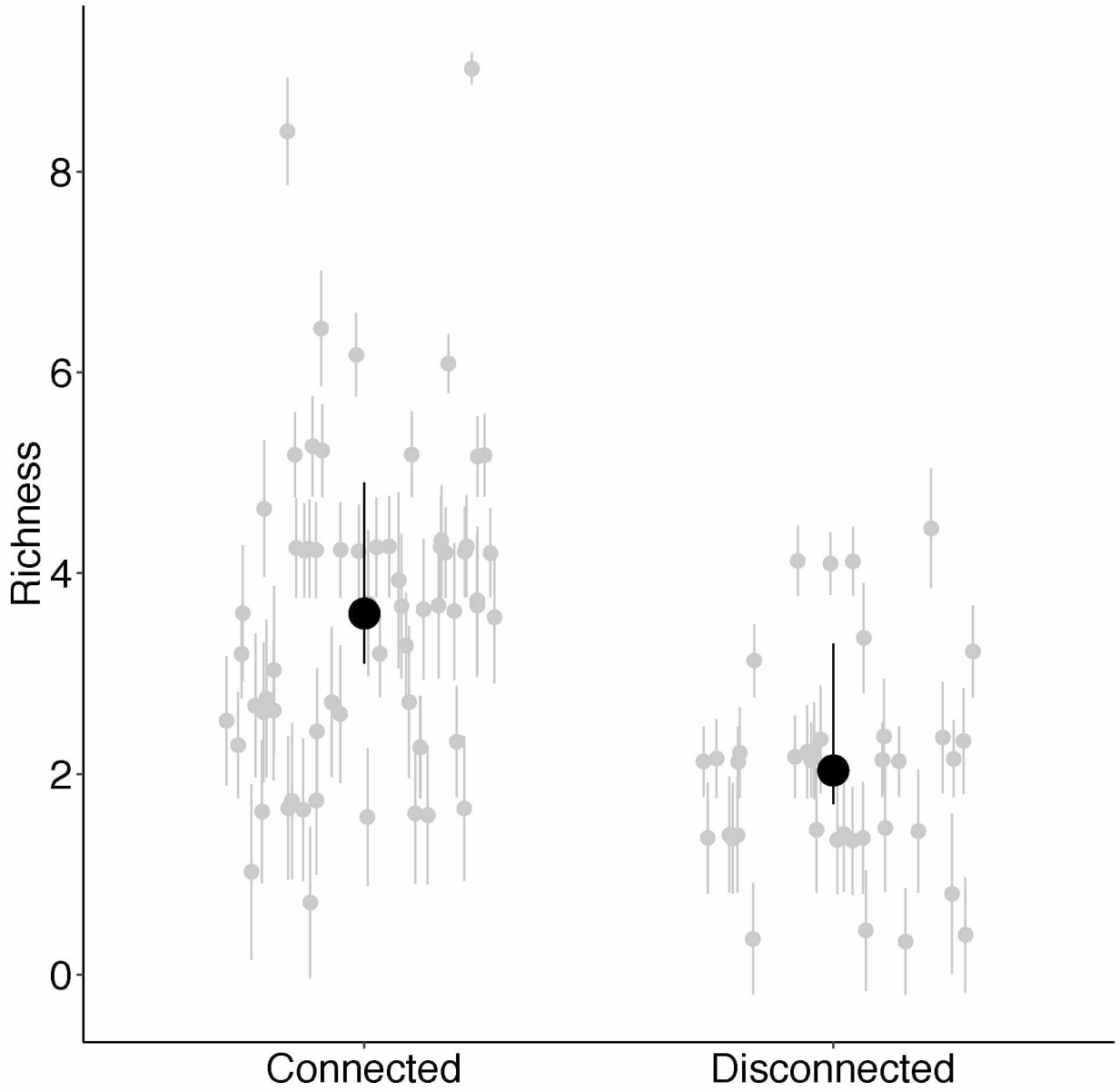

Figure 1.2. Estimated species richness for connected and disconnected lakes; gray points represent mean estimates with standard deviations for each of the individual sample lakes (points are staggered for viewing) and the large black points represent the mean and 95% credible interval for connected and disconnected lakes.

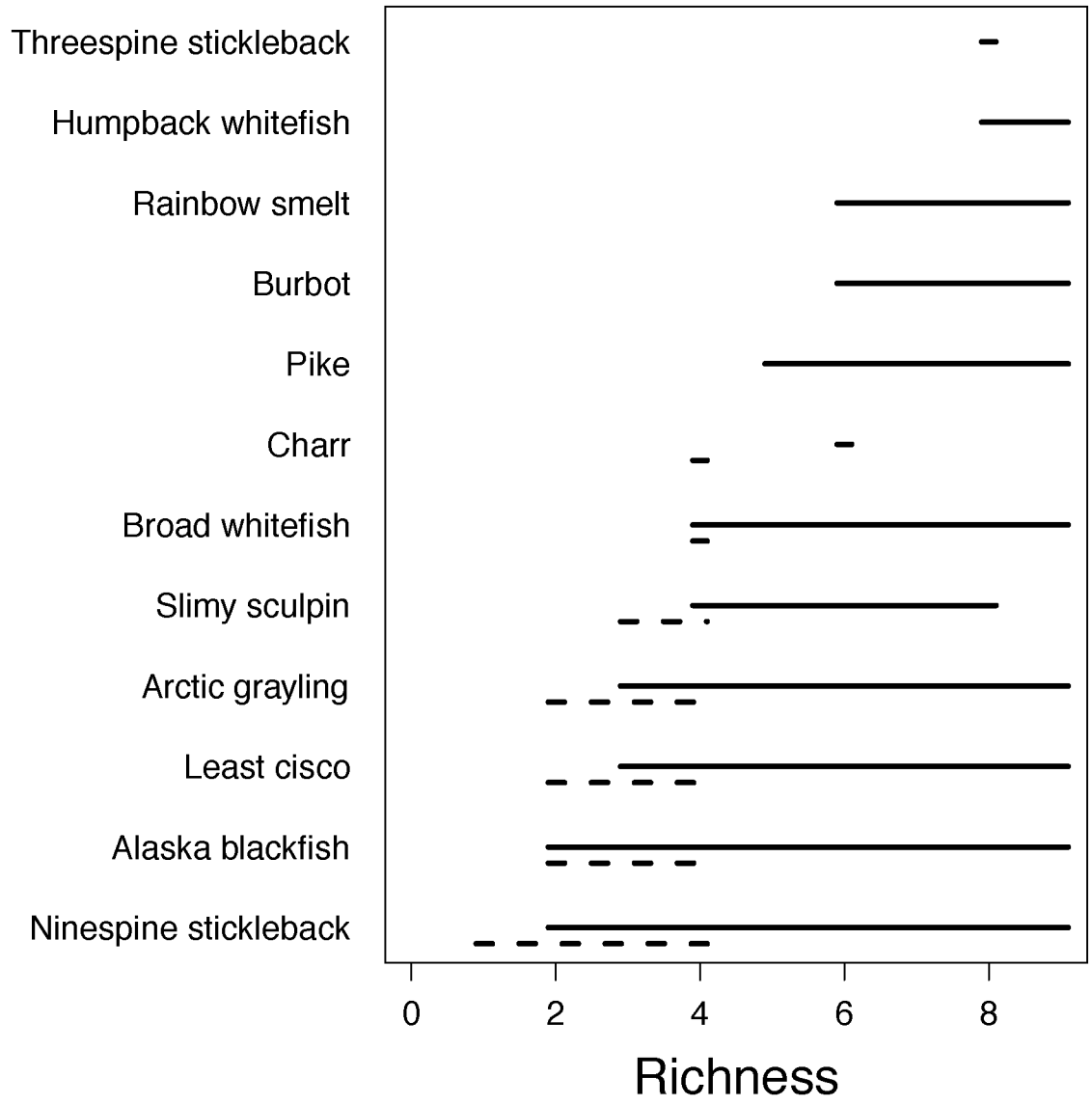

Figure 1.3. Line plots demonstrating the organisation of individual species across fish species richness levels for connected lakes (solid lines) and disconnected lakes (dashed lines). Lines correspond to the range of richness levels over which each fish species was observed. Only lakes where richness estimates equalled naïve richness were included in this plot.

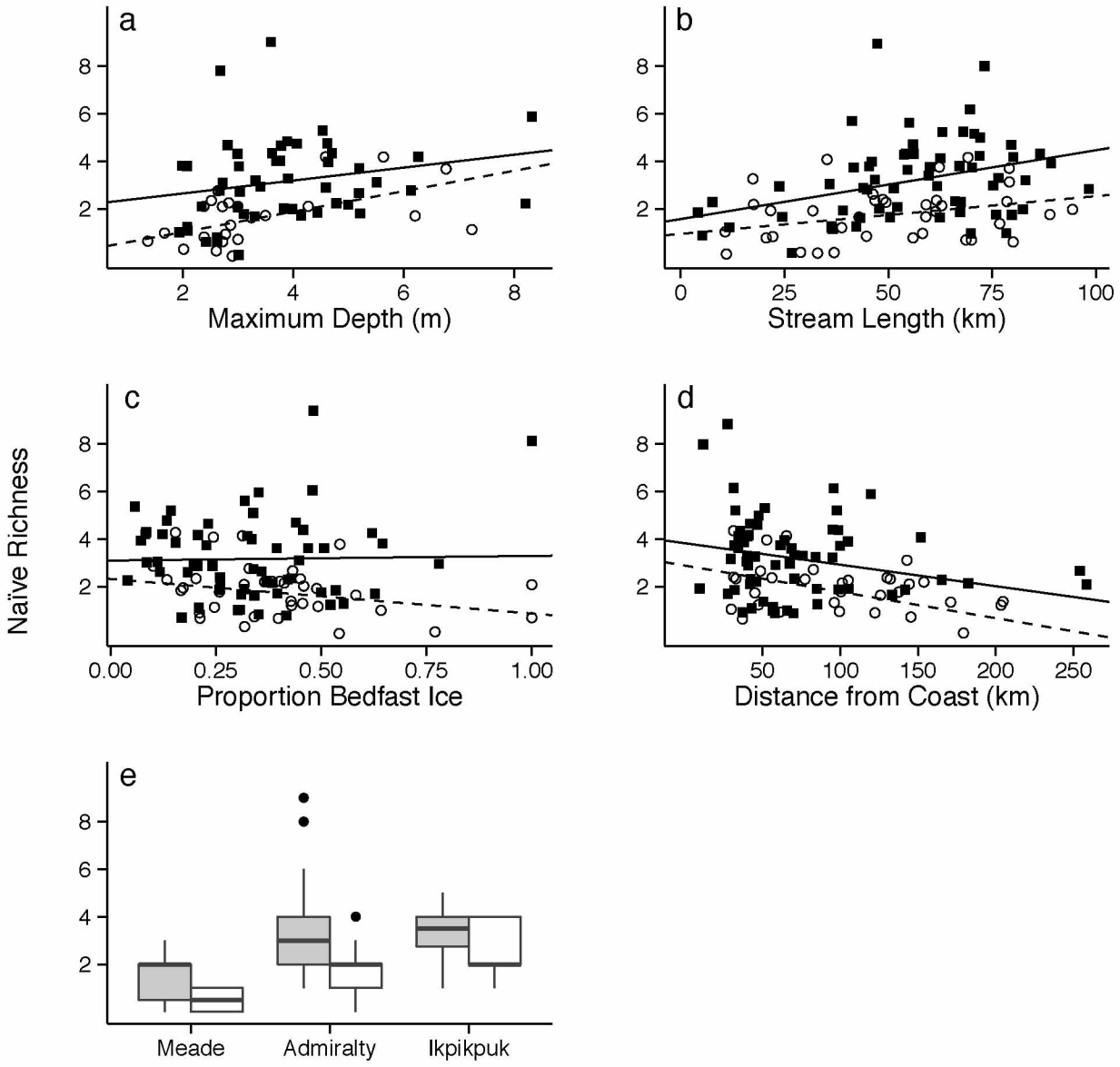

Figure 1.4. Trends of naïve species richness in connected lakes (filled – solid line) and disconnected lakes (open – dashed line; points staggered for viewing) for (a) maximum depth, (b) total local stream length, (c) proportion of lake area with bedfast ice, (d) distance from coast and (e) catchment. For the catchment plot, (e) the upper and lower box edges correspond to the first and third quartiles, points beyond the whiskers are outliers.

Table 1.1. The predicted influence of environmental covariates on fish species richness in lakes of the Arctic Coastal Plain. Covariates, grouped here by landscape scale (local or regional) and category, can have a positive (+) or negative (-) effect on richness or alter the species pool (Δ).

Scale	Category	Variable	Predicted response	Justification	Reference
Local	Connectivity	Connection	+	Direct lake access provided to more species	Tonn & Magnuson, 1982; Olden *et al,*. 2001; Haynes *et al.*, 2014
	Morphology	Surface area	+	Find more species in larger area	Tonn & Magnuson, 1982; Amarasinghe & Welcomme, 2002; Haynes *et al.*, 2014
		Bedfast ice	-	Reduction in winter refuge, strong extinction factor	Tonn *et al.*, 1990; Hershey *et al.*, 2006; Haynes *et al.*, 2014
		Maximum depth	+	Increased habitat diversity, provide winter refuge	Tonn *et al.*, 1990; Baber *et al.*, 2002; Hershey *et al.*, 2006
	Landscape Context	Total stream length	+	Increase access to stream/lake habitat, more wetted habitat	Rathert *et al.*, 1999; Kirsch & Peterson, 2014
		Total pond & lake area	+	More wetted habitat	Baber *et al.*, 2002
		Distance to near lake	-	Lake access is restricted when water bodies are distant	Haynes *et al.*, 2014
		Distance between lakes	-	Lake access is restricted when water bodies are distant	Haynes *et al.*, 2014
Regional	Landscape Context	Total stream length	+	Increase access to stream/lake habitat, more wetted habitat	Rathert *et al.*, 1999; Kirsch & Peterson, 2014
		Total pond & lake area	+	More wetted habitat	Baber *et al.*, 2002
		Distance from coast	-	Movement corridor and overwintering habitat provided near coastline	Beisner *et al.*, 2006; Uchida & Inoue, 2010; Haynes *et al.*, 2014
		Watershed	Δ	Species pool differs by watershed	Angermeier & Winston, 1998
		Ecological landscape	Δ	Species pool differs by ecosystem features	Angermeier & Winston, 1998; Argent *et al.*, 2003

Table 1.2. Covariate attributes for the Arctic lakes used to model fish species richness.

Variable	Mean	Range	Classification
Connection	–	–	present/absent
Watershed	–	–	Meade/Admiralty/Ikpikpuk
Ecological landscape	–	–	sandy/peaty/riverine
Surface area (km^2)	1.3	0.2 - 14.9	–
Bedfast ice (%)	36	4 - 100	–
Maximum depth (m)	3.6	1.4 - 8.3	–
Distance to coast (km)	86.8	9.6 - 291.9	–
Distance to near lake (m)	312	16.5 - 1,991	–
Distance between lakes (m)	202	105 - 340	–
Local stream length (km)	53.4	4.1 - 98.3	–
Local pond & lake Area (km^2)	23.5	13.2 - 33.9	–
Regional stream length (km)	4,402	3,674 - 5,064	–
Regional pond & lake area (km^2)	1,869	1,257 - 2,321	–

Table 1.3. Capture characteristics, including the number of lakes (of 102) with fish species present, the number of detections (of 910) for each species, and the total number captured in sampled lakes of the central Arctic Coastal Plain, Alaska. Family, scientific name and common name are given for all species. Number of detections was determined from 408 fyke net sets and 502 gill net sets.

Family	Scientific name	Common name	No. lakes	No. detections	*n* captured
Cottidae	*Cottus cognatus*	Slimy sculpin	9	20	29
Esocidae	*Esox lucius*	Pike	4	4	6
Gadidae	*Lota lota*	Burbot	4	5	7
Gasterosteidae	*Gasterosteus aculeatus*	Threespine stickleback	1	2	2
	Pungitius pungitius	Ninespine stickleback	94	327	76,397
Osmeridae	*Osmerus mordax*	Rainbow smelt	2	5	51
Salmonidae	*Coregonus nasus*	Broad whitefish	32	76	163
	Coregonus pidschian	Humpback whitefish	2	6	13
	Coregonus sardinella	Least cisco	54	272	2189
	Salvelinus spp.	Char	3	10	22
	Thymallus arcticus	Arctic Grayling	15	27	57
Umbridae	*Dallia pectoralis*	Alaska blackfish	48	83	182

Table 1.4. Descriptive statistics of known fish assemblages, for each richness level (*S*), found on the central Arctic Coastal Plain, Alaska. The number of lakes (*n*) and number of connected or disconnected lakes (C,D) with each known assemblage are accompanied by the mean and standard deviation (SD) for the total local stream length (m), distance from coast (km), the proportion of bedfast ice in winter (%), maximum depth (m), and the number of lakes with a particular assemblage in each of the three watersheds (MR, Meade River; AB, Admiralty Bay; IR, Ikpikpuk River). Species codes for fish species are: AB, Alaska blackfish; AG, Arctic grayling; BW, broad whitefish; BB, burbot; CH, char; LC, least cisco; HW, humpback whitefish; NS, ninespine stickleback; PK, pike; RS, rainbow smelt; SS, slimy sculpin; and TS, threespine stickleback.

S	Assemblage	*n*	C,D	Stream Length (m)		Distance from Coast (km)		Bedfast Ice (%)		Maximum Depth (m)		Watershed		
				Mean	SD	Mean	SD	Mean	SD	Mean (n*)	SD	MR	AB	IR
0	Fishless	4	0,4	27.4	11.4	171	17.9	51	19	2.4 (4)	0.5	3	1	0
1	NS	11	1,10	49.7	24.1	110.8	64.2	44	23	3 (8)	1.8	3	7	1
2	NS AB	16	5,11	53.2	18.3	104.7	43.9	39	10	3.7 (13)	1.1	1	13	2
	NS LC	3	0,3	66.6	20.2	55.4	22.2	46	47	–	–	0	1	2
	NS AG	1	0,1	21.7	–	45.1	–	17	–	2.7 (1)	–	0	1	0
3	NS AB LC	3	2,1	54	41	88.5	51.7	28	18	2.6 (1)	–	0	3	0
	NS AB AG	2	2,0	33.8	14.3	169.2	120.2	16	6	2.7 (1)	–	1	1	0
	NS LC SS	1	0,1	79.2	–	48.7	–	10	–	–	–	0	1	0
4	NS AB LC BW	13	11,2	62.7	13.8	65.6	36.2	35	20	3.7 (10)	1.2	0	6	7
	NS AB LC AG	2	1,1	40.6	7.6	63.5	2.7	22	13	4.6 (1)	–	0	0	2
	NS AB LC SS	2	2,0	78.2	15.6	35.1	0.6	12	5	5.5 (2)	1.2	0	2	0
	NS LC SS CH	1	0,1	62.3	–	31.3	–	24	–	6.8 (1)	–	0	1	0
≥ 5	NS AB LC AG BW	2	2,0	70.1	2.9	72.2	36.2	25	27	3.4 (2)	0.8	0	2	0
	NS AB LC SS BW	2	2,0	66.8	5.4	40	10.5	18	7	4.4 (2)	0.4	0	2	0
	NS AB LC AG SS	1	1,0	55.9	–	51.4	–	14	–	3.8 (1)	–	0	0	1
	NS AB LC BW NP	1	1,0	79.6	–	42.1	–	34	–	4.5 (1)	–	0	0	1
	NS AB LC AG NP RS	1	1,0	69.6	–	95.7	–	48	–	8.3 (1)	–	0	1	0
	NS AB LC AG BW BB	1	1,0	55	–	31.5	–	32	–	–	–	0	1	0
	NS LC AG SS BW CH	1	1,0	41.2	–	119.6	–	35	–	–	–	0	1	0
	NS LC AG BW RS BB HW TS	1	1,0	73.2	–	11.8	–	100	–	2.7 (1)	–	0	1	0
	NS AB LC AG BW NP RS BB HW	1	1,0	47.3	–	27.4	–	48	–	3.6 (1)	–	0	1	0

*The number of lakes included in the mean, only a subset of lakes were measured for maximum depth

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Appendix 1-A.

Co-author permissions

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Permission to use manuscript in dissertation

4 messages

Sarah Laske <slaske@alaska.edu> Wed, Mar 15, 2017 at 5:16 PM
To: "Whitman, Matt" <MWhitman@blm.gov>, "Koch, Joshua" <jkoch@usgs.gov>, thaynes@wcs.org

Greetings co-authors,

Per the UAF thesis formatting guidelines I must include permission from each of you to include the following chapter in my dissertation:

Laske, S. M., T. B. Haynes, A. E. Rosenberger, J. C. Koch, M. S. Wipfli, M. Whitman, and C. E. Zimmerman. 2016. Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology 61:1090–1104. doi:10.1111/fwb.12769

If you are willing to grant permission, please reply to this email so I can include a copy of this email exchange as an appendix to the dissertation.

Thank you,

Sarah

Trevor Haynes <thaynes@wcs.org> Wed, Mar 15, 2017 at 5:18 PM
To: Sarah Laske <slaske@alaska.edu>
Cc: "Whitman, Matt" <MWhitman@blm.gov>, "Koch, Joshua" <jkoch@usgs.gov>

Hi Sarah,
I enthusiastically grant permission for its inclusion.

Trevor

Dr. Trevor B. Haynes
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Koch, Joshua <jkoch@usgs.gov> Thu, Mar 16, 2017 at 8:21 AM
To: Sarah Laske <slaske@alaska.edu>
Cc: "Whitman, Matt" <MWhitman@blm.gov>, Trevor Haynes <thaynes@wcs.org>

Hi Sarah,

I support using that chapter in your thesis.

Thanks,
~Josh

****
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Matt Whitman <mwhitman@blm.gov> Thu, Mar 16, 2017 at 8:40 AM
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Cc: Trevor Haynes <thaynes@wcs.org>, "Koch, Joshua" <jkoch@usgs.gov>

Sarah - yes, of course.

Matthew
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CHAPTER 2

TOP-DOWN CONTROL OF INVERTEBRATES BY NINESPINE STICKLEBACK IN ARCTIC PONDS[1]

ABSTRACT

Despite their widespread presence in northern latitude ecosystems, the ecological role of Ninespine Stickleback *Pungitius pungitius* is not well understood. Ninespine Stickleback can occupy both top and intermediate trophic levels in freshwater ecosystems, so it is likely that their role in food webs as a predator on invertebrates and as a forage fish for upper level consumers is substantial. We introduced Ninespine Sticklebacks to fishless ponds to elucidate their potential effects as a predator on invertebrate communities in Arctic lentic freshwaters. We hypothesized that Ninespine Stickleback would affect freshwater invertebrate communities in a top-down manner. We predicted that the addition of Ninespine Sticklebacks to fishless ponds would: 1) reduce invertebrate taxonomic richness, 2) decrease overall invertebrate abundance, 3) reduce invertebrate biomass, and 4) decrease average invertebrate body size. We tested our hypothesis at two locations by adding Ninespine Stickleback to isolated ponds and compared invertebrate communities over time between fish-addition and fishless control ponds. Ninespine Sticklebacks exerted strong top-down pressure on invertebrate communities mainly by changing invertebrate taxonomic richness and biomass and, to a lesser extent, abundance and average invertebrate size. Our results supported the hypothesis that Ninespine Stickleback may help shape lentic food webs in the Arctic.

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[1] Laske, S. M., A. E. Rosenberger, W. J. Kane, M. S. Wipfli, and C. E. Zimmerman. 2017. Top-down control of invertebrates by Ninespine Stickleback in Arctic ponds. Freshwater Science 36:124–137. doi: 10.1086/690675

INTRODUCTION

Fish can shape the structure and composition of aquatic communities through top-down control on their invertebrate prey (Power 1990, Carpenter and Kitchell 1993). Despite the clear capacity for fishes to drive top-down effects, isolating the role of individual fish species or trophic levels is difficult given the complexity of aquatic food webs (e.g., Winkelmann et al. 2011, Helenius et al. 2015). Direct effects of predation may be masked or modified by other members of the food web, confusing specific trophic relationships (Polis 1994, Batzer et al. 2000). Also, the relative position of fish predators in a food web may affect predator–prey interactions at lower trophic levels or alter interspecific interactions (Jonsson et al. 2007). The indirect effects of predators on invertebrate communities (e.g., shifts in invertebrate behavior) may dilute the effect of direct consumption, masking important interactions (Batzer et al. 2000, Jonsson et al. 2007). Furthermore, predator effects are often reduced or altered by the spatial complexity of habitat (e.g., macrophytes), which can provide refuge for invertebrate prey (Gilinsky 1984, Zimmer et al. 2000, Hornung and Foote 2006). We are better able to describe specific interactions and the nature and pattern of the effect of specific fish species within their food webs via the use of experiments and studies comparing fishless to fish-inhabited systems (Power 1992, Polis 1994, Batzer et al. 2000, Lepori et al. 2012).

The presence of fish may change the composition, richness, abundance, biomass, or size of taxa in the invertebrate community relative to fishless systems (e.g., Gilinsky 1984, Knapp et al. 2001, Parker et al. 2001, Hornung and Foote 2006, Winkelmann et al. 2011). Consumption of a nonrandom subset of prey taxa by newly introduced fish can change richness or composition of invertebrate taxa (Gilinsky 1984, Winkelmann et al. 2011, Helenius et al. 2015). Often, within gape limitations, fish predators preferentially consume large-bodied prey, leading to a decrease in the overall size of invertebrates or to a community composed of

smaller-bodied species (Brooks and Dodson 1965, Carlisle and Hawkins 1998, Knapp et al. 2001). This preference may alter the abundance or standing crop of invertebrates as fish predators consume invertebrate prey.

Small-bodied fish species are often a link in food webs that allows energy to flow laterally across habitat boundaries before it flows up the food chain (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Solomon et al. 2011). For example, Vander Zanden and Vadeboncoeur (2002) found that benthic production indirectly supported >35% of the diet of three piscivorous fishes because their small-bodied fish prey relied on benthic food sources. One such group of small-bodied fishes are the sticklebacks, Family Gasterosteidae, which, by virtue of their omnivorous dietary habits, often serve this intermediate role in aquatic food webs (Morrow 1980, Delbeek and Williams 1988, Hornung and Foote 2006). McFarland (2015) found that Ninespine Stickleback *Pungitius pungitius* are a valuable food resource for Arctic Grayling *Thymallus arcticus* and accounted for 88% of prey biomass consumed in a study on the Arctic Coastal Plain of Alaska. However, to date, no investigators have published studies on the influence of Ninespine Stickleback predation on invertebrate communities. The few related studies are limited to observation or comparisons with other sticklebacks or Arctic Char *Salvelinus alpinus* (Delbeek and Williams 1988, Gallagher and Dick 2011, McFarland 2015).

This paucity of information on the ecological role of Ninespine Stickleback is surprising given their circumpolar distribution and dominance in Arctic lakes (Morrow 1980, Haynes et al. 2014, Laske et al. 2016). In terms of catch-per-unit-effort, the average numerical ratio of Ninespine Stickleback to other sympatric fish species in lakes of the central Arctic Coastal Plain of Alaska is ~800∶1 (SML, unpublished data), indicating they make up a large proportion of fish biomass and probably play a substantial role in food webs. Considering the rapid metabolism and

dietary flexibility of Ninespine Stickleback (Cameron et al. 1973) and the associated high demand for food resources, they are likely to affect their invertebrate prey. In experiments on related species, total invertebrate abundance increased in the presence of Threespine Stickleback *Gasterosteus aculeatus* because predation pressure on large crustaceans released small-bodied microzooplankton from predation or competition and caused their numbers to rise (Helenius et al. 2015). Brook Stickleback *Culaea inconstans* competed with large-bodied predatory invertebrates for food, which led to depletions of predatory and noninsectivorous invertebrate biomass and functional replacement of invertebrate predators by Brook Stickleback (Hornung and Foote 2006).

Ninespine Stickleback have the potential to transfer energy along multiple trophic pathways (Gallagher and Dick 2011) because of their relative position in local food webs as either the top fish predator (when found as the sole predatory fish) or as an intermediate predator (when found with additional predatory fishes). They can mediate the transfer of energy from littoral habitats to predatory fish in the pelagic zone or indicate changes in the primary source of energy production (phytoplankton vs periphyton; Gallagher and Dick 2011). However, their precise role in Arctic food webs may be difficult to describe in natural habitats where ecosystem interactions are complex. The ponds and lakes that routinely contain populations of Ninespine Stickleback are structurally diverse, with open water, shallow weed margins, submerged vegetation, and areas of flooded tundra (Cameron et al. 1973), all of which may provide different cover and habitats for invertebrate prey. Furthermore, limnology differs between ponds and lakes (surface area [SA] > 0.1 km^2). Lakes tend to be deeper, cooler, and less productive than ponds (Rautio et al. 2011) and the presence of predatory fishes in lakes may confound or mute the direct effects of Ninespine Stickleback on the invertebrate community. Zooplankton are larger

and more abundant in fishless systems than in lakes or ponds with fish (Rautio and Vincent 2006), but discerning the role of individuals in a multiple-predator environment is complex (Sih et al. 1998). Therefore, attributing influence solely to Ninespine Stickleback would be difficult. Thus, initial explorations of their ecosystem role may be best examined in simple, isolated pond systems.

The goal of our study was to investigate the role of Ninespine Stickleback as a predator in lentic freshwater food webs in Arctic Alaska via an addition–control experiment to detect top-down effects on invertebrate community structure. This experimental approach provided information on the direction and breadth of effects while controlling for external factors (e.g., waterbody type, invertebrate composition, and fish density). Essentially, we took the first step in establishing food web patterns that could be driven by the presence of Ninespine Stickleback in Arctic ponds and lakes. We predicted that the addition of Ninespine Stickleback to previously fishless ponds would have the following top-down effects: 1) reduce invertebrate taxonomic richness, 2) lower overall invertebrate abundance, 3) reduce invertebrate biomass, and 4) decrease average invertebrate body size. We repeated our experiment in small, isolated ponds over sequential years at 2 locations with differing environmental conditions, physiography, and geology (Jorgenson and Grunblatt 2013) to investigate the potential effect of local conditions on the role of Ninespine Stickleback in aquatic food webs.

METHODS

We selected trough ponds from two locations (hereafter, North and South) on the Arctic Coastal Plain, Alaska, in which to conduct our experiment (Fig. 2.1A–C). The low-relief tundra is underlain by thick, continuous permafrost, which inhibits subsurface drainage and leads to formation of various thermokarst water bodies. Troughs form in the cracks between polygonal

ground formations and deepen as the ice beneath melts. These ponds measured ~1–2 m wide and 0.5 m deep, with an average pond surface area of 25 m^2 (Table 2.1). Trough ponds have limited submerged vegetative cover for invertebrates or fish to use, and most cover consists of overhanging grasses or flooded grass margins. Water in the ponds comes from snowmelt in June and is maintained through subsurface flows and precipitation events until refreezing by October (Koch et al. 2014). North is underlain with peat and has more standing surface water than South, which is underlain by sand. The location of ponds in upland areas and lack of surface water connections provided aquatic habitats naïve to fish prior to our experiment.

At each location, we collected Ninespine Stickleback from one lake adjacent to the ponds (<1 km from the pond site). We set fyke nets with 6.4-mm mesh overnight to capture fish for transport to ponds. We moved fish in 19-L buckets, and supplied them with air with the aid of battery- operated aquarium pumps (Penn Plax Silent-Air B10, Hauppauge, New York). Fish ranged in size from ~30–60 mm total length. We did not keep any fish considered less than age-1 and assumed that no size-based diet differences would exist based on published diet data for adults (Cameron et al. 1973, Delbeek and Williams 1988). We added Ninespine Stickleback to ponds based on a previously reported mean value of 11 g/m^2 (Cameron et al. 1973), adjusting the number of fish added to attain the correct biomass given pond area. We counted the fish once we attained the desired biomass (Table 2.1). We added fish to 5 ponds at North (2013) and 6 ponds at South (2012). We selected an equal number of control ponds at each location.

One to 2 d prior to adding Ninespine Stickleback, we used a 243-µm-mesh D-frame dip-net with an opening of 604 cm^2 to sample nektonic and benthic invertebrates in all ponds. We moved the net in a J-shaped motion that began with the net grazing the bottom, then passed the net horizontally along the bottom and up through the water column. We collected two replicate

dip-net samples from each pond and noted the depth of the water at each sweep location. Replicate net samples increased the opportunity to capture rare taxa, and we did not compare within-pond variation based on these two samples. We examined taxa rarefaction curves before adding fish to assess whether collection was adequate (Appendix 2-A Figure 2-A1; Gotelli and Colwell 2001). At North, we sampled invertebrates in the same way 1, 3, and 6 wk post-introduction. At South, we sampled invertebrates 1, 2, and 8 wk post-introduction. We stored invertebrate samples in 95% ethanol for later processing. On post-introduction sampling days, we recaptured Ninespine Stickleback with unbaited minnow traps (23-cm diameter 44.5-cm length, two 2.5-cm openings, 6-mm steel mesh) and sampled the stomach contents by gastric lavage with a 22-gage intravenous catheter attached to a syringe. We flushed stomachs with 3 to 5 mL of filtered pond water and stored stomach contents in 95% ethanol. We sampled 6 (North) or 5 (South) individuals at each fish-addition pond (total 5 30 fish/location on each sampling date). We then released fish back to the pond. At North, we also sampled stomach contents 1 d post-introduction.

In the laboratory, we identified all invertebrates from dip-net collections and stomach contents to the lowest practical taxonomic level and assigned a life stage (larva, pupa, or adult). For example, macroinvertebrates were identified to family, but Ostracoda were identified no lower than to class. From the dip-net samples, for each pond and sampling period, we captured images of up to 20 individuals of each taxon with a Leica DFC425 (Leica Microsystems, Buffalo Grove, Illinois) camera mounted on a dissection microscope. We digitally measured invertebrate lengths with ImageJ (version 1.48; imagej.nih.gov). We used length–mass regression equations from the literature to estimate biomass of invertebrates (Dumont et al. 1975, Pace and Orcutt

1981, Culver et al. 1985, Benke et al. 1999, Sabo et al. 2002, Gruner 2003, Miyasaka et al. 2008, Rennie and Evans 2012).

Statistical analyses

Invertebrates

We compared number of invertebrate taxa, abundance, biomass, and size of invertebrates in control and fish-addition ponds at each sampling time to assess whether invertebrate assemblage characteristics changed in the presence of Ninespine Stickleback. Number of invertebrate taxa was the number of unique invertebrate taxa found in each pond. Rarefaction was not possible because drastic differences in invertebrate abundance among addition treatments (e.g., post-addition at South: average count in control ponds = 4713 individuals, average count in fish-addition ponds = 118 individuals) rendered standardized measures of richness incomparable. At each pond and sampling time, we divided the number of invertebrates by the sweep depth of the two samples to calculate abundance (number of invertebrates/cm depth swept). To obtain biomass, we multiplied the number of invertebrates by the average biomass on a taxon-specific basis from length–mass equations (referenced above), and divided by the depth of the sweep to obtain biomass/cm of depth swept. We used mean weighted length calculations (following methods by Helenius et al. 2015) to estimate differences in overall invertebrate size between control and fish-addition ponds at each sampling time. We tested for effects of addition treatment and time while accounting for location (fixed effect) and pond (random effect) based on linear mixed-effects models in R package *nlme* (version 3.1-126; R Project for Statistical Computing, Vienna, Austria) and accounted for temporal autocorrelation with a 1st-order autoregressive structure for all models except our model for number of invertebrate taxa, which was based on compound symmetry (model selection based on lowest Akaike Information

Criterion for small samples [AICc] score; R package *AICcmodavg*, version 2.0-4). Log(x)-transforming abundance and biomass values prior to analysis improved normality.

We used multivariate approaches to examine changes in invertebrate community composition caused by the addition treatment, time, and addition-treatment time interaction. We standardized abundances of individual taxa to species maxima and omitted taxa captured only once during the course of the study. We visually examined a non-metric multidimensional scaling (NMDS) plot (R package *vegan*, version 2.3-4) at 2 and 3 dimensions to assess which yielded the lowest stress. We then used repeated-measures multivariate analysis of variance (PERMANOVA) based on dissimilarities using Bray–Curtis distances (function *adonis*; R package *vegan*, version 2.3-4) to estimate the proportion of variation explained by location (North vs South), addition treatment, time, and the addition-treatment × time interaction in permutation tests (1000 iterations). We repeated these analyses on the mass of invertebrates to assess predation effects on invertebrate biomass.

Stomach contents

For each invertebrate taxon at all post-addition sampling times, we calculated frequency of occurrence as the number of fish in which the taxon occurred divided by the total number of fish with food in their stomachs. To calculate the mean proportion of diet items by number, we summed the invertebrates in the stomach contents of the 5 or 6 sampled fish (fish were pseudoreplicates within ponds) at each sampling time and calculated the numerical proportions for all taxa standardized to the total. We assessed the influence of time since introduction on the mean proportion of diet items by number in Ninespine Stickleback stomach contents with PERMANOVA on commonly consumed items (frequency of occurrence > 20%). This function allowed us to partition sources of variation and account for the pond effect in the permutation

tests (1000 iterations). We then calculated similarity percentage (SIMPER; vegan) between diets, by numeric proportion, at the beginning and end of the experiment using dissimilarity matrices. At South, we compared diets at week 1 to week 8, and at North, we compared diets at day 1 to week 6 and diets at week 1 to week 6. Furthermore, we estimated the contributions of potentially influential taxa (mean contribution to dissimilarity > 10%) to dietary differences.

RESULTS

Invertebrates

Our prediction that introducing Ninespine Stickleback to ponds would decrease invertebrate richness was supported. Addition of Ninespine Stickleback reduced the number of invertebrate taxa in fish-addition ponds at both locations by an average of 21.7% compared to control ponds (North: $t = -2.60$, df = 45, $p = 0.01$; South: $t = -3.11$, df = 45, $p = 0.003$; Fig. 2.2A, B). Richness attenuated over the season at all ponds, but the reduction was greatest in fish-addition ponds. Compared to control ponds, richness in fish-addition ponds was reduced by an average of 4 taxa (31.2%) at North and 1 taxon (10.5%) at South. After the initial decrease, number of taxa did not differ detectably over time (post-addition; North: $t = 0.20$, df = 45, $p = 0.84$; South: $t = -0.77$, df = 45, $p = 0.44$) or by location ($t = -1.95$, df = 45, $p = 0.06$). Support for our prediction that introducing Ninespine Stickleback would decrease invertebrate abundance was limited (Fig. 2.2C, D). Abundance initially decreased but then increased at North (addition treatment time interaction: $t = 3.61$, df = 40, $p < 0.001$) but remained lower at South (addition treatment: $t = -8.88$, df = 18, $p < 0.001$). After an immediate decrease (week 1), abundance stayed low throughout all sampling periods at South (time: $t = 1.05$, df = 40, $p = 0.30$). Fish-addition ponds at South contained 98% fewer invertebrates/cm depth swept than their control-pond counterparts, but at North, fish addition interacted with time to confound the

influence of fish introduction on invertebrate abundance. Abundance rebounded after an initial 84% decrease (compared to control ponds). By the 6th wk post-addition, abundance of invertebrates in fish-addition ponds exceeded control-pond values by 23%. This increase in abundance was not accompanied by an increase in biomass (Fig. 2.2C, E).

At both locations, fish addition decreased invertebrate biomass (North: $t = -3.06$, df = 18, $p = 0.007$; South: $t = -5.13$, df = 18, $p < 0.001$; Fig. 2.2E, F), providing support for our hypothesis. As with abundance at South, after an initial decrease in biomass, invertebrate losses stabilized and did not continue through time. At all post-addition sampling times, invertebrate biomass was ~90% lower in fish-addition than in control ponds.

Our prediction that introduction of Ninespine Stickleback would decrease the overall size of invertebrates in the ponds was not supported. At both locations, fish addition did not affect mean weighted size of invertebrates (North: $t = -1.36$, df = 45, p 5 0.18; South: $t = -1.13$, df = 45, $p = 0.26$; Fig. 2.2G, H). At North, length tended to diverge over time between addition treatments (addition-treatment × time interaction: $t = -1.90$, df = 45, $p = 0.06$), but sampling time and the addition-treatment sampling time interaction were not significant at South, though the pattern of mean weighted lengths over time was similar for North and South ponds (Fig. 2.2G, H).

NMDS plots showed the relative similarity of samples (centroids of all ponds in the addition-treatment-time group) for location, addition treatment, and time (Fig. 2.3A– F). Three dimensions reduced stress (0.16) and provided better fit for the data than 2 dimensions. Plots based on the first 2 dimensions (NMDS1 vs NMDS2; Fig. 2.3A, D) showed strong separation of samples by addition treatment and location and showed that pre-addition communities were more similar to communities in control than in fish-addition ponds. Proximity among samples

suggested that fish addition had a greater influence than time on community structure. Plots based on the 1st and 3rd dimensions (NMDS1 vs NMDS3; Fig. 2.3B, E) showed separation by addition treatment along the 1st axis. Evaluation of the 2nd and 3rd dimensions (NMDS2 vs NMDS3; Fig. 2.3C, F) showed separation by location.

PERMANOVA supported the trends visible in the NMDS plot. Fish addition was an important factor in shaping invertebrate communities at North and South regardless of whether dissimilarities were based on abundance ($R^2 = 0.38, p < 0.001$) or biomass ($R^2 = 0.35, p < 0.001$). Time accounted for little of the variation in biomass among communities ($R^2 = 0.02, p = 0.02$). Time and the addition-treatment × time interaction accounted for little of the variation in abundances among communities (time: $R^2 = 0.02, p = 0.02$; addition-treatment × time interaction: $R^2 = 0.01, p = 0.05$). The amounts of variation in biomass or abundance among communities explained by sampling time (the repeated-measure) were ≤2%. Location, which appeared distinctly in our NMDS plots, was a secondary source of variation in abundance ($R^2 = 0.20, p < 0.001$) and biomass ($R^2 = 0.22, p < 0.001$) among communities.

Stomach contents

Based on frequency of occurrence, the diets of Ninespine Stickleback were more diverse at North than South (Tables 2.2, 2.3). Three taxa occurred regularly in the diets of Ninespine Stickleback at both North and South. At South, Chironomidae (larva and pupa), Cyclopoida, and Harpacticoida had a frequency of occurrence >30% at each sampling time. At North, Chironomidae (larvae and pupae) and Cyclopoida had a frequency of occurrence >30% at all time periods and Harpacticoida had a frequency of occurrence ≥30% at wk 3 and wk 6. Harpacticoida, Chydoridae, and Ostracoda increased in frequency of occurrence (Tables 2.2, 2.3) and numeric proportion in fish stomach contents (Fig. 2.4) after the abundance of large-bodied

prey declined. Chironomidae frequency of occurrence was consistent throughout the experiment (Tables 2.2, 2.3), and the numeric proportion of all Diptera (larvae and pupae), including Chironomidae, in the diets was relatively consistent (Fig. 2.4). We saw a shift from larger prey (e.g., Daphniidae) to small-bodied prey (e.g., Harpacticoida) at both locations (Fig. 2.4). Consumption of Daphniidae and Baetidae occurred only within the 1st wk after introduction, and differences in abundance indicated that these taxa were removed from the invertebrate communities of fish-addition ponds (Fig. 2.5A, B).

Given the differences in invertebrate communities by location, we analyzed the numeric proportion of diet contents separately for North and South. At both locations, we observed a change in stomach contents over time (PERMANOVA, North: $R^2 = 0.16$, $p = 0.005$; South: $R^2 = 0.24$, $p < 0.001$). The dissimilarity matrix indicated changes in both proportion of diet items and identity of prey. Diets differed by 82% from week 1 to week 8 at South (SIMPER), primarily because of changes in Harpacticoida, Daphniidae, and Cyclopoida, with mean contributions to diet dissimilarity of 23 ± 16 (SD), 17 ± 19, and 15 ±14%, respectively. At North, diets differed by 81% from day 1 to week 6 and by 68% from week 1 to week 6. From day 1, Daphniidae and Harpacticoida drove these differences, with mean contributions to diet dissimilarity of 26 ± 15 and 13 ± 11%, respectively. From week 1, Ostracoda and Harpacticoida supported these differences, with mean contributions to diet dissimilarity of 17 ± 19 and 12 ± 12%, respectively.

DISCUSSION

We found support for our hypothesis that Ninespine Stickleback exert top-down controls on invertebrate communities of small Arctic ponds common across the Alaskan Arctic landscape. The effects of fish on the invertebrate community occurred rapidly and persisted throughout the short growing season, and communities quickly shifted from pre-addition and

control values. Selective feeding by Ninespine Stickleback (e.g., Ingram et al. 2011, Helenius et al. 2015) targeted specific taxa. This preferential feeding resulted in complete losses of large-bodied, nektonic taxa like Daphniidae and Baetidae, providing evidence that top-down effects can be strong enough to drive local extinctions. By the end of the experiment, Ninespine Stickleback consumption had shifted toward benthic prey like harpacticoid copepods. Behavioral differences between nektonic and benthic taxa probably contributed to the order in which these prey were consumed. Active prey or those swimming in the water column, like Baetidae and Daphniidae, may have a higher risk of encounter with fish predators (Wellborn et al. 1996) and might have been more likely to be consumed than taxa that use cover (e.g., tuft-weaving or tube-building midges; Gilinsky 1984, Power et al. 1992). By selecting specific taxa from the available pool (Delbeek and Williams 1988), Ninespine Stickleback effectively altered the community of invertebrates. Our experimental approach was useful for discerning the potential effects of fish on lower trophic levels because it controlled for confounding factors, including differences arising from location, shifts in diet composition over time, and changes in invertebrate communities unrelated to fish predation (e.g., emergence).

Location of the experimental ponds was a secondary source of variation for invertebrate abundance and biomass, but experimental outcomes demonstrated the importance of Ninespine Stickleback presence across spatial gradients of climate or physiography. Initial invertebrate communities at North and South varied before introducing Ninespine Stickleback into ponds. We found a greater number of taxa at North, which was reflected in the diets of fish, and two taxa (Chydoridae and Baetidae) appeared consistently at North but not at South. Fish consumed both of these taxa— Baetidae early on and Chydoridae later. However, when we excluded these items, diets of fish at North and South appeared similar. Fish consumed six primary taxa:

Daphniidae, cyclopoid copepods, harpacticoid copepods, ostracods, copepod nauplii, and assorted Diptera. In North ponds, replacement of larger invertebrates by smaller ones (e.g., Daphniidae for copepods) damped losses in overall abundance but resulted in a loss of biomass. However, at South, the presence of Ninespine Stickleback led to dramatic losses of invertebrate abundance in fish-addition ponds, whereas invertebrate abundance nearly doubled in control ponds. Continued invertebrate population growth in control ponds would lead to greater abundance, but in all ponds at South, the water level fell by up to 0.25 m in the last week of July (SML, unpublished data) because of dry conditions in 2012 (Koch et al. 2014). This loss of volume concentrated invertebrates in open water, away from grassy pond margins, enhanced our ability to capture most taxa, and increased the availability of invertebrates to fish in fish-addition ponds (Gilinsky 1984, Hornung and Foote 2006), which could have increased the difference between addition treatments at South ponds.

Predation pressure on specific taxa led to shifts in invertebrate community structure (similar to findings by Bendell and McNicol 1987, Herbst et al. 2009, Winkelmann et al. 2011). Fish diet breadth is hypothesized to be narrower and selection of larger prey to be stronger when prey exist at high densities (Werner and Hall 1974, Maszczyk and Gliwicz 2014). Ninespine Stickleback exhibited this type of prey selectivity early in the experiment, when 50 to 70% of their diet consisted of one or two relatively abundant taxa, Daphniidae and Baetidae. Selective feeding exerted top-down control on invertebrate communities (Herbst et al. 2009, Helenius et al. 2015), so Ninespine Stickleback predation shaped the community over time as they sequentially consumed prey in accordance with availability (Delbeek and Williams 1988).

The shift to small-bodied taxa was more prominent in ponds at North than South. At North, abundance of small-bodied cyclopoid and harpacticoid copepods increased in fish-

addition ponds relative to control ponds, but we did not see this pattern at South. At North, these two taxa became so abundant relative to other taxa that they made up nearly the total invertebrate composition in fish-addition ponds in contrast to the declines in abundance of all taxa observed at South. Increased abundance of small taxa is common in the presence of selective foragers like Ninespine Stickleback (Helenius et al. 2015). Increase in small-bodied taxa could result by predator release if Ninespine Stickleback reduced the abundance of large-bodied insectivorous or planktivorous taxa that feed upon smaller individuals without consuming the small-bodied pond residents themselves (Batzer et al. 2000). Another explanation is that, under intense predation, size selection for Daphniidae by Ninespine Stickleback could ease competition between Daphniidae and small copepods, thereby allowing small-bodied zooplankton to dominate (Brooks and Dodson 1965). Furthermore, small taxa, like Harpacticoida and Ostracoda, generally are associated with the bottom, whereas cladocerans are in the water column. The cover of benthic sediments may allow these taxa to avoid predators, especially when other large-bodied prey are available (Bendell and McNicol 1987).

However, no significant reduction of invertebrate size was evident over time. Size selection by Ninespine Stickleback might have been less apparent because overall variation in the sizes of invertebrates present in the ponds was small. In other words, size selection might have been less apparent than taxonomic selection (i.e., Daphniidae consumed first). However, Ninespine Stickleback have gape limitations (largest reported taxa from diets studied by Cameron et al. 1973 was 10 mm). Some resident pond taxa (e.g., Gastropoda or Trichoptera) that were physically too large to be consumed (SML, personal observation) persisted over time and could have maintained the average size of invertebrates during the experiment. Our inability to capture all large-bodied taxa (e.g., Dytiscidae) efficiently prevented us from including them in

our analyses and reduced our ability to discern size-based trends.

Data collected prior to introduction of Ninespine Stickleback provided important baseline information for understanding the shift in invertebrate community taxonomic richness, abundance, biomass, and invertebrate size in the presence of fish. For example, pre-addition communities were more similar to those in control than in fish-addition ponds at all sampling times. Some taxa, like Culicidae and Chaoboridae, underwent metamorphosis to their adult stages early in the experiment (week 1). This emergence probably led to a drop in abundance of these taxa in control and fish-addition ponds. Sampling for emergent adults could provide more detail for understanding predation effects in the aquatic and terrestrial environment and would be an excellent future step in assessing Ninespine Stickleback effects on community structure. How many of these emergent taxa were lost from fish-addition ponds because of ingestion by Ninespine Stickleback vs natural phenology is unknown because losses occurred over the same time period. Examination of the diets of Ninespine Stickleback at North on day 1 suggested that they consumed some of these invertebrates (Chaoboridae and Baetidae), but these items were not found in stomach contents 1 wk post-addition. Rapid consumption of these taxa probably reduced their numbers, but Baetidae abundance did not differ between fish-addition and control ponds by week 3 despite combined losses from both ingestion and emergence from fish-addition ponds and only emergence from control ponds.

The potential of Ninespine Stickleback to influence the structure of simple aquatic communities must be understood before results can be scaled to larger, more complex systems where effects could be obscured (Gilinsky 1984, Zimmer et al. 2001). The trough ponds to which we introduced Ninespine Stickleback would not have naturally occurring populations of these fish because of their isolated locations. However, other troughs that connect and form a

hydrologic network (similar to a stream) or that are in proximity to larger thermokarst ponds may occasionally support Ninespine Stickleback. By examining the effects of Ninespine Stickleback introduction on invertebrate communities at small, fish-naïve ponds with simple morphometry, we tried to control for bottom-up factors that may confound top-down effects so that we could isolate potential effects on the invertebrate community.

Changes in nutrient, light, and thermal regimes that occur as water bodies increase in size cause the emergence of different physical habitats, which support different invertebrate communities (Hobbie 1984, Rautio et al. 2011, Koch et al. 2014). Relatively complex ponds with diverse substrates may contain a heterogeneous assemblage of invertebrates (Power 1994, Zimmer et al. 2001) that respond differently to fish predators. The effect of fish on invertebrate communities can vary with spatial complexity, habitat heterogeneity, or connectivity (Gilinsky 1984, Power 1994, Shurin 2001). For example, submerged vegetation in larger, thermokarst ponds adds complexity to habitats and supplies cover for invertebrate taxa (Zimmer et al. 2000, Hornung and Foote 2006). In lakes and ponds with complex shorelines, terrestrial invertebrates may be more available as prey items, thereby potentially releasing pressure on aquatic invertebrates (Nakano et al. 1999, Mehner et al. 2005). Connection to adjacent habitats or regional surface-water networks provides dispersal pathways for certain colonizing invertebrates (Shurin 2001). Together these factors, along with indirect effects, confound trophic relationships or mitigate the role of predators (Winkelmann et al. 2011), leading to premature conclusions on the effects of fish, especially in larger systems (Batzer et al. 2000).

The heterogeneous landscape of ponds, lakes, and streams of the central Arctic Coastal Plain in Alaska presents a variety of potential habitats for occupancy of Ninespine Stickleback. Local- and regional-scale differences in water-body characteristics, such as surface area, depth,

watershed connectivity, location, and habitat complexity, affect presence and abundance of Ninespine Stickleback, but also influence the presence and abundance of sympatric fishes and the invertebrate prey base (Cameron et al. 1973, Shurin 2001, Haynes et al. 2014, Laske et al. 2016). We were able to demonstrate consistent top-down effects resulting from the presence of Ninespine Stickleback on invertebrate community structure because our study design accounted for potential variation caused by physiographic locations and pond phenology. By first studying these simplistic food webs, we gained knowledge on trophic effects of ubiquitous Ninespine Stickleback. This study provides needed baseline information on a regionally common fish species, and is a first step in discerning food web patterns in the central Arctic Coastal Plain.

Ninespine Stickleback have a wide-ranging, global distribution that includes Asia, Siberia, Europe, Greenland, and North America (Morrow 1980). Thus, they probably exert top-down pressures in other biomes. The Arctic Coastal Plain of Alaska is a unique ecosystem where this species is an extremely successful opportunist (Haynes et al. 2014). However, its adaptability and tolerance suit it well for any number of habitats with a range of physical characteristics and associated biota (e.g., high Arctic: Gallagher and Dick 2011, brackish waters: Arai and Goto 2005, deep temperate lakes: Nelson 1968). In these settings, this relatively small species might play an important role in the transfer of energy via an array of aquatic food webs.

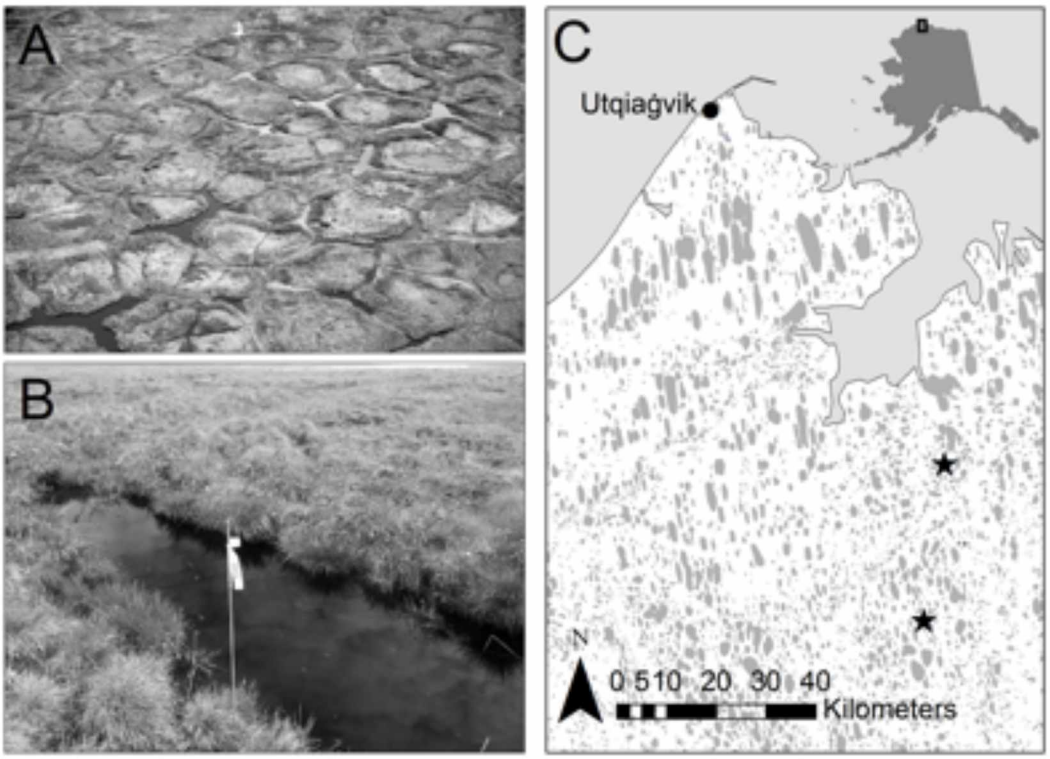

Figure 2.1. Aerial view of trough ponds (A), an on-site view of one experimental pond (B), and maps showing the two study locations (North and South; indicated by stars) and the site location in Alaska (C).

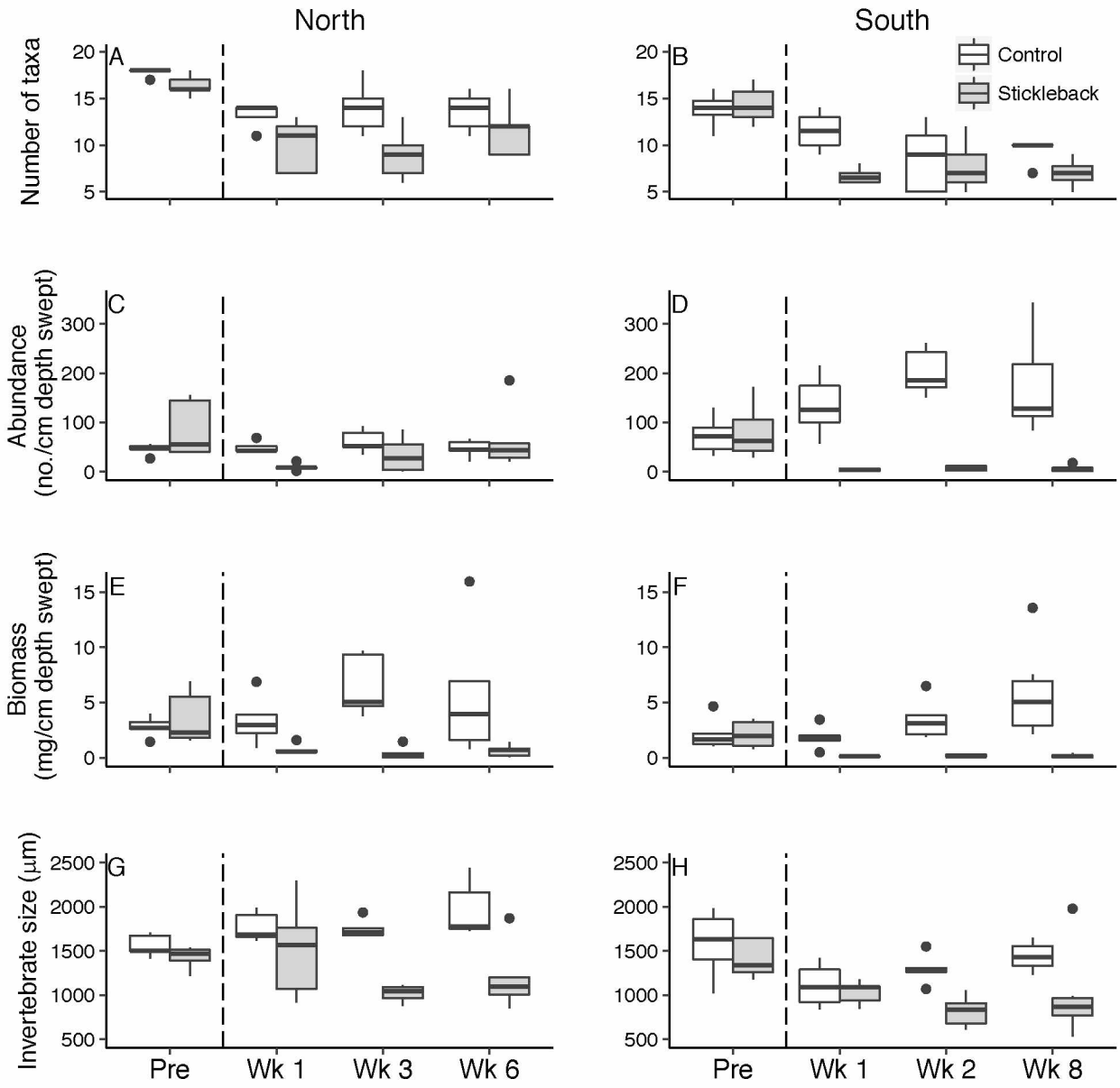

Figure 2.2. Box-and-whisker plots for the number of taxa (A, B), abundance (C, D), biomass (E, F), and size (G, H) of invertebrates before and after Ninespine Stickleback addition to ponds in the North (A, C, E, and G) and South (B, D, F, and H) locations. Lines in boxes are medians, box-ends are quartiles, whiskers are 1.5 inter-quartile range, and dots show outliers. The vertical dashed line separates pre-addition and post-addition sampling dates. No. = number, Wk = week, pre = pre-addition.

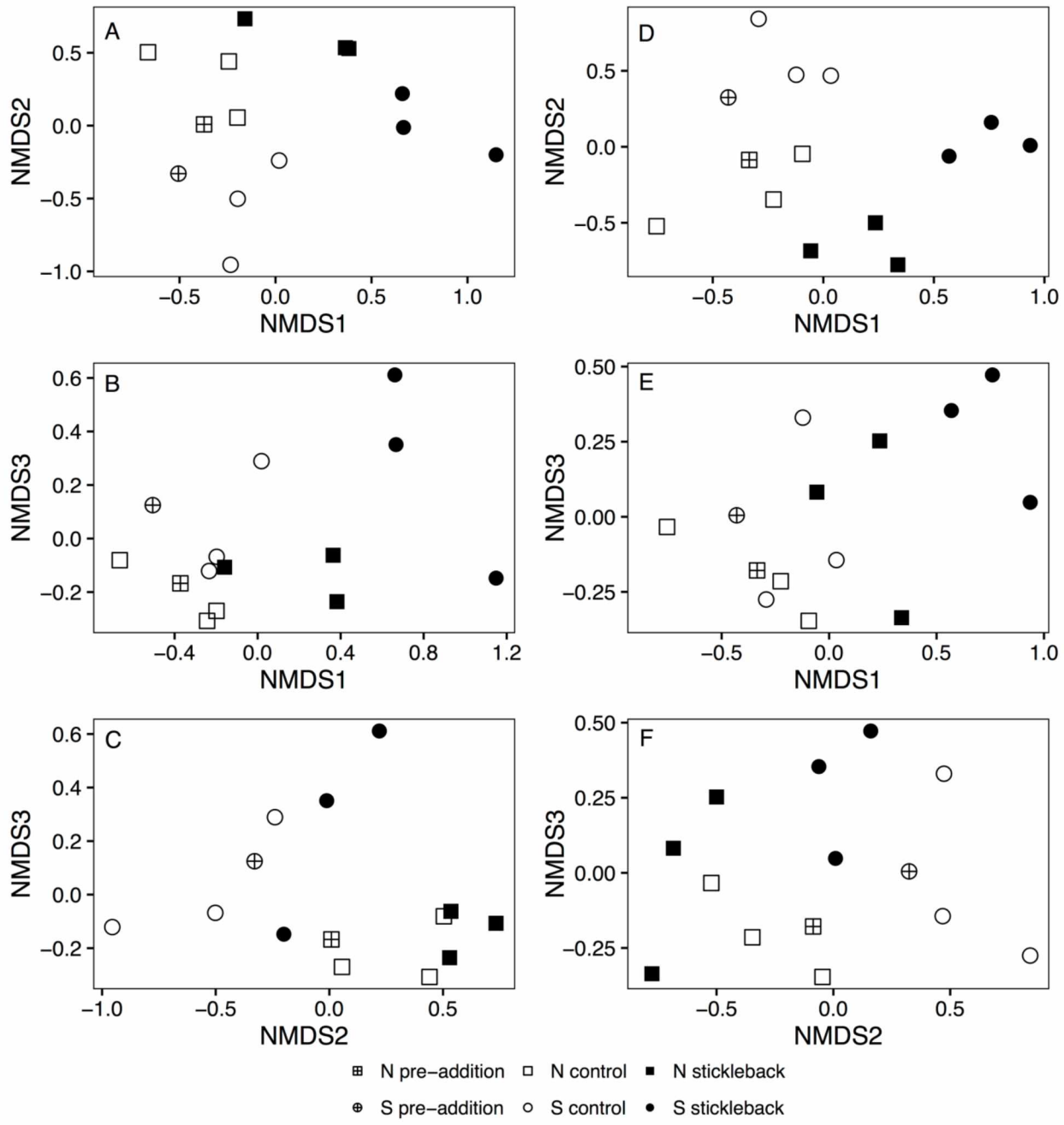

Figure 2.3. Nonmetric multidimensional scaling (NMDS) plots for invertebrate communities based on abundance (A–C) and biomass (D–F). Individual points represent the centroids of invertebrate communities for North (N) and South (S) pre-addition, control, and stickleback addition ponds at each sampling time. Proximity indicates similarity among communities.

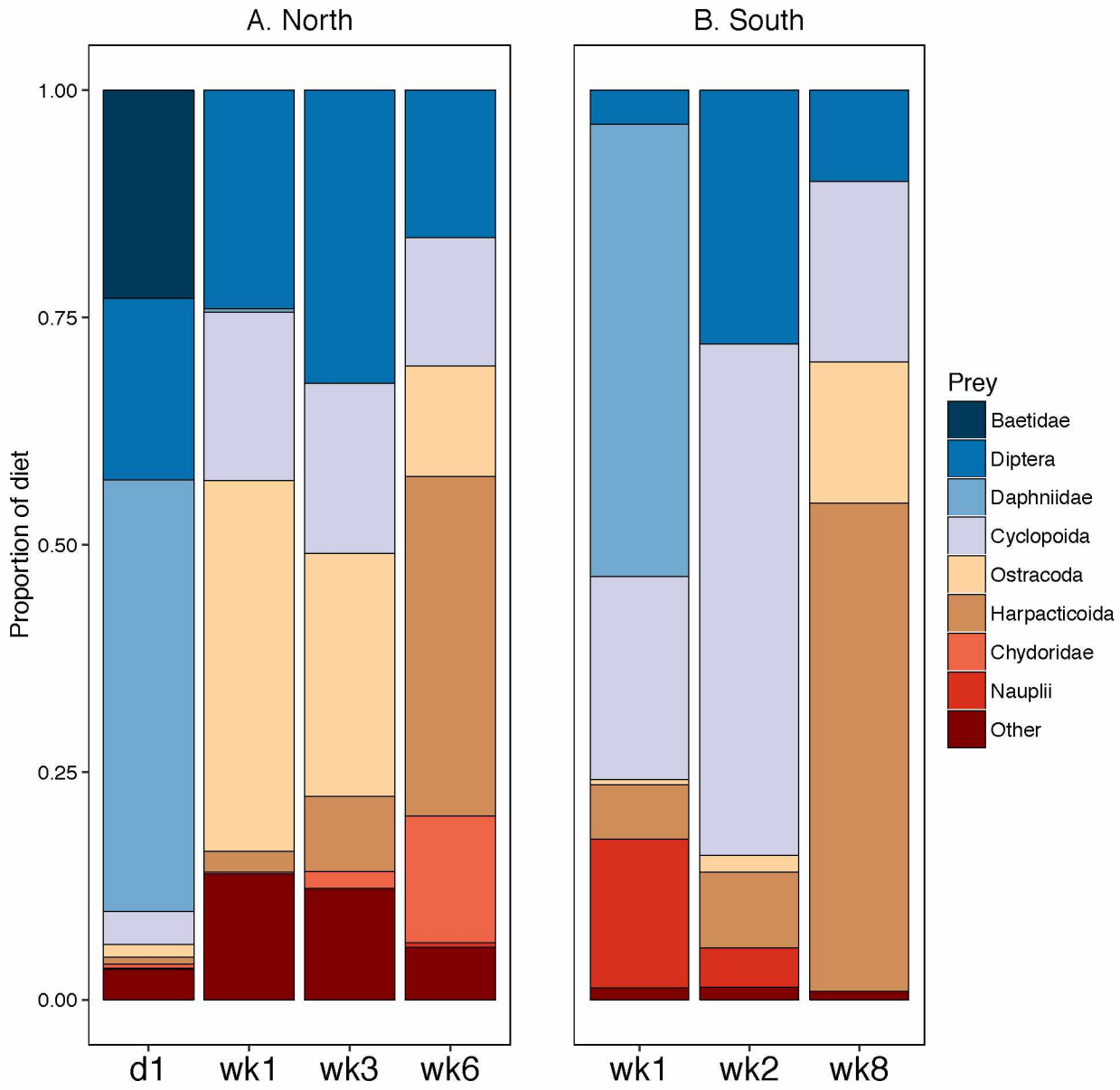

Figure 2.4. Diet proportions, by number, of common prey items found in Ninespine Stickleback stomach contents at each sampling time. At North (A), we collected contents 1 day (d1), 1 wk (wk1), 3 wk (wk3), and 6 wk (wk6) post-addition, and at South (B) we collected contents 1 wk (wk1), 2 wk (wk2), and 8 wk (wk8) post-addition. Diptera includes larvae and pupae of Chironomidae, Chaoboridae, Ceratopogonidae, Dixidae, Empididae, Tipulidae, and digested (unknown) Diptera. Nauplii are the larval stage of all copeopod taxa.

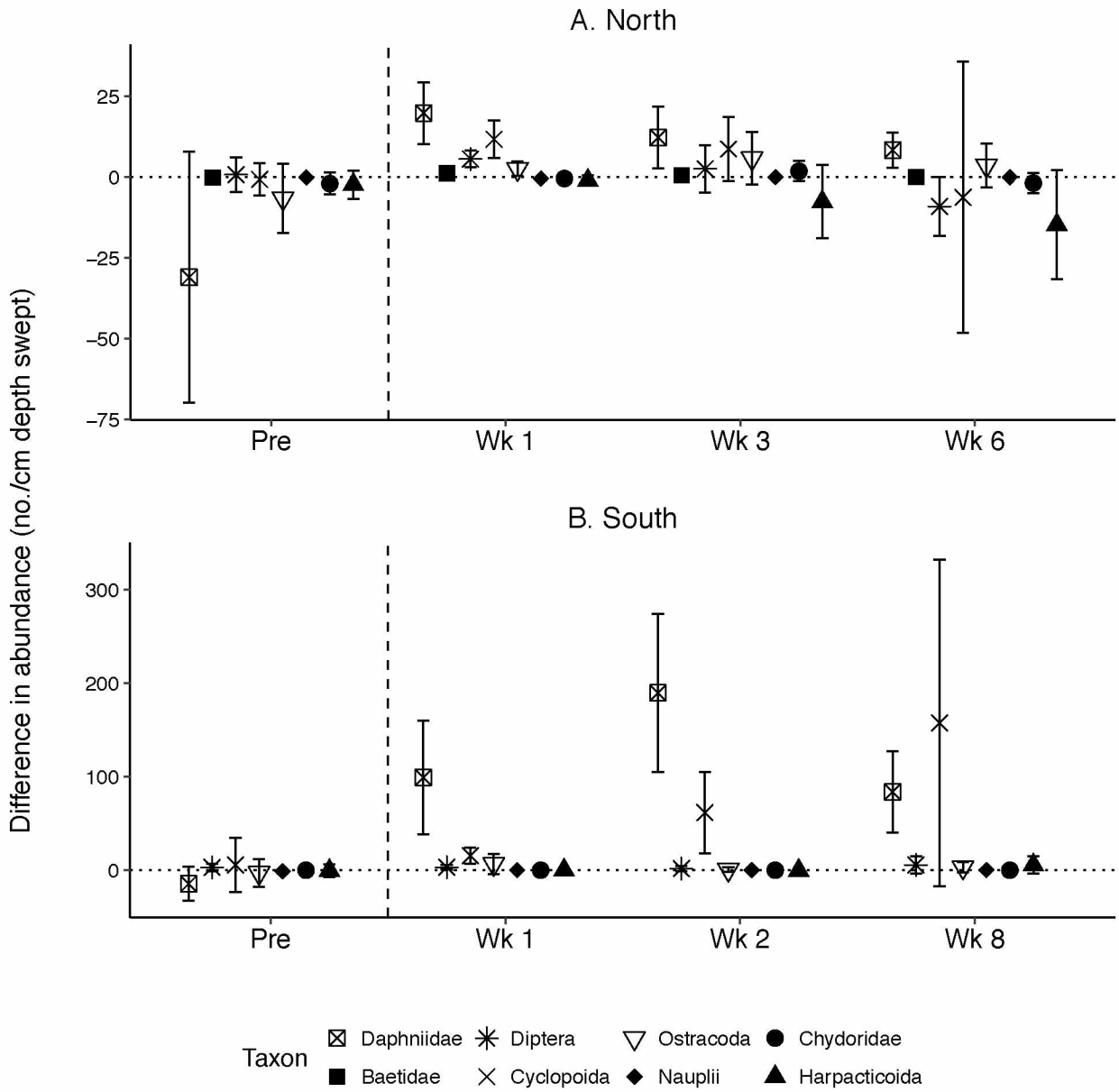

Figure 2.5. Mean (95% CI) difference in abundance between control and fish-addition ponds of invertebrate taxa common in the stomach contents of Ninespine Stickleback at North (A) and South (B). Points represent the mean control-pond abundance minus the mean fish-addition-pond abundance. Values > 0 indicate control ponds had greater abundance than fish-addition ponds. Values < 0 indicate fish-addition ponds had greater abundance than control ponds. The vertical dashed line separates pre-addition and post- addition sampling dates. Diptera includes larvae and pupae of Chironomidae, Chaoboridae, Ceratopogonidae, Dixidae, Empididae, Tipulidae, and digested (unknown) Diptera. No. = number, Wk = week, pre = pre-addition. Nauplii are the larval stage of all copeopod taxa.

Table 2.1. Pond location, addition treatment, and surface area (SA). The biomass (g) and number (*n*) of fish stocked are given for fish-addition ponds. ID = identifier.

Location	Addition treatment	Pond ID	SA (m^2)	Fish added (g)	Fish added (*n*)
North	Control	N2	19.0	–	–
		N4	45.0	–	–
		N5	36.0	–	–
		N6	70.0	–	–
		N9	20.8	–	–
	Fish-addition	N1	10.5	116	103
		N3	58.0	396	393
		N7	35.0	385	344
		N8	54.6	601	551
		N10	38.0	418	353
South	Control	3	26.0	–	–
		4	19.6	–	–
		7	7.2	–	–
		8	5.3	–	–
		9	18.9	–	–
		11	18.1	–	–
	Fish-addition	1	15.2	167	153
		2	6.5	70	60
		5	11.1	122	101
		6	8.7	96	93
		10	4.3	47	34
		12	22.3	245	303

Table 2.2. Frequency of occurrence (% of Ninespine Stickleback with a given taxon in stomach contents) at North 1 d (d1), 1 wk (wk1), 3 wk (wk3), and 6 wk (wk6) post-addition.

Taxon	Frequency of occurrence (%)			
	d1	wk1	wk3	wk6
Chironomidae	77	40	80	77
Daphniidae	63	7	0	0
Chaoboridae	43	0	0	0
Cyclopoida	43	67	47	77
Baetidae	37	0	0	0
Unknown Diptera	33	93	37	40
Dytiscidae	20	20	3	0
Harpacticoida	10	23	30	73
Ostracoda	10	23	23	20
Hydrachnidia	10	7	0	3
Calanoida	10	0	3	3
Terrestrial	7	23	60	13
Chydoridae	7	3	23	50
Ceratopogonidae	7	0	3	7
Dixidae	3	7	0	3
Unknown Trichoptera	3	7	0	0
Tipulidae	3	3	0	0
Copepod nauplii	3	0	0	17
Collembola	0	13	23	13
Physidae	0	13	3	0
Nematoda	0	7	0	7
Unknown Cladocera	0	3	0	0
Unknown Ephemeroptera	0	3	0	0
Unknown Copepoda	0	0	3	0

Table 2.3. Frequency of occurrence (% of Ninespine Stickleback with a given taxon in stomach contents) at South 1 wk (wk1), 2 wk (wk2), and 8 wk (wk8) post-addition.

	Frequency of occurrence (%)		
Taxon	wk1	wk2	wk8
Cyclopoida	59	85	70
Daphniidae	52	4	0
Harpacticoida	48	44	93
Chironomidae	33	67	57
Copepod nauplii	30	15	0
Empididae	11	15	0
Hydrachnidiae	11	4	7
Ostracoda	7	22	47
Dytiscidae	7	0	0
Collembola	0	11	7
Dixidae	0	7	0
Limnephilidae	0	4	0
Oligochaeta	0	4	0
Tardigrade	0	0	3
Terrestrial	0	4	3

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Appendix 2-A

Rarefaction Curves

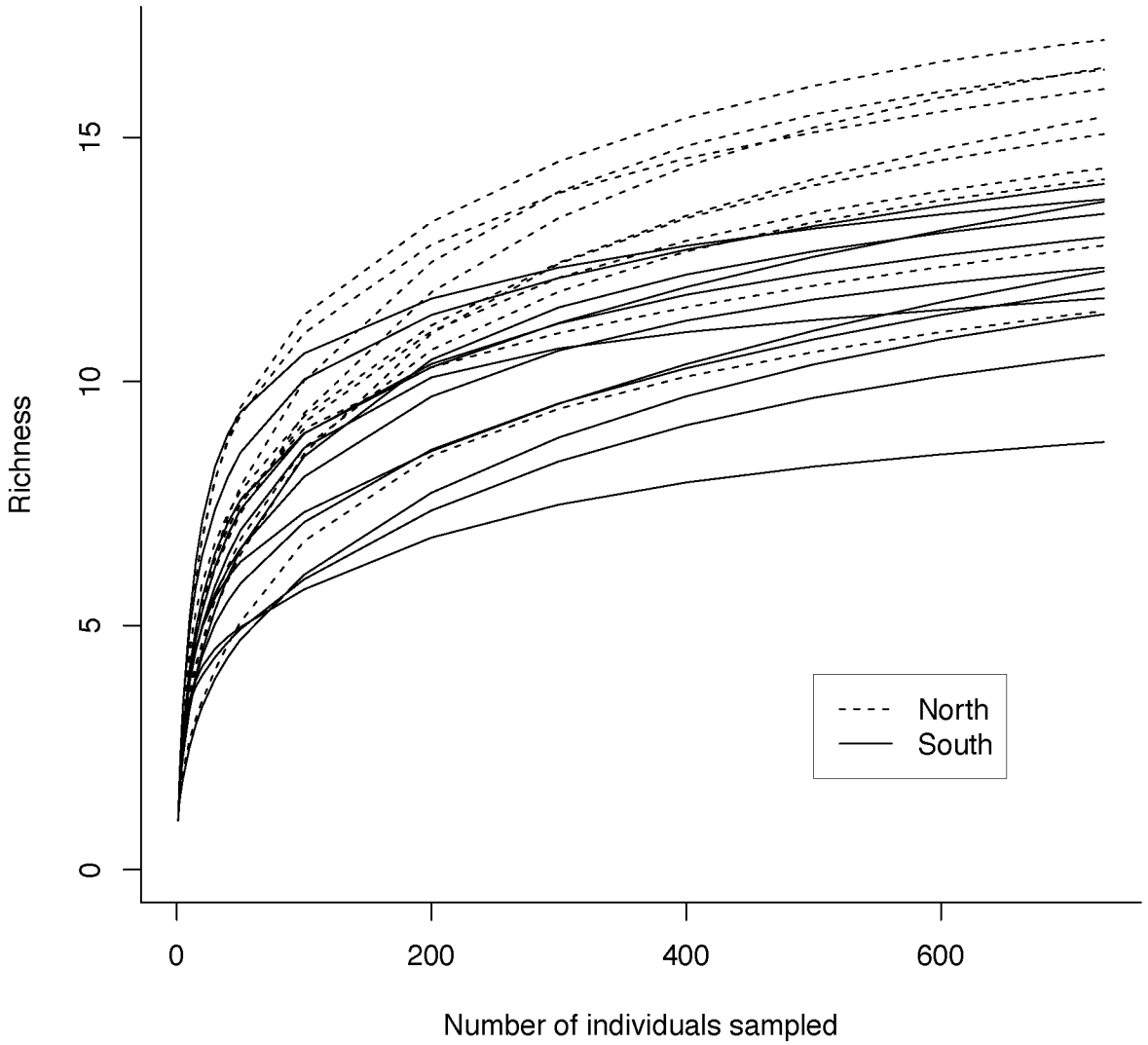

Figure 2-A1. Taxa rarefaction curves for North and South prior to the addition of Ninespine Stickleback. Curves approached an asymptote indicating adequate sampling of pond invertebrates. All curves were truncated at 728 individuals, the minimum number of individuals captured from a single pond.

Appendix 2-B

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2 messages

Sarah Laske <slaske@alaska.edu> Wed, Mar 15, 2017 at 5:16 PM
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Hi Sarah,

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CHAPTER 3

GENERALIST FEEDING STRATEGIES IN ARCTIC FRESHWATER FISH: A MECHANISM FOR DEALING WITH HARSH ENVIRONMENTS[1]

ABSTRACT

Variation in food resource availability is common in cold climate regions. Fluctuation in resource density favors generalist species that can feed across multiple habitat types and trophic levels. Further, consumption of prey from multiple carbon sources imparts stability on food webs through the use of readily available, alternative energy pools. In lakes, generalist fish species take advantage of fluctuating prey availability by switching from benthic to pelagic prey to meet their energy demands. Using stomach content and stable isotope analyses, we examined the feeding habits of fish species in lakes of the central Arctic Coastal Plain (ACP), Alaska, to determine the prevalence of generalist feeding strategies as a mechanism for persistence in harsh environments with short growing seasons. Generalist feeding strategies were evident in adults of five common fish species. Analysis of diet composition suggested fish switch food items and feed on benthic and pelagic prey and across trophic levels. Diptera and Cladocera consistently appeared in the diets of all fish, and 70% of the variation in diets between fish could be demonstrated with 12 prey taxa, yet all pairwise comparisons between fish species showed dietary differences exceeded 65%. ACP fishes had similarly sized dietary niches with apparent overlap in $\delta^{13}C$ signatures. The accumulation of energy from diverse sources by Arctic fishes creates redundancy in food webs, making them more resistant to perturbations or stochastic

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events. Therefore, the generalist and omnivorous feeding strategies employed by ACP fish maintain energy flow and food web stability in harsh or variable environments.

INTRODUCTION

Within aquatic food webs, generalist fish species often link benthic and pelagic energy sources, transferring energy to higher trophic levels (Schindler & Scheurell, 2002; Vander Zanden & Vadeboncoeur, 2002). Adaptive foraging strategies not only allow fish to rapidly respond to changes in food abundance or availability, but insure food availability in fluctuating environments (Hayden, Harrod, & Kahilainen, 2014; Rooney, McCann, Gellner, & Moore, 2006). Further, alternative energy pathways and prey switching imparts stability on food webs by dampening oscillations in food resources brought about by predation (Beckerman, Petchey, & Warren, 2006; Rooney, McCann, Gellner, & Moore, 2006) and maintaining energy flow when prey species are lost (Dunne, Williams, & Martinez, 2002; Gravel, Canard, Guichard, & Mouquet, 2011). Generalist fishes couple food web compartments (e.g., benthic and pelagic) and provide energy subsidies across habitat boundaries that could profoundly affect community interactions, nutrient cycling, and top-down regulation of the food web (Schindler & Scheurell, 2002; Vander Zanden & Vadeboncoeur, 2002).

Fluctuating availability of food resources is common in cold-climate regions (Hayden, Harrod, & Kahilainen, 2013; Rautio, Sorvari, & Korhola, 2000), and seasonal variation in prey abundance can affect the trophic ecology of predators (Hayden, Harrod, & Kahilainen, 2014). Fish often respond to food limitations with high rates of consumption when food becomes available in space or time (Craig, 1984; Prowse et al., 2006). Further, some species migrate to seasonal feeding sites to access food resources (Buzby & Deegan, 2000; Heim, Wipfli, Whitman, & Seitz, 2016). Arctic grayling (*Thymallus arcticus*) exhibit site fidelity to stream habitats in the

Alaskan Arctic, migrating long distances between summer foraging habitats and winter refuges (Buzby & Deegan, 2000). At summer feeding sites, grayling take advantage of seasonally abundant food resources that provide energy for rapid growth and accumulation of energy reserves (Heim, Wipfli, Whitman, & Seitz, 2016; McFarland, Wipfli, & Whitman, 2017). Accumulation of mass and lipid reserves during summer provides fish with energy needed for winter survival (Biro, Morton, Post, & Parkinson, 2004). These reserves are particularly important for species that reside in harsh environments like the Arctic, where organisms are vulnerable to environmental extremes (Rautio et al., 2011).

Food webs with generalist feeders will be more resilient to climatic variability and harshness (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001). In lentic habitats of the Arctic, temporal and spatial variation in pelagic zooplankton and benthic macroinvertebrate abundance may require fish predators to adapt their feeding strategies or alter their trophic niche to access sufficient resources (Amundsen, 1995; Eloranta, Knudsen, & Amundsen, 2013). Also, the importance of generalist fishes in coupling energy sources may be prominent in oligotrophic, high-latitude lakes, where only simple communities persist (Christoffersen, Jeppesen, Moorhead, & Tranvik, 2008; Eloranta, Knudsen, & Amundsen, 2013). European whitefish (*Coregonus lavaretus*) switch from benthic macroinvertebrates to zooplankton when zooplankton abundance peaks in late summer, a switch that coincides with increased body condition and somatic growth important for overwinter survival (Biro, Morton, Post, & Parkinson, 2004; Hayden, Harrod, & Kahilainen, 2013; Hayden, Harrod, & Kahilainen, 2014). Arctic charr (*Salvelinus alpinus*) also shift from littoral to pelagic foods with increasing lake size (decreased littoral area) and in the presence of sympatric fish species (Eloranta et al., 2015), demonstrating potential for trophic niche plasticity. For example, if littoral resources are dominated by co-occurring brown trout

(*Salmo trutta*), Arctic charr will shift away from littoral macroinvertebrates to pelagic zooplankton, which facilitates coexistence with sympatric species by reducing competitive interactions and consumer-resource oscillations (Eloranta et al., 2015; Eloranta, Kahilainen, & Amundsen, 2013; Rooney, McCann, Gellner, & Moore, 2006).

The Arctic Coastal Plain (ACP) of Alaska is a 50,000 km^2 area of low relief tundra that spans from the foothills of the Brooks Range to the Arctic coast. The region is underlain by thick permafrost, which is primarily responsible for the formation of related surface features, including ice wedges and associated thermokarst water bodies (Martin et al., 2009). Streams and lakes form a heterogeneous hydrologic network that fish use for migratory routes, feeding areas, and seasonal refuge (Craig 1984; Hershey et al., 2006; Heim, Wipfli, Whitman, & Seitz, 2016). Extreme seasonal fluctuation in photoperiod (0–24 hours between winter and summer) influences air and water temperature, primary production, and ecological cues used by species for migration or physical development (Kittel, Baker, Higgins, & Haney, 2011; Reist et al., 2006). Ice dynamics play an important part in the survival and success of fish by restricting access to habitat and creating a physically harmful environment (Reist et al., 2006). The severe winter makes the short growing season critical for fish to grow and accumulate sufficient energy stores (Biro, Morton, Post, & Parkinson, 2004; McDonald, Hershey, & Miller, 1996;).

The extreme seasonality of the Alaskan Arctic with its long, cold winters and short, relatively warm summers limit biota by physiological thresholds (Prowse et al., 2006). Only fifteen species of fish are known to occupy habitats on the ACP (Alaska Freshwater Fish Inventory, Alaska Department of Fish and Game, accessed October 2016); but little is known regarding their dietary habits, trophic niches, or associated food webs in this region. A handful of studies in the central ACP offer information regarding individual species' diets, but fall short of

cross-species comparisons or community analyses (e.g., Alaska blackfish [*Dallia pectoralis*] in Ostdiek & Nardone, 1959; ninespine stickleback [*Pungitius pungitius*] in Cameron, Kostoris, & Penhale, 1973). Additional studies in the neighboring foothills region, near Toolik Lake, provide information regarding trophic ecology for several of these species (e.g., lake trout [*Salvelinus namaycush*], round whitefish [*Prosopium cylindraceum*], and Arctic grayling in Merrick, Hershey, & McDonald, 1992; slimy sculpin [*Cottus cognatus*] in Cuker, McDonald, & Mozley, 1992) that could than provide useful comparison across physiographic regions of the Arctic (Jorgenson & Grunblatt, 2013).

Determining the current trophic ecology of fishes in the ACP is important for understanding energy flow and mechanisms that may be disrupted due to climate change. The region's climate has warmed rapidly in recent decades, with temperature increases at twice the global average. Future climate projections for the region indicate an annual temperature increase of 7.3 °C by the end of the century (Martin et al., 2009). These changes coincide with milder winters, warmer summers, and longer ice free seasons that will likely enhance planktonic primary production (Rautio et al., 2011; Wrona et al., 2006). Warmer temperatures will also increase fish metabolic needs and their associated food requirements; the balance between available food and metabolic need will ultimately determine future fish production (Carey & Zimmerman, 2014; McDonald, Hershey, & Miller, 1996; Reist et al., 2006). Under changing conditions, a generalist feeding strategy may allow fish to shift to readily available resources, imparting food web resilience to new climatic patterns (Eloranta et al., 2015; Hayden, Harrod, & Kahilainen, 2014).

We aim to describe the diets of fishes residing in lakes of the ACP, Alaska, where little information is currently available. We then describe the dietary strategies of these fishes by

examining stomach contents and isotopic niches. At the level of species (or size class), we anticipate that fishes of the ACP will exhibit generalist or flexible feeding patterns and trophic omnivory – either consuming prey across compartment boundaries (i.e., benthic and pelagic) or on different trophic levels. A suite of generalist characteristics describing resource use by Arctic fishes should represent an overall strategy for persistence in a harsh Arctic environment. At the community level, we anticipate trophic redundancy among fish species and overlapping trophic niches, which may contribute to overall stability and resilience in food web structure.

METHODS

We sampled fish from 16 lakes (mean surface area 0.7 km^2, mean depth 2 m) at two locations on the Arctic Coastal Plain of Alaska (Figure 3.1). Lakes in the region are shallow, underlain by permafrost, and ice free from late June or early July through September. Over three summer seasons (2011–13), we collected fishes using unbaited minnow traps (6 mm steel mesh, 23 cm diameter, and 44.5 cm length with two 2.5 cm openings), fyke nets (0.6 cm mesh, 15.2 x 1.2 m wings, and a 1.1 m square opening; or 0.6 cm mesh, 9 x 1 m wings, and a 1 m diameter opening), and gill nets (24.8 x 1.8 m, eight panels with mesh size from 19 to 64 mm [North American standard, Lester, Bailey, & Hubert, 2009]). Each lake was sampled a minimum of four times over the span of the study, with a minimum of 6 h of fishing per sampling event. We deployed gear over short time intervals (3-4 h) to reduce losses due to digestion and to limit the potential for net feeding. Additional overnight net sets were employed during 2013 to capture more fish for stable isotope samples.

At each lake, we sampled stomach contents up to approximately 30 individuals of each species, depending on availability. All sample collection was performed under a University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol (#233290), by sedating

fish with a 20-30 mg/L clove oil solution (non-lethal sampling) or by severing the head from the spinal cord (lethal sampling). We sampled diets with gastric lavage using a 60 ml syringe filled with filtered water and a 5 Fr catheter tube, or through direct collection of the stomach. We preserved contents from all stomachs with 95% ETOH. To determine feeding positions relative to one another and species dietary niches (Layman, Arrington, Montaña, & Post, 2007; Post, 2002), we collected muscle tissue for stable isotopes for each species at eight lakes (northern site only) – up to 11 individuals per species per lake. With a scalpel, we extracted a small plug of dorsal muscle from the left side of the fish, anterior to the dorsal fin, and preserved muscle plugs in 95% ETOH. Small fishes (< 45 mm length) were preserved and ground whole for stable isotope analysis (Swanson, Kidd, & Reist, 2010).

We identified stomach contents to the lowest practical taxonomic level. For example, for items in good condition, we identified to the family level for macroinvertebrates and cladoceran zooplankton and to order for copepods. When digestion interfered, we identified organisms as low as possible, typically to the order level, or classified them as well digested material. We also specified the life stage of prey (e.g., larva). Any invertebrate prey of non-aquatic origin was considered terrestrial and identified to order when possible.

We placed muscle tissue into individual 4 ml glass vials and freeze-dried at -50°C for 48 hours (LABONCO FreeZone 1 Liter Benchtop Freeze Dry Systems 77400 Series, Kansas City, MO). Once dry, we used petroleum-ether to extract any remaining lipids (Kelly & Martínez del Rio, 2010). Storing tissues in ETOH removed much, if not all, of the tissue's lipid prior to formal extraction, therefore, only 48 hours of submersion in petroleum-ether was required. Tissues air-dried for 24 hours. We sent all samples to the Stable Isotope Facility at the University of Wyoming, Laramie, where they ground and analyzed samples for of $\delta^{15}N$ and $\delta^{13}C$ with a

continuous flow stable isotope ratio mass spectrometer (Costech 4010, Carlo Erba 1110, Thermo Flash Elemental Analyzer coupled to a Thermo Delta Plus XP and Delta V IRMS). Analytic precision was ± 0.2‰, with standards L-glutamic acid and liver (36-UWSIF-Glutamic 1, $\delta^{15}N_{AIR}$ = -4.6‰, $\delta^{13}C_{VPDB}$ = -28.3‰; 39-UWSIF-Glutamic 2, $\delta^{15}N_{AIR}$ = 27.9‰, $\delta^{13}C_{VPDB}$ = 24.4‰; and UWSIF01 [Liver], $\delta^{15}N_{AIR}$ = -6.8‰, $\delta^{13}C_{VPDB}$ = -17.8‰).

Data Analysis

All analyses of stomach contents were performed at the order level or higher to establish consistency across samples and the degree of digestion, although we acknowledge that this reduces our taxonomic resolution. We did not include parasites within prey items (e.g., Nematomorpha or Cestoda) in the analyses because they were not directly consumed. Empty stomachs were not included in analyses. We examined the feeding strategy of each fish species by plotting the prey-specific abundance against frequency of occurrence based on number of prey consumed. Prey-specific abundance is the proportion prey item *i* constitutes of all prey items in predators that contain prey *i* (see Amundsen, Gabler, & Staldvik, 1996 and Chipps & Garvey, 2007 for more detail). Frequency of occurrence (FO) is defined as the number of fish with a given prey item in its stomach (Chipps & Garvey, 2007). Mean numeric proportion was calculated for individual fish species within each lake (Chipps & Garvey, 2007). Differences were determined through a multivariate analysis of variance with function adonis in R (PERMANOVA; vegan, R package 2.4-1) on the Bray-Curtis distances of the mean numeric proportions, excluding unidentifiable well digested items. We determined the contribution of potentially influential diet items (Table 3-A1, in Appendix A1, for a list of all prey and numeric proportions) as those that contributed up to 70% of the dissimilarities between species pairs

(pairwise comparison of each fish species) and determined the overall percent dissimilarity in diets between each fish species pair (SIMPER; vegan, R package version 2.4-1).

For the same fish species that we included in stomach content analyses, we conducted an analysis of isotopic niche area, overlap, and community measures of trophic structure (Jackson, Inger, Parnell, & Bearhop, 2011; Layman, Arrington, Montaña, & Post, 2007; SIBER, R package version 2.0.3). Fourteen fish (55 – 60 mm length), of two genera (*Pungitius* and *Coregonus*), were used to test for mean differences between whole body and muscle sample carbon and nitrogen signatures. In each sampled lake, we determined the niche area (SEA_B) of each species using a Bayesian method, which is unbiased with respect to sample size and propagates uncertainty in the mean (Jackson, Inger, Parnell, & Bearhop, 2011). We then used the species posterior means (from Markov chain Monte Carlo [MCMC] simulations in rjags, R Package version 4-6) from each lake to calculate the overall mode and 95% credible intervals for SEA_B for all species groups. Variation in isotopic baselines across sampling locations prevented pooling of isotopic data across all individuals; calculation of SEA_B in an isotopically heterogeneous region would artificially inflate the size of the niche. We visually assessed niche overlap by examining plots of 95% credible interval ellipses around the mean of each group. Further, we determined values of three community-wide measures of trophic structure to provide measures of trophic diversity (mean distance to centroid, CD), redundancy (mean nearest neighbor distance, MNND), and distribution of niches (standard deviation of nearest neighbor distance, SDNND; Layman, Arrington, Montaña, & Post, 2007).

RESULTS

We collected stomach contents and muscle tissues from 10 fish species: Alaska blackfish, ninespine stickleback, least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*),

Arctic grayling, slimy sculpin, humpback whitefish (*Coregonus pidschian*), Arctic charr, pike (*Esox lucius*), and rainbow smelt (*Osmerus mordax*). Five species provided limited dietary information (< 10 individuals from ≤ 2 lakes) and were not included in the analysis: slimy sculpin, humpback whitefish, Arctic charr, pike, and rainbow smelt (Table 3.1). Detailed information on their diets and the diets of the fishes used in the analysis can be found in the Appendix 3-A (Table 3-A1). We examined least cisco diets according to size class; small least cisco ≤ 100 mm FL and adults >100 mm FL to account for potential ontogenetic shifts. Small whitefish, < 130 mm FL, either broad whitefish or humpback whitefish, could not be distinguished to the species level in the field and were considered as one group (Table 3.1).

Feeding strategy plots indicated that most fishes, with the exception of small least cisco, had either a generalist or flexible feeding strategy (Figure 3.2). All fishes had high frequency of occurrence of Diptera larvae (mainly Chironomidae) in their stomach contents. The feeding strategy plot showed that Diptera was a dominant prey for Arctic grayling. Ninespine stickleback, as a species, consumed the greatest variety of prey; however, few individual fish consumed as great a variety, indicating that feeding may have been habitat or location specific. The flexible feeding strategy seen in Alaska blackfish, ninespine stickleback, least cisco, broad whitefish and whitefish spp. indicated that variation in diets ranged from narrow to high, with some individuals consuming a specialized diet, while others a varied diet. Small least cisco had the most constrained diet, with specialization on Cladocera and Diptera larvae.

Numeric proportion of stomach contents differed by species (PERMANOVA of 1000 permutations; $R^2 = 0.29$, $p < 0.001$). Further examination of pairwise differences in diets through SIMPER provided estimates of average percent dissimilarity between species. Dietary differences often exceeded 70%, with 19 of 21 pairwise comparisons showing little similarity in

overall stomach content composition. Ninespine stickleback and Arctic grayling differed by an average of 67%, and ninespine stickleback and small least cisco differed by an average of 57%. Further, we identified prey items that cumulatively explained up to 70% of the variation in pairwise difference between fish species stomach contents. This amount of variation was described with three to six prey items per fish species pair, and a total of 12 prey items accounted for all of the differences: Notostraca, Gastropoda, Ostracoda, Hydrachnidia, Nematoda, Diptera larvae, Trichoptera larvae, Calanoida, Cladocera, Diptera pupae, aquatic Diptera adults, and fish (Figure 3.3).

Alaska blackfish (n = 26, 7.7 % empty) regularly consumed (frequency of occurrence ≥ 50% and/or mean numeric proportion ≥ 0.1) benthic invertebrate taxa of Diptera larvae, Gastropoda, and Ostracoda, and fish (93% identified as ninespine stickleback; Figure 3.2 and 3.3). Stomachs of ninespine stickleback (n = 468, 8.3% empty) contained 30 different taxa – more than any other fish species – but cladoceran zooplankton and Diptera larvae and pupae made up the largest numeric proportion with the greatest frequency of occurrence (Figure 3.2 and 3.3). Small least cisco (n = 43, 7.0% empty) also consumed cladoceran zooplankton and Diptera larva and pupa (Figure 3.3), but had reduced frequency of occurrence and a narrower selection of diet items, 13, than ninespine stickleback (Figure 3.2). The ontogenetic shift in least cisco adults (n = 49, 0 empty) led to an increase in the variety of diet items (n = 24), including fish (90% identified as ninespine stickleback), Hydrachnidia, Gastropoda, and Diptera pupae.

Small whitefishes (n = 47, 19.1% empty) consumed Diptera and Trichoptera larvae, Diptera pupae, and Cladocera (Figure 3.3). However, they did not consume benthic organisms that adult broad whitefish (n = 16, 6.3% empty) consumed, such as snails (Gastropoda) and bivalves (Bivalvia; Figure 3.2). Arctic grayling (n = 20, 0 empty) consumed small proportions of

prey items, and mean numeric proportion never exceeded 0.20 for any taxa; only Diptera larvae, Nematoda, and Notostraca averaged > 0.10 (Figure 3.3). However, frequency of occurrence was high for six taxa, including fish (95% identified as ninespine stickleback) and Trichoptera larvae.

For small fish, when comparing whole body signatures to tissue only signatures (δC^{13}_{tissue} - δC^{13}_{body} = -0.21± 0.07 ‰ and δN^{15}_{tissue} - δN^{15}_{body} = 0.38 ± 0.15 ‰); no biologically meaningful differences were found. Carbon values did not differ from analytical precision (0.2 ‰) and nitrogen difference was far less than 3.4‰ that constitutes a trophic level, therefore, whole fish were used for analyses. The overall mode of isotopic niche area for each fish species ranged from 0.14‰^{2} for small least cisco to 2.22‰^{2} for ninespine stickleback (Table 3.2) and visually appeared to correspond with the known diversity of dietary items. For example, small least cisco and whitefish spp., which consume mainly zooplankton, had smaller niche areas than fish with more diverse diets like ninespine stickleback. Species ellipse areas (SEA_B) for all individuals did not differ by species based on overlapping 95% credible intervals. Differences in between-species niche areas did occur in individual lakes; for example, broad whitefish niche area was greater than whitefish spp., Arctic grayling, and small least cisco in lake 1. This broad whitefish ellipse (5.86‰^{2}, 2.79 LCI – 13.08 UCI) was the largest of any species and was significantly larger than the other measured broad whitefish ellipse (1.16‰^{2}, 0.58 LCI – 2.32 UCI). Only one other species, Alaska blackfish, showed within-species variability of niche area; the ellipse area in two lakes differed significantly (lakes 4 and 5). For the remaining species, there was no difference in within-species niche area across lakes.

Overlap in isotopic niche area and metrics of community-wide trophic structure varied with the number and identity of fish species present in a lake (Figure 3.4). We visually examined overlap in six of the eight lakes, because in two of the lakes, isotopic data were available for only

one species, ninespine stickleback. Carbon values of the fish assemblages centered near –28 - –27‰ $\delta^{13}C$ in each of the six lakes, with many of the species overlapping in carbon signatures – suggesting either averaging of disparate carbon resources (e.g., pelagic and benthic) or use of a single carbon resource (e.g., benthic only). The degree of trophic diversity, measured by CD, was greatest in lakes where species occupied discrete isotopic niches, with no overlap (e.g., lake 2). In several lakes, species' trophic niches showed a higher degree of overlap; for example, multiple fish species isotopic niches overlapped in Lake 1, the most species-rich lake. The MNND, which declines in webs with overlapping trophic ecology or increasing trophic redundancy, was reduced in lakes with more fish species (e.g., Lake 1) or small, tightly clustered species niches (e.g., Lake 4). In agreement with the other two metrics, SDNND, which measures the evenness of species isotopic distributions was highest also where species niches occupied discrete evenly spaced niches as seen in Lake 2.

DISCUSSION

Common fish species of the ACP primarily demonstrated use of generalist or flexible feeding strategies, common in stressful or harsh environments where generalist ecological traits are beneficial (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Eloranta et al., 2015; Sternberg, Balcombe, Marshall, Lobegeiger, & Arthington, 2012;). Fluctuations in prey density found in cold-climate regions often result from local extinction events (e.g., winterkill), and result in predation on organisms nearer the base of the food web or higher omnivory (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001). Adults of the five species included in our analysis consumed prey across food web compartments, consistently relying on benthic Diptera larvae and pelagic (water column dwelling) Diptera pupae and cladoceran zooplankton. Based on stomach contents and stable isotope signatures, three fish species could clearly be considered

omnivorous – consuming both fish and invertebrate prey. However, young-of-year or sub-adult fish (least cisco and whitefish spp. < 100 mm FL) exhibited narrower diets, but sampling multiple age classes revealed an ontogenetic shift and life-history omnivory, or change in diet with body size (Kratina, LeCraw, Ingram, & Anholt, 2012).

Our findings, and those from other studies at northern latitudes (boreal and Arctic regions), showed omnivory and the use of benthic and pelagic prey (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Hayden, Harrod, & Kahilainen, 2014; Merrick, Hershey, & McDonald, 1992). For example, Alaska blackfish sampled southeast of Utqiaġvik (formerly Barrow, Alaska), consumed high proportions of benthic Diptera larvae and Ostracoada, and pelagic Cladocera (Ostdiek & Nardone, 1959); stomach contents similar to Alaska blackfish captured in this study. Arctic grayling from the Toolik Lake region consumed benthic macroinvertebrates and snails, and pelagic zooplankton (Merrick, Hershey, & McDonald, 1992). In contrast to grayling sampled at Toolik, the Arctic grayling of the central ACP consumed fish (see also McFarland, Wipfli, & Whitman, 2017), which could elevate their relative trophic position. However, analysis of trophic niches indicated that fish spanned two trophic levels, with species like Arctic grayling in intermediate positions. In fact, top predators in this environment may have more omnivorous or generalist diets due to reliance on macroinvertebrates, zooplankton, and fish (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Eloranta, Kahilainen, & Amundsen, 2013; Merrick, Hershey, & McDonald, 1992).

Trophic omnivory, or consuming prey across trophic levels, was clearly demonstrated by three of the fish species in our analysis, Alaska blackfish, adult least cisco, and Arctic grayling. Overwhelmingly, the fish prey most often consumed was ninespine stickleback; and the fish that consumed ninespine stickleback also consumed their shared prey resources. The isotopic

signatures of adult least cisco were less than one trophic level above their fish prey (one trophic level is 3.4‰ $\delta^{15}N$; Post, 2002). Even Lake 2, where fish clearly separated according to nitrogen signatures and with higher trophic diversity, least cisco adults were only enriched 2.6‰ $\delta^{15}N$ from ninespine stickleback, due to the trophic generalization of the top predator (Eloranta et al., 2015). Interestingly, the trophic positioning of Alaska blackfish and Arctic grayling was typically equal or lower than their fish prey (ninespine stickleback), which suggests an averaging of their nitrogen signature between lower trophic level invertebrates and fish prey. The integration of food web compartments, via omnivory, is prominent in small, climatically variable lakes, where piscivores feed on a mixture of fish and abundant invertebrate resources at lower trophic levels (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Eloranta et al., 2015). The use of zooplankton during the summer months coincides with seasonal availability in northern lakes (Hayden, Harrod, & Kahilainen, 2013; Rautio et al., 2011;). Zooplankton could provide fish with a pelagic energy pathway that brings stability to the food web (Rooney, McCann, Gellner, & Moore, 2006), and provide energy required during summer periods of rapid fish growth (Hayden, Harrod, & Kahilainen, 2014).

The size and proximity of trophic niches was similar across species, with a few exceptions (e.g., discrete trophic niches in lake 2), indicating similarity or sharing of energy resources, which supports our anticipation of trophic redundancy that ultimately contributes to food web stability and resilience. Given their SEA_B, fishes likely had equally broad diets over the long-term. We expected that the muscle tissues collected would reflect months to a year of assimilation, given the cold climate and slow growth of fish in the Arctic (Eloranta, Kahilainen, & Amundsen, 2013; Hesslein, Hallard, & Ramlal, 1993). Young-of-year and sub-adult least cisco and whitefish spp. had slightly smaller trophic niches than adults, arguably due to a

combination of age and diet. Ontogenetic shifts in these fishes likely will expand and shift the dietary and isotopic niche to incorporate large crustaceans, snails, and fish, becoming more similar to adults of the same species, indicating a discrete niche shift (Hammerschlag-Peyer, Yeager, Araújo, & Layman, 2011). Isotopic niches of adult least cisco were relatively narrow and occurred along the midrange of values, indicating that this species may be the top-generalist predatory fish of these Arctic lakes (Eloranta et al., 2015; Hecky & Hesslein, 1995). Dietary flexibility and omnivory seen in the diet are consistent with this role in the food web. Broad whitefish, on the other hand, had variability in trophic niche size. The range of carbon values may have resulted from variability in the basal resource pool or from the range of resources used (Hammerschlag-Peyer, Yeager, Araújo, & Layman, 2011) – either mechanism has potential. Migratory broad whitefish may sample prey over a wide range of habitats; fish visiting one lake in summer may individually represent a different overwintering area due to the slow turnover of muscle tissue. Alternatively, seasonal dietary shifts and individual diet specialization, within a generalist population, could widen the isotopic niche (Eloranta, Kahilainen, & Amundsen, 2013; Hecky & Hesslein, 1995). However, we do not have data that support either argument, and more research regarding seasonal dietary shifts would be needed to clarify this pattern.

The overlap of isotopic ellipses indicated that fish species used similar carbon sources in ACP lakes (Sierszen, McDonald, & Jensen, 2003; Vander Zanden & Vadeboncoeur, 2002). Trophic redundancy, or fish with similar trophic ecologies, seems likely in lakes with higher fish species richness and multiple top-predators, due to consistent generalist use of prey resources by fish (Layman, Arrington, Montaña, & Post, 2007; Thomas et al., 2016). Whether the similarities arose from averaged use of pelagic (lower $\delta^{13}C$ values) and benthic (higher $\delta^{13}C$ values) carbon or from one unique source remains unclear and requires further study. However, research on the

productivity of shallow Arctic lakes indicates that benthic carbon (in the form of periphyton) supplies much of the energy to the system (Hecky & Hesslein, 1995; Sierszen, McDonald, & Jensen, 2003). Clear water, constant summer sunlight, and expansive littoral areas accommodate a high proportion of benthic production in lakes. Some species of cladoceran zooplankton may graze benthic mats directly or filter out resuspended material (Rautio & Vincent, 2006), creating an alternative pathway for benthic algae to reach fishes. In fact, periphyton stable isotope signatures in the region averaged -28.6 ± 0.8 ‰ $\delta^{13}C$ (B. Uher-Koch, U.S. Geological Survey, Unpublished data). This value is in line with the carbon signatures we found in sampled fishes. Therefore, it is plausible that fishes in these lake food webs rely on periphyton-derived carbon (Sierszen, McDonald, & Jensen, 2003).

Our investigation of the dietary habits of common ACP fishes supports the idea that fish will use the broad array of food resources available to them across aquatic boundaries in the Arctic. Generalist and flexible feeding strategies couple energy pathways, reduce the amount of competitive interaction, and reduce predation pressure on specific prey groups or energy channels, ultimately stabilizing trophic dynamics and the food web (Eloranta et al., 2015; Rooney, McCann, Gellner, & Moore, 2006; Vander Zanden & Vadeboncoueur, 2002). This study highlights the overarching patterns in trophic dynamics among fish in ACP shallow lakes. Even with limited dietary information on common species in several lakes, distinct food web arrangements depended on the identity and number of species present. Additional information regarding the diets of spatially rare species, like pike, prevents a complete assessment of all trophic interactions. Certainly, pike have the potential to occupy higher trophic positions than the fishes included in this analysis and may have the ability to fundamentally change the food web structure and function (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Eloranta et al.,

2015). However, in boreal regions, pike tend to have diverse or omnivorous diets, rather than specializing on fish because invertebrates are a more reliable source of food than highly fluctuating fish populations (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001; Danylchuk & Tonn, 2003).

Understanding the roles of fishes in the region is critical to determining possible shifts in trophic dynamics of Arctic lakes due to climate change. The anticipation of warmer summers and longer ice free seasons brings with it potential changes in fish distributions, increased metabolic rates, and a longer period of fish movement and growth (Laske et al., 2016; Reist et al., 2006). The changes resulting from warming may indirectly alter the flow of energy through the food web (Reist et al., 2006; Wrona et al., 2006) via changes in timing or abundance of phytoplankton and zooplankton production (Carter & Schindler, 2012). It is unclear whether adequate resources will be available to all fish species or age classes in the future Arctic. Climate warming is likely to increase primary productivity, but the current balance between benthic and pelagic energy compartments remains unknown (Rautio et al., 2011). In a climate scenario study, young-of-year lake trout have difficulty acquiring adequate zooplankton resources to compensate for increased metabolic rates (McDonald, Hershey, & Miller, 1996). For pelagic-dependent species, like young lake trout, continued increases in summer water temperatures could prove lethal. In contrast, the effects of warming were less dire for least cisco, a species with generalist feeding behaviors; a bioenergetics model predicted increased growth among all age classes of fish provided they can maintain their current feeding rates (Carey & Zimmerman, 2014). Therefore, it is critical that we fully understand trophic ecologies of the species that will be affected by climate change. For common fish species of the ACP, generalist feeding strategies

likely provide adequate redundancy in feeding habits to maintain energy flow and food web stability in the future.

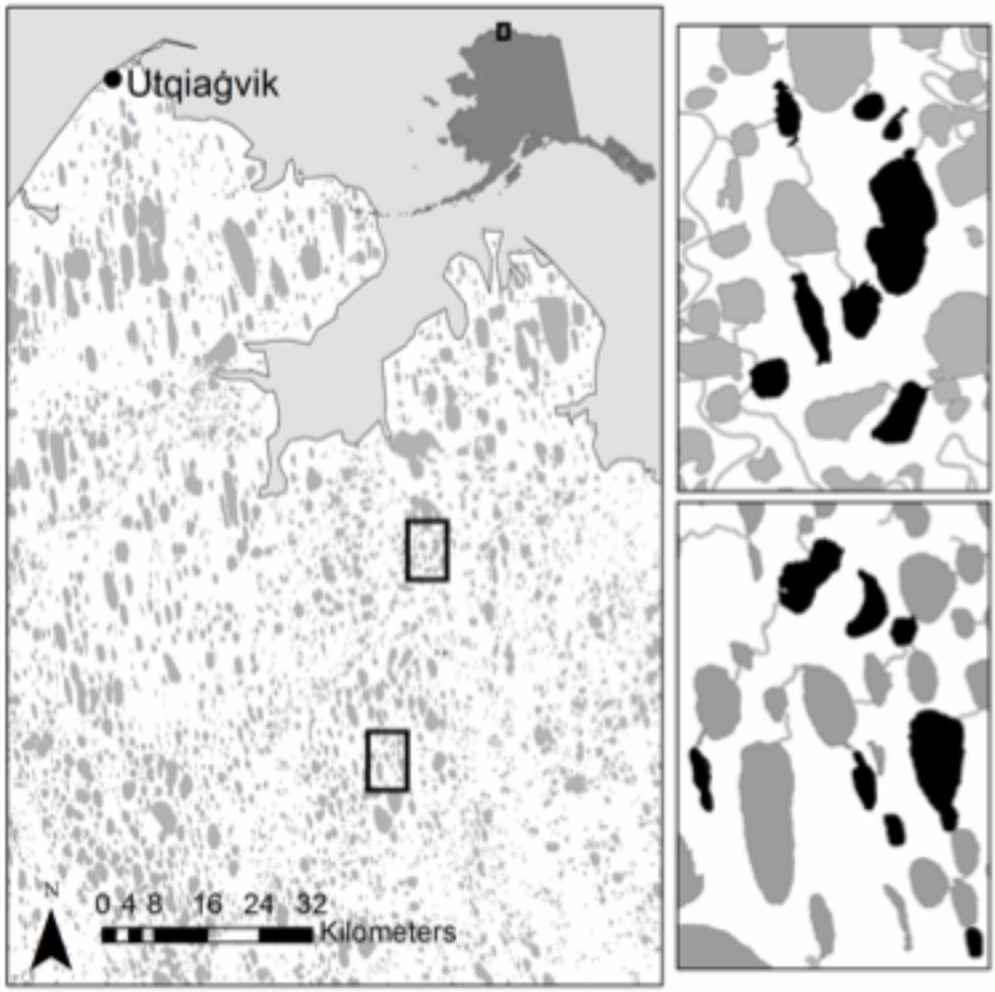

Figure 3.1. Lakes on the Arctic Coastal Plain of Alaska where common fish species were sampled for stomach content analysis and stable isotope analysis. The region (left) shown as inset on state of Alaska. The two study areas are shown in more detail (right), with unstudied lakes shaded grey and study lakes shaded black.

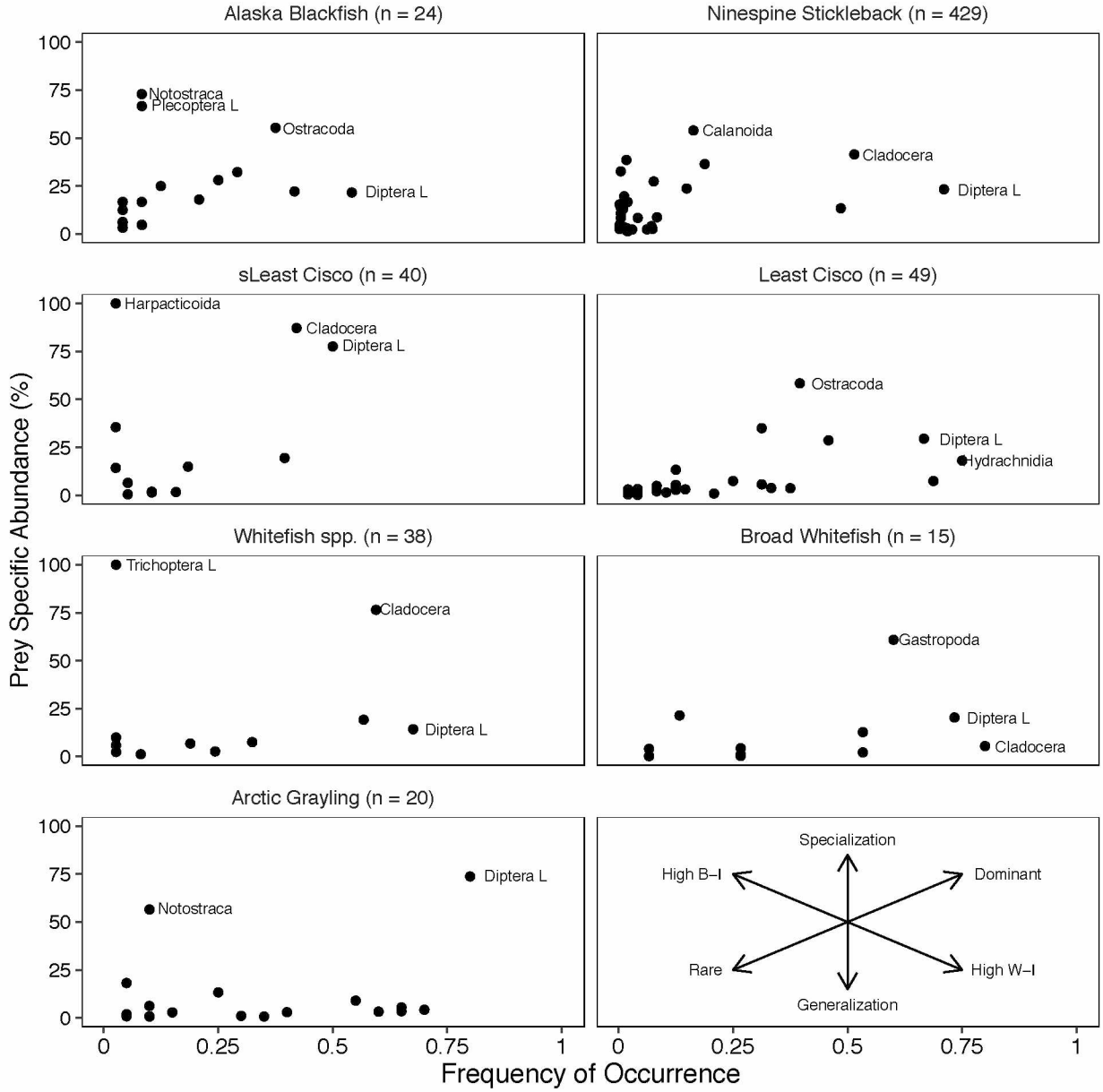

Figure 3.2. Feeding strategy plots for common fishes in lakes on the Arctic Coastal Plain. The lower right plot offers an explanatory diagram for point distribution (adapted from Amundsen 1995). Above each plot, the names of the species and the number of stomachs included in the analysis are given. Small Least Cisco, those ≤ 100 mm FL, are sLeast Cisco and Least Cisco are > 100 mm. Within each plot names of some specific prey taxa are adjacent to the associated data points.

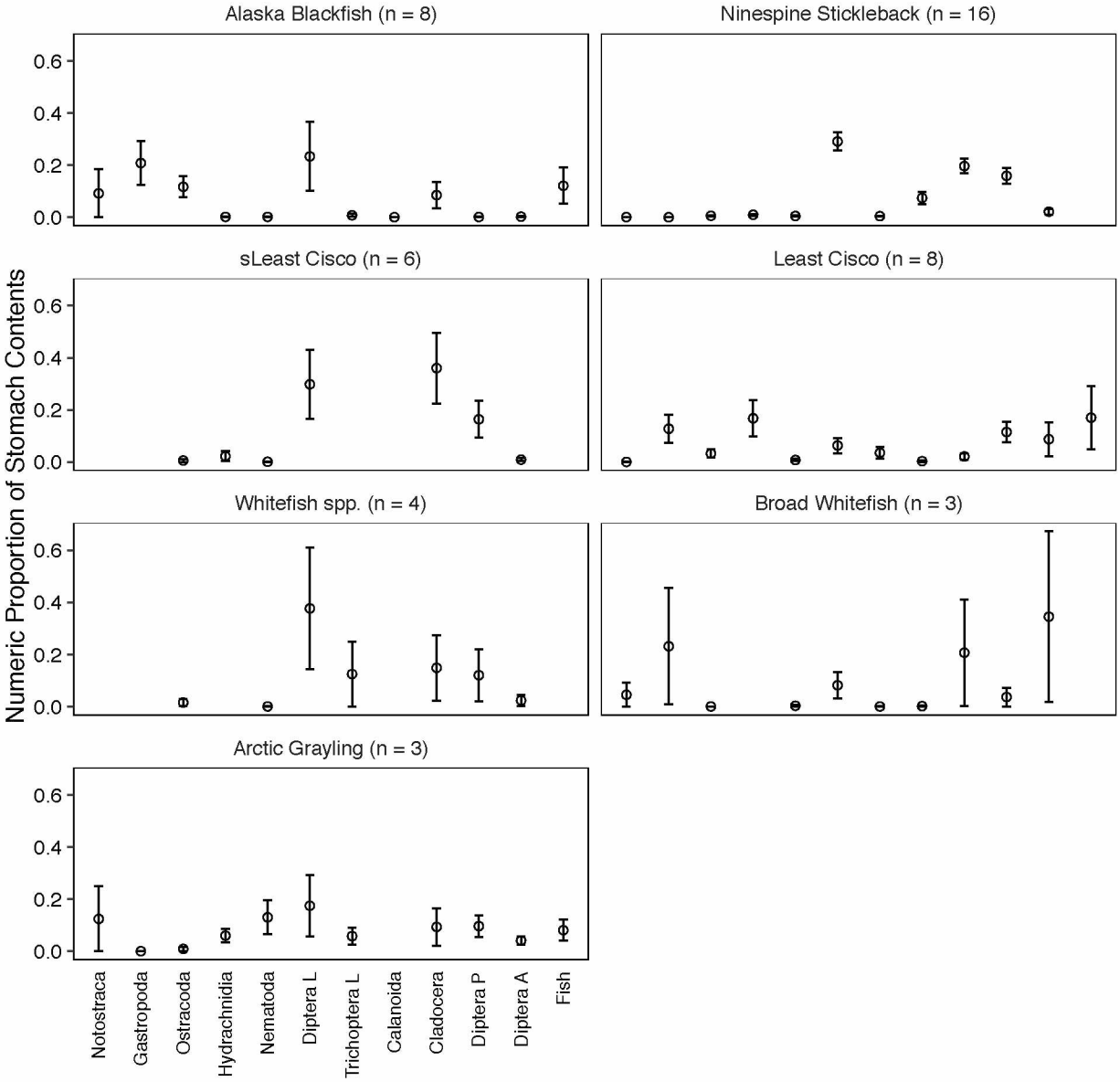

Figure 3.3. Mean numeric proportion (with 95% SE) of important prey items found in the stomachs of common ACP lake fishes. Prey shown here accounted for up to 70% of the variation in pairwise differences in fish diet, and are arranged from left to right from benthic to pelagic. Above each plot, the species name and number of lakes where the species occurred is given. Small Least Cisco (sLeast Cisco) are ≤ 100 mm FL, and Least Cisco are > 100 mm.

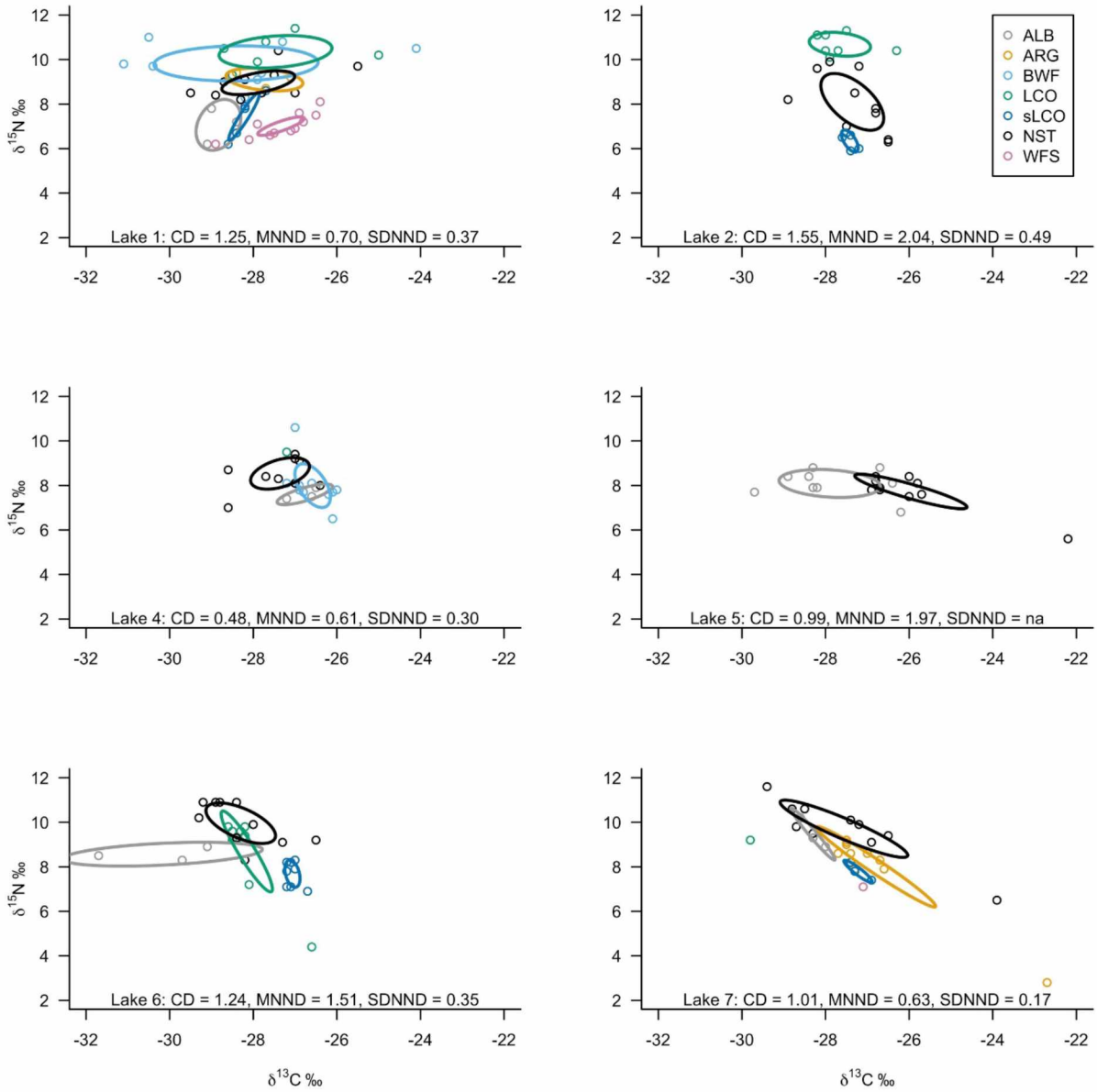

Figure 3.4. Stable isotope ellipse areas representing the 95% credible interval around the mean for each species captured in six lakes on the Arctic Coastal Plain, Alaska. Points for individual fish are shown. Layman metrics for each fish community are shown in the plots, CD – mean distance to centroid, MNND – mean nearest neighbor distance, SDNND – standard deviation of nearest neighbor distance. ALB – Alaska Blackfish, ARG – Arctic Grayling, BWF – Broad Whitefish, LCO – Least Cisco (> 100 mm FL), sLCO – small Least Cisco (≤ 100 mm FL), NST – Ninespine Stickleback, and WFS – Whitefish species.

Table 3.1. Fish species, mean and standard deviation of length and sample sizes for stomach content analysis (SCA) and stable isotope analysis (SIA). Length for Alaska Blackfish and Ninespine Stickleback are given in total length, the remaining species lengths are given as fork length.

Species	Common name	Length (SD)	n SCA	n SIA
Dallia pectoralis	Alaska Blackfish	63 (34)	24	21
Pungitius pungitius	Ninespine Stickleback	47 (11)	429	81
Coregonus sardinella	Least Cisco	50 (23)	40	22
		229 (58)	49	24
Coregonus spp.	Whitefish spp.	65 (18)	38	12
Coregonus nasus	Broad Whitefish	400 (147)	15	18
Thymallus arcticus	Arctic Grayling	173 (58)	20	13

Table 3.2. The number of fish, lake ID and mean stable isotope signatures (‰) for $\delta^{13}C$ and $\delta^{15}N$ are shown for each species. Stable isotope ellipse area estimates, with 95% lower and upper credible intervals, are shown for each lake, with the average ellipse area and credible interval for each species below. Least Cisco (> 100 mm FL) and sLeast Cisco (≤ 100 mm FL).

Species	n Fish	Lake ID	$\delta^{13}C$ (SE)	$\delta^{15}N$ (SE)	SEA_B (‰^{2})	95% LCI	95% UCI
Alaska Blackfish	3	1	-28.8 (0.2)	7.1 (0.5)	0.78	0.15	3.35
	3	4	-26.8 (0.2)	7.6 (0.2)	0.22	0.05	0.99
	9	5	-27.9 (0.4)	8.1 (0.2)	2.11	1.07	4.39
	3	6	-30.2 (0.8)	8.6 (0.2)	0.97	0.29	4.43
	3	7	-28.3 (0.2)	9.5 (0.4)	0.37	0.09	1.72
					0.29	0.05	3.65
Ninespine Stickleback	10	1	-27.9 (0.4)	9.0 (0.2)	1.93	1.04	4.02
	10	2	-27.4 (0.2)	8.1 (0.4)	2.64	1.19	5.18
	11	3	-28.1(0.2)	10.0 (0.7)	3.05	1.62	5.90
	10	4	-27.4 (0.2)	8.5 (0.2)	1.41	0.78	2.92
	10	5	-26.0 (0.4)	7.7 (0.3)	1.90	1.01	3.86
	10	6	-28.3 (0.3)	10.0 (0.3)	1.99	1.02	4.01
	10	7	-27.6 (0.5)	9.7 (0.4)	3.36	1.84	6.95
	10	8	-26.5 (0.6)	7.9 (0.2)	2.63	1.33	5.38
					2.22	0.90	5.30
sLeast Cisco	5	1	-28.2 (0.1)	7.4 (0.4)	0.58	0.20	1.72
	5	2	-27.4 (0.1)	6.3 (0.2)	0.12	0.05	0.37
	8	6	-27.1 (0.1)	7.7 (0.2)	0.24	0.13	0.59
	4	7	-27.2 (0.1)	7.8 (0.2)	0.14	0.04	0.48
					0.14	0.04	1.07

Table 3.2. Continued

Species	n Fish	Lake ID	δC^{13} (SE)	δN^{15} (SE)	SEA_B (‰^{2})	95% LCI	95% UCI
Least Cisco	6	1	-27.5 (0.6)	10.4 (0.3)	2.67	1.09	6.85
	7	2	-27.7 (0.2)	10.7 (0.2)	0.85	0.35	1.98
	1	4	-27.2	9.5	-	-	-
	9	6	-28.2 (0.2)	8.7 (0.6)	1.74	0.88	3.77
	1	7	-29.8	9.2	-	-	-
					0.95	0.26	5.22
Arctic Grayling	3	1	-27.7 (0.4)	9.1 (0.2)	0.51	0.17	2.37
	10	7	-26.8 (0.5)	8.0 (0.6)	3.82	2.04	7.82
					0.57	0.15	6.65
Whitefish spp.	11	1	-27.3 (0.2)	7.0 (0.2)	0.82	0.42	1.53
	1	7	-27.1	7.1	-	-	-
					0.82	0.42	1.53
Broad Whitefish	8	1	-28.4 (0.8)	9.8 (0.3)	5.86	2.79	13.08
	10	4	-26.6 (0.4)	8.0 (0.3)	1.16	0.58	2.32
					1.17	0.46	11.03

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Appendix 3-A

Numeric proportions of prey from Arctic Coastal Plain fish stomachs.

Table 3-A1. Mean (SE) numeric proportions (as %) of prey for each of the fish species sampled from Arctic Coastal Plain lakes. The first 12 taxa accounted for known variation in pairwise fish species comparisons. Least Cisco (> 100 mm FL) and sLeast Cisco (≤ 100 mm FL).

Taxa	Alaska Blackfish		Ninespine Stickleback		Least Cisco	
	MN	SE	MN	SE	MN	SE
Notostraca	9.20	9.20	0.08	0.06	0.03	0.03
Gastropoda	20.84	8.35	0.01	0.01	12.74	5.42
Ostracoda	11.72	4.03	0.58	0.27	3.28	1.60
Nematoda	0.18	0.18	0.51	0.29	0.77	0.49
Diptera L	23.36	13.21	29.08	3.51	6.33	2.91
Trichoptera L	0.83	0.55	0.43	0.22	3.55	2.20
Hydrachnidia	0.18	0.18	0.95	0.38	16.76	7.00
Calanoida	0.09	0.09	7.44	2.33	0.28	0.26
Cladocera	8.54	5.06	19.67	2.81	2.15	1.28
Diptera Pupa	0.15	0.15	15.91	2.95	11.51	3.89
Diptera Adult	0.23	0.23	2.15	1.10	8.76	6.46
Fish	12.11	6.95	0		17.02	12.20
Amphipoda	0		2.84	2.31	0	
Annelida	0		0.06	0.04	0	
Anostraca	0		0.44	0.41	0	
Bivalvia	0.33	0.26	0.05	0.05	7.29	6.44
Coleoptera A	0		0.01	0.01	0.31	0.16
Coleoptera L	0.42	0.42	0.14	0.08	0	
Collembola	0		0.27	0.19	< 0.01	< 0.01
Copepoda (Unk)	0.09	0.09	4.79	1.53	0.19	0.19
Crustacea (Unk)	0		0.02	0.01	0	
Cyclopoida	4.68	3.33	4.73	1.47	1.36	1.24
Diptera E	0		0.04	0.03	0.13	0.12
Ephemeroptera L	0		0.01	0.01	0	
Fish Eggs	0		0.10	0.09	0	
Harpacticoida	1.24	1.24	1.70	0.77	0.20	0.14
Oligochaeta	0		0.07	0.07	0.03	0.03
Plecoptera L	5.00	3.62	0.15	0.08	0.11	0.11
Seed	0		0.53	0.27	0	
Terrestrial	0.79	0.79	0.82	0.44	2.07	1.40
Trichoptera A	0		0		3.26	2.13
Trichoptera P	0		0.01	0.01	0.05	0.05

Table 3-A1. Continued

Taxa	sLeast Cisco		Whitefish spp.		Broad Whitefish	
	MN	SE	MN	SE	MN	SE
Notostraca	0		0		4.58	4.57
Gastropoda	0		0		23.19	22.33
Ostracoda	0.54	0.54	1.59	1.42	0.08	0.04
Nematoda	0.09	0.06	0.10	0.10	0.36	0.23
Diptera L	29.85	13.24	37.71	23.31	8.23	5.10
Trichoptera L	0		12.50	12.50	0.12	0.12
Hydrachnidia	2.25	1.87	0		0	
Calanoida	0		0		0.23	0.23
Cladocera	36.02	13.57	14.92	12.55	20.71	20.36
Diptera Pupa	16.38	7.07	12.09	9.96	3.67	3.59
Diptera Adult	0.93	0.60	2.37	2.10	34.51	32.76
Fish	0		0		0	
Amphipoda	0		0		0	
Annelida	0		0		0.01	0.01
Anostraca	0		0		0	
Bivalvia	0		0		4.31	4.31
Coleoptera A	0		0		0	
Coleoptera L	0		0		0	
Collembola	0.40	0.40	0.03	0.03	0	
Copepoda (Unk)	4.93	3.45	0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	0.99	0.64	0.08	0.08	0	
Diptera E	1.52	1.52	0		0	
Ephemeroptera L	0		0		0	
Fish Eggs	0		0		0	
Harpacticoida	1.11	1.11	0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	2.36	2.00	5.93	5.81	0	
Trichoptera A	0		0.17	0.17	0	
Trichoptera P	0		0		0	

Table 3-A1. Continued

Taxa	Arctic Grayling		Humpback Whitefish		Pike	
	MN	SE	MN	SE	MN	SE
Notostraca	12.47	12.47	0.20	-	0	
Gastropoda	0.05	0.05	65.80	-	5.30	-
Ostracoda	0.97	0.77	0.40	-	1.20	-
Nematoda	13.07	6.54	0		5.30	-
Diptera L	17.53	11.74	0.40	-	5.30	-
Trichoptera L	5.81	3.25	5.20	-	0	
Hydrachnidia	6.06	2.66	3.20	-	0	
Calanoida	0		0.40	-	0	
Cladocera	9.38	7.14	2.30	-	3.00	-
Diptera Pupa	9.72	4.14	0		0	
Diptera Adult	4.20	1.60	0		0	
Fish	8.13	4.03	22.20	-	67.70	-
Amphipoda	0		0		0	
Annelida	0		0		0	
Anostraca	0		0		0	
Bivalvia	0		0		12.30	
Coleoptera A	0.04	0.04	0		0	-
Coleoptera L	1.29	0.88	0		0	
Collembola	0.09	0.09	0		0	
Copepoda (Unk)	0		0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	2.02	2.02	0		0	
Diptera E	0		0		0	
Ephemeroptera L	0.22	0.22	0		0	
Fish Eggs	2.02	2.02	0		0	
Harpacticoida	0.11	0.09	0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	5.39	4.45	0		0	
Trichoptera A	1.43	1.37	0		0	
Trichoptera P	0		0		0	

Table 3-A1. Continued

Taxa	Rainbow Smelt		Slimy Sculpin		Arctic Char	
	MN	SE	MN	SE	MN	SE
Notostraca	0		0		0	
Gastropoda	0		0		0	
Ostracoda	0		0		0	
Nematoda	0		0		0	
Diptera L	0		75.00	27.50	26.90	-
Trichoptera L	0		11.10	-	1.10	-
Hydrachnidia	0		0		0	
Calanoida	0		0		0	
Cladocera	62.30	-	5.50	-	0	
Diptera Pupa	37.70	-	0		25.40	-
Diptera Adult	0		0		13.30	-
Fish	0		0		0	
Amphipoda	0		0		0	
Annelida	0		0		0	
Anostraca	0		0		0	
Bivalvia	0		0		0	
Coleoptera A	0		0		0	
Coleoptera L	0		0		0	
Collembola	0		0		0	
Copepoda (Unk)	0		0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	0		0		0	
Diptera E	0		0		0	
Ephemeroptera L	0		0		0	
Fish Eggs	0		0		0	
Harpacticoida	0		0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	0		0		0	
Trichoptera A	0		0		0	
Trichoptera P	0		0		0	

CHAPTER 4

SURFACE WATER CONNECTIVITY INFLUENCES LAKE FOOD WEB COMPLEXITY ON MULTIPLE SPATIAL SCALES[1]

ABSTRACT

Across large spatial scales, habitat complexity may translate to food web stability by promoting species persistence and energy flow. Examining species' access to habitat patches with differing connectivity can enhance our understanding of the influence of spatial variation in physical processes on patterns of community assembly and food web function within a larger metacommunity. In the Alaskan Arctic, surface water connectivity plays a vital role in structuring lake fish communities and, therefore, food web structure. However, potential changes to the hydrologic regime due to climate and landscape changes could influence community composition, food web organization, and energy flows in Arctic lakes. Therefore, it is imperative that we examine current patterns of lentic food web structure and how they relate to surface water connectivity at the local and regional spatial scale. We examined how fish species richness and lentic food web structure responded to surface water connectivity in Arctic landscapes at the local scale, using a gradient of connectivity, and at the regional scale, we compared the two different locations. In 32 water bodies, we collected fish diet information from stomach contents and stable isotopes to determine the number of feeding links and trophic relationships that occurred among fish species. We found that local food web complexity, assessed by number of trophic links and trophic levels, was dependent on the lake's relative isolation. Lakes with permanent channel connections were highest in food web complexity. At regional scales, food

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webs were more complex when represented as an aggregate, or meta-food web of all potential fish species, compared to the average or "typical" food web for a particular region. Spatial variation in hydrological processes that drive individual fish species occupancy and community richness contributed to food web diversity across the Arctic landscape.

INTRODUCTION

Physical mechanisms that structure aquatic communities are directly relevant to the development of aquatic food web structure and complexity (e.g., Hershey et al. 1999, Jackson et al. 2001, Giam and Olden 2016). Landscapes regulate carbon inputs at the resource base, constraining the availability and assimilation of energy to food webs (Smits et al. 2015), and control the distributions of mobile species (e.g., fish) that shape trophic structure within food webs (Hershey et al. 1999). At the local scale, complex food webs with numerous, tightly linked species (Williams et al. 2002), may be more vulnerable to alteration via extinctions (Dunne et al. 2002). However, at the regional scale, food web complexity may promote species persistence through colonization-extinction dynamics of predators and their prey (Gravel et al. 2011). Complexity across greater spatial scales may translate to food web stability by increasing the redundancy of certain predator-prey links and by offering alternative and heterogeneous habitat patches to prey species where they can take refuge from predators (Gravel et al. 2011, Bellmore et al. 2015, Ziegler et al. 2017). Spatial heterogeneity is an important part of metacommunity organization (Heino et al. 2015), and examining local communities or food webs in a metacommunity framework can enhance understanding of spatial processes on patterns of species distribution and diversity (Leibold et al. 2004, Henriques-Silva et al. 2013). Further, spatial complexity may provide a mechanism for stabilizing food web structure and function

(Bellmore et al. 2015) and highlights the importance of maintaining heterogeneity of habitats across the landscape.

Dispersal of species in a metacommunity facilitates food web branching (i.e., regional persistence of multiple consumers through consumption of a shared resource) and diversity (Pillai et al. 2011). The regional persistence of a predator requires that it follow its prey through space, and the number of patches occupied is determined by rates of colonization and extinction (LeCraw et al. 2014). Generalist species may be quicker to colonize, given their wide trophic breadth and ability to consume early-colonizing prey, followed by specialist species with narrow, prey-specific foraging patterns (Piechnik et al. 2008). Ultimately, food web complexity should result from the aggregation of foraging links for each species in the community (Beckerman et al. 2006). Therefore, with the addition of more species, predators may "stack vertically up" food chains or cause further branching of the food web (Pillai et al. 2011). Complexity due to branching is a stabilizing force, particularly for generalist consumers that respond rapidly to change and dampen destabilizing resource oscillations (Rooney et al. 2006, Pillai et al. 2011)

Omnivores may act as an external predator in a metacommunity framework by feeding on prey in multiple habitat patches and switching prey based on availability or profitability (Kratina et al. 2012). Prey switching can be either spatial (e.g., Reid et al. 2012, Eloranta et al. 2015) or temporal (e.g., Hayden et al. 2014), with generalists shifting between energy sources across trophic levels. Shifting to alternative energy sources, or mulitchain trophic omnivory (Vadeboncoeur et al. 2005, Rooney et al. 2006), may help maintain food web function even if sympatric species are lost (Gravel et al. 2011, Pillai et al. 2011). The higher proportion of weak interactions between predator and prey as local food webs are aggregated across a complex landscape may indicate a mechanism that links complexity and stability (Bellmore et al. 2015).

The stability of food webs increases in highly connected webs when many species operate as weak interactors, generally as omnivores or trophic generalists (McCann et al. 1998, Dunne et al. 2002, LeCraw et al. 2014, Ziegler et al. 2017).

In stream-lake networks, surface water connectivity, local colonization and extinction factors, and predator-prey interactions often determine the species assemblage, and, ultimately, metacommunity organization (Beisner et al. 2006, Heino et al. 2015, Giam and Olden 2016). However, short growing seasons, low temperatures, and low light intensity supersede biotic controls for communities and food webs in harsh high-latitude environments (van der Wal and Hessen 2009), and physical controls of the landscape likely play a greater role in structuring species occupancy, communities, and food webs (Hershey et al. 1999, Haynes et al. 2014, Smits et al. 2015). In the Alaskan Arctic, surface water connectivity plays a vital role in determining distribution patterns of fishes and formation of local assemblages (Hershey et al. 2006, Laske et al. 2016). Surface water connectivity influences the pool of species (regional) and shapes the rates of species colonization between habitat patches (local) and is, therefore, a driver of aquatic ecosystem structure and function (Tonn 1990, Reid et al. 2012, Henriques-Silva et al. 2013). Additionally, the relative simplicity of Arctic lake assemblages may improve our ability to recognize patterns in food web architecture as it relates to the environment at multiple spatial scales (e.g., Hershey et al. 1999).

However, climate-induced changes to the hydrologic cycle may affect the function of these food webs (Prowse et al. 2006, Wrona et al. 2006). Evaporative losses and flow regime changes will affect connectivity of lakes and ponds differentially depending on their current state (Koch 2016). Ponds may evaporate completely or disconnect altogether from the hydrologic network, leading to greater numbers of fishless pond habitats (Smol and Douglas 2007). Water

levels in lakes will decrease due to evaporative loss, reducing overflow and affecting both connectivity and water depth (Lesack and Marsh 2010, Koch 2016). Reduced water levels will limit overwintering refuges for fish, and, without a sustaining pulse of colonists, species and associated trophic links would be lost from those lakes (Hershey et al. 2006, Haynes et al. 2014).

Large heterogeneous landscapes support an array of habitats and associated species that are important to the function of freshwater ecosystems and biodiversity (Heino et al. 2009), but may be vulnerable to changes in hydrologic networks and lake and pond connectivity. Therefore, we examine how fish species richness and lentic food web structure respond to surface water connectivity in Arctic landscapes at two spatial scales. Locally, we considered a gradient of connectivity that differentiates between strong permanent connections, ephemeral connections, and isolation (for details regarding the connectivity scale, see Riera et al. 2000). Regionally, we compared two locations that varied in physiography, climate, and surface water availability associated with colonization potential.

We expected that fish species richness would increase with the degree of surface water connectivity, with lowest richness in isolated lakes and highest richness in lakes with strong, permanent channel connections. Regionally, we predicted that the average richness of lakes would be greater at the site with higher overall surface water connectivity. We anticipated that food web complexity would be greater in lakes of higher connectivity; we therefore predicted that the number of trophic links, link density, and maximum trophic position would increase along the local gradient of surface water connectivity. We examined regional webs in two ways – as an average of the region's lakes and as a metacommunity. We anticipated that both the average food web and the aggregate metacommunity food web would have higher complexity in the wetter location, with a greater number of trophic links and link density in that region.

Further, we discuss the complexity of food webs in a metacommunity framework. Considering colonization, dispersal ability, and the heterogeneity of habitats available to fishes in the two study locations, we discuss how changes due to climate warming may affect local food webs (i.e., lakes) and regional meta-food webs (i.e., location) with respect to local scale channel connectivity and regional scale differences in surface water availability.

STUDY AREA

The Arctic Coastal Plain of Alaska (ACP) is a 50,000 sq km area located north of the Brooks Range and south of the Beaufort Sea. The region is underlain by permafrost and is covered in snow from October to June (Martin et al. 2009). In the central ACP (156°50'W – 154°00'W and 70°00'N – 70°50'N), where permafrost processes are chiefly responsible for lake formation and distribution, lakes occupy approximately 40% of the landscape (Grosse et al. 2013). Mean annual temperature is -10.3°C, and mean summer (June–August) temperature is 7.1°C (U.S. Geological Survey Ikpikpuk Metrological Station 2006–2012; Urban and Clow 2014). The spring freshet results in flooding and movement of water across the low gradient landscape, causing water to spill across stream and lake boundaries. This temporarily increases water body volume and surface water availability, ephemerally connecting otherwise isolated lakes and ponds to the hydrologic network.

We sampled ponds (surface area [SA] < 0.02 km^2) and lakes (SA > 0.1 km^2) at two locations on the central ACP in 2012–13 (Figure 4.1 A–D). Study locations were selected in coordination with other research interests in the region, but provided a contrast in temperature and physiography. Summer temperatures at the northern location were consistently cooler, due to the prevalence of fog near the Beaufort Sea coast. In 2012 and 2013, the daily average temperature in July was consistently 1.3°C warmer the southern location (J. Koch, U.S.

Geological Survey, unpublished data), and spring melt was advanced six days at the southern location based on final dates of snow loss in 2012 (24-June at south and 30-June at north, Gurney and Uher-Koch 2012, Uher-Koch 2012). The locations but are starkly different in the amount of surface water drainage (Figure 4.1 A, B). The northern location is low gradient and is underlain by peat, whereas the southern location has a slight gradient, some topography, and is underlain by sand (Jorgenson and Grunblatt 2013). The differences in drainage above the permafrost boundary created a wetter landscape matrix surrounding northern lakes compared to the drier, broadly spaced lake arrangement to the south.

METHODS

At each location, we selected eight ponds and eight lakes of varying surface water connectivity – no connection, ephemeral connection, or permanent connection – for inclusion in the study to incorporate water bodies of varying species richness and composition. We used the metric of lake order proposed in Riera et al. (2000) as a guide, which specifies various connectivity states of lakes based on their position relative to a chain of lakes. Isolated water bodies with no surface water connection are designated -3, while water bodies with ephemeral connections are -1. For water bodies with permanent connections, there are three groups: 0, headwater lakes with no inflow and only an outflow; 1, first order lakes with a first order stream outflow; and 2, second order lakes with a second order stream outflow. Stream channels on the ACP are not typical of Strahler (1957) stream orders, so the use of the Riera et al. (2000) lake order metric is modified. For example, a 1st order lake would have one inflow and one outflow, with the inflowing channel coming from a similarly connected lake or a headwater lake. A 2nd order lake would possess at least two inflows and one outflow, or would have one inflow from an upstream lake possessing at least two inflows. Lake order was determined by examining the

perimeter of each pond or lake sampled and by investigating the direction and permanence of stream connections in the field.

We sampled fish from lakes using fyke nets, hoop nets, minnow traps, and experimental gill nets. In shallow ponds, we sampled fish with only hoop nets and minnow traps. Two fyke net designs were used, including one constructed with 0.6 cm mesh, 15.2 x 1.2 m wings, and a 1.1 m square opening; and another with 0.6 cm mesh, 9 x 1 m wings, and a 1 m diameter opening. Nets either blocked lake inlets or outlets or were set perpendicular to the shoreline. We often used two nets, set end to end, to capture fish traveling in both directions along the shoreline. Hoop nets made of 0.6 cm mesh, with a 61 cm opening, had leads of 4.6 m. One lead was attached from the center or two leads attached as wings depending on the location of fish capture. We used two wings blocking a lake inlet or outlet and one lead if the net was set perpendicular to shore. Unbaited minnow traps, often used in ponds, with 6 mm steel mesh, 23 cm diameter, and 44.5 cm length had two 2.5 cm openings captured small-bodied and juvenile fish. Experimental gill nets measured 24.8 by 1.8 m, with eight panels ranging in mesh size from 19 to 64 mm (North American standard, Lester et al. 2009). Time of net deployments was generally four hours or less, to limit digestion of stomach contents or potential net feeding. Further, we checked gill nets every hour to limit fish mortality and stomach content digestion or regurgitation. Collection took place over two (2011) to four days (2012–13) for each lake we sampled. Often, we sampled in the crepuscular hours; however, given the 24-hr cycle of light in the Arctic, there is little diel variation in fish movements and our ability to detect them (Kahilainen et al. 2004; Haynes et al. 2013). We also collected 10 snails (Gastropoda) from each lake and pond at North to establish baseline stable isotope signatures; we preserved snails in 95% ETOH.

We measured fork length and total length of each fish species captured. Fish weight, to the nearest gram, was collected for all species except ninespine stickleback (*Pungitius pungitius*) due to their small mass (often less than 1g) and the accuracy of our field scales. We took stomach contents for up to 30 of every species collected in all ponds and lakes and preserved them in 95% ETOH. Only char (*Salvelinus* spp.) stomach content retrieval was done via gastric lavage with a 60 ml syringe and 1.7 mm diameter catheter tube, so these fish could be released unharmed. Whole stomachs were removed from all other fish after euthanasia via severing the spinal cord (per IACUC approved protocol, see Appendix A). We collected muscle tissues for stable isotope analysis from these fish as well by removing a small section of dorsal tissue from the left side of the fish and preserving it in 95% ETOH.

We prepared fish muscle tissue and snails minus their shells (up to 10 individuals) from each sampled lake at North for stable isotope analysis and determination of $\delta^{15}N$ and trophic position (Post 2002; Vander Zanden et al. 2004). We placed tissues into open 4 ml glass vials, and freeze-dried at -50°C for 48 hours (LABONCO FreeZone 1 Liter Benchtop Freeze Dry Systems 77400 Series, Kansas City, MO). Once dry, we used petroleum-ether to extract remaining lipids. Storing tissues in ETOH removed much, if not all, of the tissue's lipid prior to formal extraction; therefore, only 48 hours of submersion in petroleum-ether was required (Kelly and Martínez 2010). Tissues were air-dried for 24 hours before capping vials. We sent all samples to the Stable Isotope Facility at the University of Wyoming, Laramie, where they ground and analyzed samples for of $\delta^{15}N$ with a continuous flow stable isotope ratio mass spectrometer (Costech 4010, Carlo Erba 1110, Thermo Flash Elemental Analyzer coupled to a Thermo Delta Plus XP and Delta V IRMS). Analytic precision was ± 0.2‰, with standards L-

glutamic acid ($\delta^{15}N$ = -4.6‰, AIR, 36-UWSIF-Glutamic 1 and $\delta^{15}N$ = 27.9‰, AIR, 39-UWSIF-Glutamic 2).

Data Analysis

Use of the lake order metric throughout our analyses combines the effects of surface water connectivity and observations of fish species richness. We examined relations between fish species richness and lake order via analysis of variance (ANOVA, Package R 3.3.1) and test of multiple comparisons using a false discovery rate (FDR) correction method. Further, analyses were conducted independently for ponds and lakes. These two systems differ fundamentally, especially considering that the ponds are shallow and freeze to the bottom annually, whereas the lakes do not.

For each species and water body, we counted the number of trophic links – identified to the Family level for aquatic macroinvertebrates and cladoceran zooplankton – between fishes and their prey. In lakes where dietary data were unavailable for a present species, we interpolated by including prey with frequency of occurrence greater than 10% for the species. We determined the average link density, or number of links per taxa, across the connectivity gradient of lake order. Link density in lake food webs was analyzed across the connectivity gradient with a one-way analysis of variance (ANOVA, Package R 3.3.1) and test of multiple comparisons using a false discovery rate (FDR) correction method. Link density data were assessed for normality. To examine differences in regional food webs, we counted the total number of links and determined the total link density for each location. We also examined differences in average link density using a Welch two sample t-test (Package R 3.3.1) comparing all pond and lake food webs from northern and southern locations.

We assembled food web diagrams for each surface water connectivity grouping (lake orders) and for northern and southern sampling locations; keeping ponds separate from lakes (R package *diagram*, version 1.6). Dietary items shown in the webs are weighted according the mean numeric proportion of items found in the diets of fish (see Laske et al. in prep, for more detail on fish diets). Only items with a mean numeric proportion > 0.06 were included in the web diagrams. When species dietary information was missing for a category, we interpolated using the mean diet for that species. For diagrams demonstrating food webs along the connectivity gradient, black lines indicate fish that occurred in all lakes of a category and gray lines indicate fish that occurred in at least one, but not all lakes in the category. This coloring scheme is meant to show another level of complexity, distinguishing fishes that are consistently present from those that are potentially present. Webs prepared for the sampling locations (north and south) were prepared as meta-food webs with all of the species found in the region.

To correct for variation in $\delta^{15}N$ at the base of the lake's food web, we estimated species trophic positions (TP) using the following equation from Vander Zanden et al. (2004) for individual fish:

$$TP_{consumer} = [(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4] + 2,$$

where 3.4 is the trophic enrichment factor, and primary producers are at level two. The stable isotope nitrogen signature of snails (Gastropoda) was averaged within each water body and used as the baseline. We then calculated the average trophic position for each species across the spectrum of surface water connectivity (lake order) for ponds and lakes independently. We visually examined the data for correlations between length and trophic position for each species. For any species where length appeared to be an influential factor, we fit linear mixed-effects models as a function of length in mm (fork length or total length dependent on species

morphology) and included the identity of the water body as a random effect (R version 3.3.1, package *lme4*). We then examined effect plots to determine significance – a positive trend in trophic position with increasing length (R version package *effects* version 3.3-1). We determined differences in species trophic positions with one-way ANOVA and used a false discovery rate (FDR) correction method to test multiple comparisons among species (R version 3.3.1). Also, we plotted the average trophic position for each species for each category of lake connectivity (lake order) to look for trends in the data within and across species. Further, we calculated the maximum trophic position for each category of lake connectivity. Maximum trophic position was determined as the average trophic position for the species that occupied the top position in each category. The differences in maximum trophic position across the gradient of surface water connectivity in lakes were assessed with a one-way ANOVA (R version 3.3.1).

RESULTS

Local scale

We sampled 32 water bodies of varying connectivity at two locations: 12 isolated water bodies (8 ponds, 4 lakes), 12 ephemerally connected water bodies (8 ponds, 4 lakes), and 8 permanently connected lakes (Table 4.1). Ponds fell only into two surface water connectivity categories, lake order of -3 or -1. Isolated ponds (-3) never contained fish, while ephemerally connected ponds (-1) contained only ninespine stickleback. Three isolated lakes (-3) also contained only ninespine stickleback, while one isolated lake contained ninespine stickleback and Alaska blackfish (*Dallia pectoralis*). Ephemerally connected lakes (-1) contained up to four fish species, ninespine stickleback, Alaska blackfish, least cisco (*Coregonus sardinella*), and slimy sculpin (*Cottus cognatus*). In lakes with permanent connections (0, 1, and 2), we observed three to nine fish species, including those mentioned above and broad whitefish (*Coregonus*

nasus), humpback whitefish (*C. pidschian*), Arctic grayling (*Thymallus arcticus*), Arctic char (*Salvelinus alpinus*), pike (*Esox lucius*), rainbow smelt (*Osmerus mordax*), and burbot (*Lota lota*). However, we captured only larval burbot and have no dietary information on the species.

In ponds, the relationship between fish richness and connectivity (lake order) was constant. If an ephemeral connection was present in a pond, then one fish species was present. Without a surface water connection, ponds were void of fish. In lakes, fish species richness increased with the degree of surface water connectivity (ANOVA, $F = 11.7$, $p < 0.001$). Multiple comparisons showed isolated lakes, with a richness of 1.2 species, differed in richness from all other lake order types (Figure 2). Ephemerally connected lakes, headwater lakes, and first order lakes did not differ in fish richness. Estimates of mean richness ranged from 2.5 to 4 species across this range of connectivity. However, richness of a second order lake differed from richness in isolated lakes by 4.6 species and from ephemerally connected lakes by 3.4 species on average. Second order lakes did not differ from permanently connected headwater and first order lakes.

Number of links and link density increased with the degree of surface water connectivity (Table 4.1). The number of links increased with the addition of fish species; however, fish species did not contribute equally to the web's complexity. Generalist species like Arctic grayling averaged 15 trophic links, while a benthic fish like Slimy Sculpin averaged 2.5 links (Table 4.2). Therefore, the addition of different fish species to lake food webs resulted in differences in overall complexity. Food web diagrams (Figure 4.3) showed increasing complexity with the addition of fish species. However, the identity of fish included in any given web can change its architecture. The number of consistently present fish species did not increase beyond one – ninespine stickleback – until lake connectivity was relatively high (Figure 4.3 E

and F). Headwater lakes (Figure 4.3 D) also have potential for greater web complexity, but this complexity was dependent on species identity rather than on a suite of consistently present fish species – chiefly least cisco and broad whitefish. A comparison of link density given surface water connectivity demonstrated that the number of links per taxa did not differ across any lakes with a channel connection, whether permanent or ephemeral (Figure 4.4). Difference in link density occurred between food webs in isolated lakes (predicted link density = 0.99; Figure 4.3 B) and food webs in lakes with strong permanent connections (predicted link density = 1.82; Figure 4.3 F), with an increase of about 0.8 links per taxa when the lake was strongly connected rather than isolated.

We found a correlation between length and trophic position for one species, least cisco (r = 0.77). However, the distribution of fish lengths in our sample allowed us to partition this species into two groups that sorted young-of-year fish (44 ± 6 mm FL) from adults (224 ± 38 mm FL); mean trophic position for least cisco < 100 mm FL was 3.2 ± 0.1 (confidence interval), while least cisco ≥ 100 mm FL was 3.7 ± 0.2. None of the fish species included in our stable isotope model occupied whole number trophic positions, and many appeared similar (Figure 4.5). Among fish that resided in lakes, trophic position varied with species identity (F = 5.09, df = 10, p < 0.001), and a test of multiple comparisons indicated clear differentiation between the smaller fish, Alaska blackfish, juvenile whitefish, and least cisco < 100 mm FL, and large predators like humpback whitefish and pike (Figure 4.5). Many species had overlapping trophic positions, like Arctic grayling, broad whitefish, least cisco ≥ 100 mm FL, ninespine stickleback, pike, rainbow smelt, and slimy sculpin.

When we examined maximum trophic positions (MTP) across the spectrum of surface water connectivity, three species occupied that role: ninespine stickleback (lake order -3), least

cisco (lake order -1 and 0), and humpback whitefish (lake order 2; Figure 4.6). Analysis of variance indicated that the change in maximum trophic position was significant between isolated lakes and strongly connected lakes ($df = 3$, $F = 4.23$, $p = 0.014$), and the change was equal to approximately one trophic level (2nd order lake MTP = 4.3 ± 0.5, isolated lake MTP = 3.3 ± 0.1). Within lakes of higher surface water connectivity, fish species spanned a broader range of trophic positions, from small whitefish spp. at 3.3 ± 0.1 to humpback whitefish at 4.3 ± 0.5, also ranging approximately one trophic level. Isolated lakes, with only one or two fish species, had the smallest range of trophic positions. Ninespine stickleback in isolated lakes had a mean trophic position of 3.3 ± 0.1, which was similar to that of ninespine sticklebacks in ponds, with a mean trophic position of 3.5 ± 0.2. Interestingly, ninespine stickleback, least cisco, Alaska blackfish, and broad whitefish trophic positions increased with surface water connectivity (Figure 4.6).

Regional scale

The fish assemblage at the southern location was composed of five species – Alaska blackfish, Arctic grayling, broad whitefish, least cisco, and ninespine stickleback. Those fishes, plus an additional six – Arctic char, burbot, humpback whitefish, pike, slimy sculpin, rainbow smelt – occurred at the northern location (Table 4.3). When examining food webs at a broader scale, comparatively, lakes at the northern location contained more trophic taxa and 1.9 times more links in the regional food web. Also, link density of regional lake food webs was seven times greater at wetter northern locations (link density = 3.18) than dryer southern locations (link density = 0.45). Diagrams of regional food webs (Figure 4.7) increased in complexity with the addition of fish species found at the northern location, including the appearance of two additional piscivores, pike and humpback whitefish (Figure 4.7 B). In ponds at both locations, ninespine

stickleback was the only fish species present. Pond food webs differed little; southern webs contained 22 links with a link density equal to 1.0 link per taxa, while northern pond webs contained 17 links with a link density of 0.94 links per taxa. One incidence of cannibalism occurred among ninespine stickleback in a pond at South.

In terms of averages for the two locations, observed richness in southern lakes was 2.8 ± 1.0 fish species, while northern lakes averaged 3.9 ± 1.7 fish species (Table 4.3). Lakes at the southern location tended to have fewer links on average, at 28 trophic taxa, than the northern lakes, with 40 trophic taxa. However, the difference in average number of links had little influence on link density, with an average of 1.35 links per taxa in southern lakes and 1.47 links per taxa in northern lakes (one-way t-test, $t = 0.55$, $df = 13.97$, $p = 0.29$). In ponds, fish species richness was constant. One species, ninespine stickleback was present if the pond had an ephemeral connection, regardless of the location. Contrary to the effects seen in lakes, northern pond webs had a slightly less complex structure than southern ponds, but average link density did not differ (south link density = 0.95 links per taxa; north link density = 0.90 links per taxa at North; one-way t-test, $t = -2.02$, $df = 6$, $p = 0.96$).

DISCUSSION

The diversity of individual food webs resulted from the variation in surface water connectivity among individual lakes and within study locations. At the local scale, food web complexity increased with surface water connectivity. The average species richness of isolated lakes was four times lower than a lake with a 2nd order stream outflow, and the lack of surface water connection translated to reduced fish species richness and 1.8 times loss in food web complexity, measured by link density. At the regional scale, increased food web complexity arose from the aggregation of trophic species as part of a metacommunity, but not as an average

of all lake types at each location. The additional fish species in the wetter, northern region meta-food web added trophic links between fish and invertebrates and fish and fish, increasing web complexity and potentially lengthening the food chain. This aggregation of eleven fish species led to a more complex food web with seven times the link density of the drier, southern region food web, which contained only five fish species. However, average lake food web complexity did not differ by location, suggesting increased complexity resulted from the aggregation of multiple diverse of food webs rather than from regional differences in the food webs of a "typical" lake.

We hypothesized that fish species richness, the number of trophic links, and link density would increase with lake surface water connectivity (LeCraw et al. 2014). At the local scale, using lake order as a metric for surface water connectivity (Riera et al. 2000), we found support for this hypothesis. While we may expect a positive correlation between species richness and the number or density of trophic links (Hershey et al. 1999, Dunne et al. 2002), large changes in surface water connectivity were required to obtain differences in food web link density. This is because the relationship between surface water connectivity and fish species richness was non-linear, and richness overlapped in lakes of differing connectivity strengths. For example, in lakes with ephemeral channel connections richness ranged from two to four fish species, while in lakes with a permanent channel connection richness ranged from three to nine fish species, including top-predators.

We also hypothesized that the maximum trophic position, a proxy of food chain length, would increase with surface water connectivity, primarily due to the addition of top-predators in lakes with higher colonization potential (Pillai et al. 2011, LeCraw et al. 2014). Interestingly, food chain length only increased substantially (i.e., ~ 1 trophic level) in a 2nd order lake where

Pike and Humpback Whitefish occurred. In other lakes, regardless of which fish was the apex predator (either Ninespine Stickleback or Least Cisco), food chain length was similar. The high degree of omnivory in the diets of Arctic fishes (Laske et al. in prep) likely promotes this similarity in the food chain length; however, the diversity of diets simultaneously promotes complexity, albeit in a shorter web (Gravel et al. 2011).

Foraging strategies and the dietary habits of individual fish species may provide a mechanism to explain patterns of food web complexity (Beckerman et al. 2006). Omnivorous feeding links may be critical for assembling complex webs via creation of network braches, where a species (potentially with a competitive disadvantage) feeds on a different trophic level or from different branches of the food web (Pillai et al. 2011). Most predators fed on zooplankton, macroinvertebrates, and fish, promoting complexity in these webs and drawing on resources from benthic, pelagic, or terrestrial energy compartments (Solomon et al. 2011). A majority of fish in the region demonstrated generalist feeding strategies, which allowed them to switch food resources in accordance with their availability, thereby increasing the number of trophic links for these fish species (Beaudoin et al. 2001, Eloranta et al. 2015, Laske et al. in prep). Species like Arctic Grayling, Least Cisco, and Ninespine Stickleback had the greatest dietary diversity, readily using resources from benthic and pelagic sources and from multiple trophic levels link energy compartments (Schindler and Scheuerell 2002, Eloranta et al. 2013), conferring stability on the local food web (Williams et al. 2002, Rooney et al. 2006).

If we consider each pond or lake food web within a region as a network of habitat patches, or a metacommunity, then food web function would depend on the accessibility of a patch (i.e., the surface water connectivity; Pillai et al. 2011) and the preexisting presence of its prey in that patch (LeCraw et al. 2014). LeCraw et al. (2014) point out that most empirical food

web studies demonstrate the idea of bottom-up control on food chain length – predators follow prey through space, and ultimately, prey constrain predators – yet few studies address the concept. We cannot provide any direct evidence that fish in these Arctic lakes were responding to bottom-up controls at the local scale. Given the generalist feeding behaviors demonstrated by common fish species, like Ninespine Stickleback, Alaska Blackfish, Least Cisco, Broad Whitefish, and Arctic Grayling (Laske et al. in prep), limited access to prey is unlikely, and many fishes relied heavily on similar prey (e.g., Diptera and Cladocera) in all lake types. We suspect similar outcomes even for fish commonly considered top predators, like Arctic Char or Pike, because they too are generalists (Beaudoin et al. 2001, Eloranta et al. 2015). Furthermore, given the abiotic constraints to productivity in the extreme Arctic environment, generalists may be best able to track limited resources and stabilize food webs through prey switching (Beaudoin et al. 2001, Hayden et al. 2014, Laske et al. in prep). It is far more likely that environmental controls such as stream size, permanence, or discharge influenced patterns of fish species distribution, richness, assemblage composition, and the resultant food web structure (Heino et al. 2015, Laske et al. 2016). Therefore, access to habitat patches is likely more limiting than prey availability, and access to habitat patches then becomes a major factor in distributing food webs in space.

Dispersal modes vary among Alaska's Arctic fishes, and colonization potential of lakes and ponds in the region depends upon the connectivity of the water body and the ecology of the fish species in question (Die Bie et al. 2012, Laske et al. 2016). For example, Ninespine Stickleback likely disperse in an undirected manner in pathways opened by flood waters during each spring melt; Ninespine Stickleback inhabit more aquatic habitats than other fishes in the region and often occur in ponds and lakes with limited surface water access (Laske et al. 2016).

On the other end of the spectrum, Arctic Grayling migrate, with site-specific fidelity, to foraging habitats (Buzby and Deegan 2000). Their movement patterns coincide with stream flow cues; movements into feeding areas occur with high flows during the spring freshet and movements out of feeding areas occur with summer base flows (Heim et al. 2016).

Shallow pond habitats (depths ≤ 1 m) freeze solid annually, essentially resetting the fish population of Ninespine Stickleback each spring, and if surface water connections are not available for outmigration in fall, then the ponds function as a sink for Ninespine Stickleback. The persistence of specific ponds as Ninespine Stickleback food webs on an annual basis is unknown; local factors like variation in snow accumulation, spring flood severity, and summer precipitation or evaporation would dictate a pond's connectivity to the hydrologic network or accessibility to fish (Woo and Guan 2006, Haynes et al. 2014). Given the stochasticity of pond habitats with respect to connectivity and permanence, spatial processes (e.g., dispersal ability) may be more relevant to community structure (Heino et al. 2015). Therefore, it is not surprising that food web structure was similar in ponds supporting Ninespine Stickleback at both locations. The ability of Ninespine Stickleback to access a pond is not contingent upon the pond's location, but rather its connectivity during periods of high water availability. However, one important distinction should be noted: we observed that locating a pond without Ninespine Stickleback was much more difficult at our northern location, where peaty soils and lower relief tundra resulted in a greater potential for overland flow and ephemeral channel connections. Therefore, it is more likely that fishless food webs would occur in ponds at the drier, less connected, southern location.

Each of the lakes included in our analysis supported fish food webs. The variation in local surface water connectivity was primarily responsible for patterns of species richness (Laske

et al. 2016). Examination of surface water connectivity along an ordered gradient (lake order; Riera et al. 2000) improved the resolution of surface water connectivity and provided insight into distributions of food webs at the local scale (i.e., lake). Isolated lakes, which lacked connection to hydrologic networks, supported only the hardiest fish species – Ninespine Stickleback and Alaska Blackfish (Haynes et al. 2014, Laske et al. 2016) – and supported distinctive invertebrate assemblages comprised of large-bodied Cladocera, Anostraca, and Amphipoda (SML, personal observation). Amphipoda comprised a notable proportion of the web in isolated lakes only. Food webs in complete isolation lacked large fish predators (e.g., Least Cisco, Arctic Grayling, or Pike), either because of lower colonization rates to those patches (Pillai et al. 2011, LeCraw 2014), or due to extreme conditions (e.g., low dissolved oxygen) that tend to negatively affect survival of larger predator species (Jackson et al. 2001). Therefore, it is unknown whether these lakes had, but then lost, these predators due to local extinction factors (Hershey et al. 2006, Ledger et al. 2012, Haynes et al. 2014) or whether larger fish were prevented from following prey to the isolated habitat patch (Holt 1996). In either case, the resultant food web in isolation was less complex, with reduced link density and food chain length than webs found in lakes with greater surface water connectivity.

Lakes with ephemeral or 1st order channel connections (headwater and 1st order lakes) had similar fish species richness and link density. Differences in food webs in these lakes, and the species components, depended indirectly on the degree of surface water connectivity and likely a suite of other environmental characteristics or landscape controlled food web characteristics (e.g., geomorphic-trophic hypothesis, Hershey et al. 1999). Access to lakes varied by fish species. For example, Least Cisco was the only salmonid that occupied ephemerally connected lakes (for more detail see Laske et al. 2016), and was the top predator in those

systems, yet they remained omnivorous – which allows species to invade systems at lower colonization rates (Pillai et al. 2011). Other fishes, like Arctic Char and Slimy Sculpin, may require greater area or water depth (Hershey et al. 1999; Eloranta et al. 2015) to colonize. However, a generalist, like Arctic Char, can stabilize food web compartments by changing their trophic niche, which reduces competition with other fish and reduces oscillations in the resource base (Rooney et al. 2006, Eloranta et al. 2015). Perhaps these stabilizing species – those that shift between available sources of production (e.g., Arctic Char, Eloranta et al. 2015; Ninespine Stickleback, Gallagher and Dick 2011) – were well suited to physically remote lakes, such as headwater, ephemerally connected, or isolated systems.

As the strength of channel connections increased, so did the number of piscivorous fishes and the length of the food chain (Pillai et al. 2011). However, the relatively short chains did not increase substantially with surface water connectivity due to the high degree of omnivory within the food webs (Morin and Lawler 1996, Beaudoin et al. 2001). Surprisingly, even for omnivorous or generalist species, the average link density of food webs in ephemeral, headwater, and 1st order lakes did not differ from average link density of food webs in isolated lakes, even when fish species richness was greater. This was counter to our expectation that number of links and link density would be positively correlated with habitat connectivity (LeCraw et al. 2014). In part, the similarity in link density was due to high variation in number of feeding links in food webs of differing connectivity. Small sample sizes of fish, like Broad Whitefish, Arctic Grayling, and occasionally Least Cisco, and limited dietary data from some individuals (i.e., stomachs not "full") weakened our ability to determine differences in food web complexity. For example, in 1st order lakes, the minimum number of trophic links was 17 for a lake with Ninespine Stickleback, Broad Whitefish, and Least Cisco adults and young-of-year. However, based on the average

number of feeding links for each of those species, we expected the number of trophic links to approach 40, with a link density value intermediate of that found for headwater lakes and 2nd order lakes.

The 2nd order lakes had the most complex food webs, with four fish species that occurred consistently in each individual web. At this level of surface water connectivity, colonization is unconstrained for fish species; also, given bottom-up constraints of food webs, their prey would also be established and available (Pillai et al. 2011, LeCraw et al. 2014). Second order lakes spanned the greatest range of fish species richness and included fish species that did not occur in in lakes of lower surface water connectivity, indicative of higher colonization potential (Hershey et al. 2006, Laske et al. 2016). One of the most prominent features of these lakes was the span of trophic positions. Longer food chains in 2nd order lakes may result from increasing colonization potential with the number of species that "stack vertically up" (Pillai et al. 2011), or as a function of greater access to refuge habitats (e.g., other lakes or streams) for intermediate predators (Ziegler et al. 2017). Fish in lakes with strong channel connections are also more likely to come and go from them; particularly fish with strong swimming abilities, migratory behaviors, or roving prey-search patterns. The maintenance of species richness and web structure in these lakes depends on their location within the hydrologic network, number of dispersal corridors (i.e., stream channels), distance between patches, and presence of lakes or patches that provide colonists or refuge (Holyoak 2000).

At both locations, the aggregation of individual lake food webs to one meta-food web increased the overall food web complexity, with greater complexity arising with increased species richness. Interestingly, when we compared the average web complexity for both locations, they were similar. The difference between the aggregate web and the average web

highlights the importance of the diversity of local food webs, including webs in isolated lakes with one fish species and webs from 2nd order lakes with five or more species. The differences in connectivity and colonization potential for each lake type are ultimately responsible for the array of local food webs and the overarching meta-food web. The aggregation of individual patches from a complex landscape can decrease the average strength of predator-prey interactions and increase the number of weak interactors in the larger, aggregated species pool, which may promote food web stability (McCann et al. 1998, Bellmore et al. 2015, Cross et al. 2013). The availability of multiple habitat patches in a metacommunity, which provide refuge for prey species or forage for predators, provides populations with stable resources used to sustain them (Ziegler et al. 2017). Predators, often generalists or omnivores, may rapidly switch to an increasing prey in accordance with its availability, and in doing so the predator releases the declining prey from top-down pressure (Rooney et al. 2006). In this way, the predator balances the asynchrony in food web energy channels (Rooney et al. 2006, Hayden et al. 2014, Eloranta et al. 2015). In a highly integrated system, such as they hydrologic network of Coastal Plain lakes, these connections may well exist in multiple patches (i.e., lakes). The meta-food web of a complex landscape may contribute to both community diversity and persistence by increasing the spatial heterogeneity of habitats and reducing associated species interaction strengths that constrain prey dispersal or survival (Holyoak 2000, Leibold et al. 2004, Bellmore et al. 2015). Much of the food web diversity we found across lakes and locations was due to fish species access, resulting from hydrological processes that drive fish species occupancy and richness in Arctic Coastal Plain lakes (Haynes et al. 2014, Laske et al. 2016). However, we expect the distribution of species and associated food webs to change across the landscape because of climate induced changes to surface water dynamics (Prowse et al. 2006, Wrona et al. 2006). If

landscape drying occurs as projected (23–37% drier by 2075–2084, Martin et al. 2009), we would expect reduced surface water connectivity to lakes with ephemeral or limited (e.g., headwater lakes) channel connection and a resultant shift in their associated food webs (Prowse et al. 2006). Isolated lakes could comprise as much as 25% (up from 3%, currently; estimated from site visits and aerial photography) of the nearby lakes at the northern location and 39% (up from 23%, currently) of the nearby lakes at the southern location, increasing the proportion of lake food webs that are vulnerable to extinction events like winter kill (Hershey et al. 2006, Gravel et al. 2011, Heino et al. 2015). Landscape complexity (e.g., variety of connectivity states) may be critical for maintaining regional food web stability by maintaining diversity of energy pathways through support of colonization processes in the meta-food web (Gravel et al. 2011, Bellmore et al. 2015, Smits et al. 2015). However, the effects of metacommunity properties, like colonization and extinction rates, on these on Arctic lake food webs require further study before we can fully evaluate the impacts of climate change.

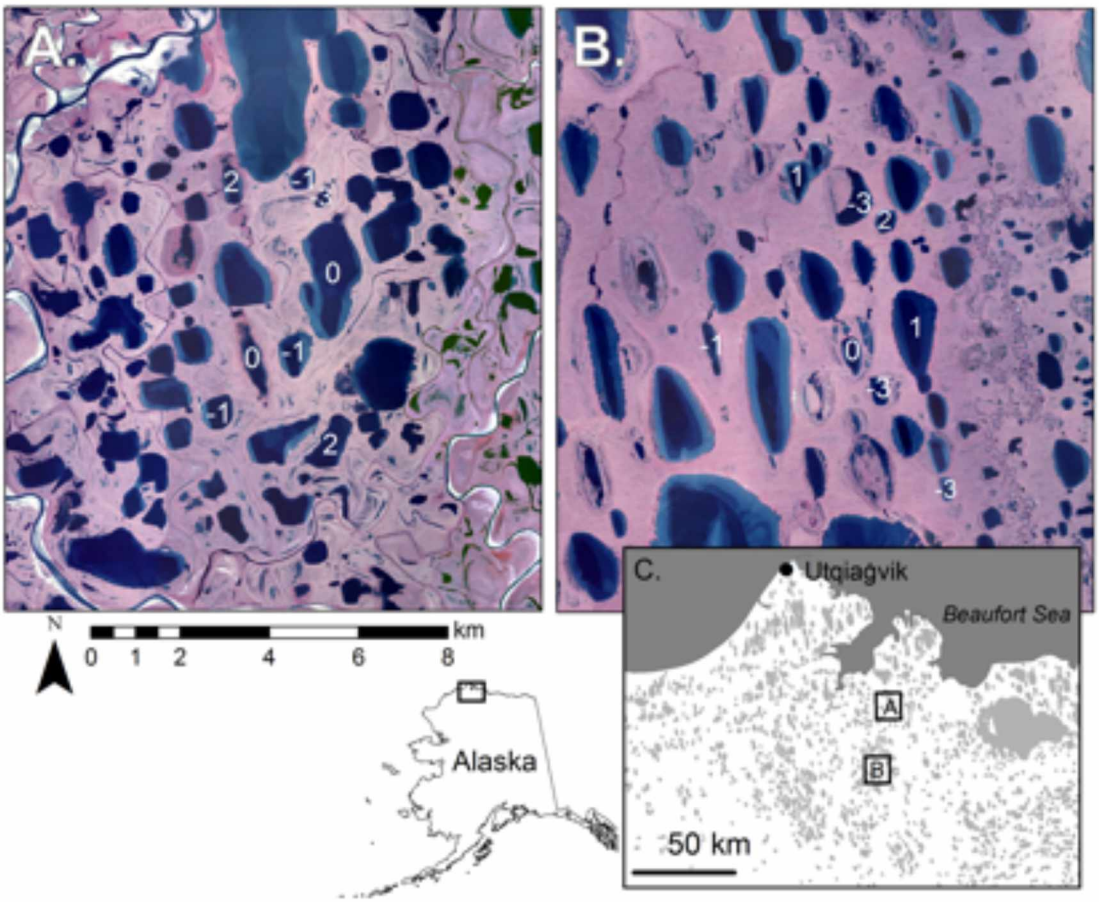

Figure 4.1. Locations of lakes and ponds sampled for fish food webs (A, B) on the central Arctic Coastal Plain (C) of Alaska. Surface water connectivity metrics for sampled lakes are indicated for the northern (A) and southern (B) locations. Connectivity categories are: -3, isolated; -1, ephemerally connected; 0, headwater lake with outflow only; 1, first order lake with 1st order stream inflow; and 2, seconder order lake with a 2nd order stream outflow. Sampled ponds are not indicated on the map.

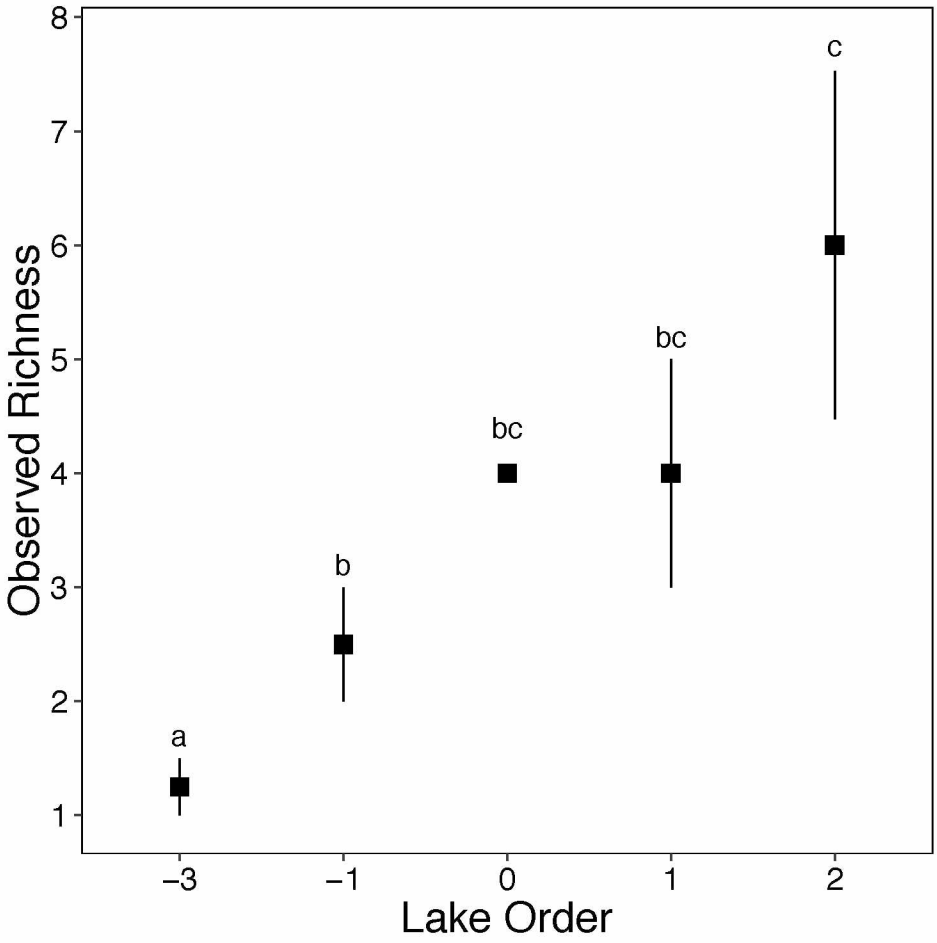

Figure 4.2. Mean (± 1 SE) observed fish species richness across the range of local surface water connectivity, or lake order, for lakes at two locations on the Arctic Coastal Plain of Alaska. Lake orders, adopted from Riera et al. (2000), indicate a lake's relationship with the hydrologic network as either -3, isolated; -1, ephemerally connected; 0, headwater lake with outflow only; 1, first order lake with 1st order stream inflow; and 2, seconder order lake with a 2nd order stream outflow. Multiple comparisons are indicated with letters above each point, mean richness values that share a letter are not statistically different.

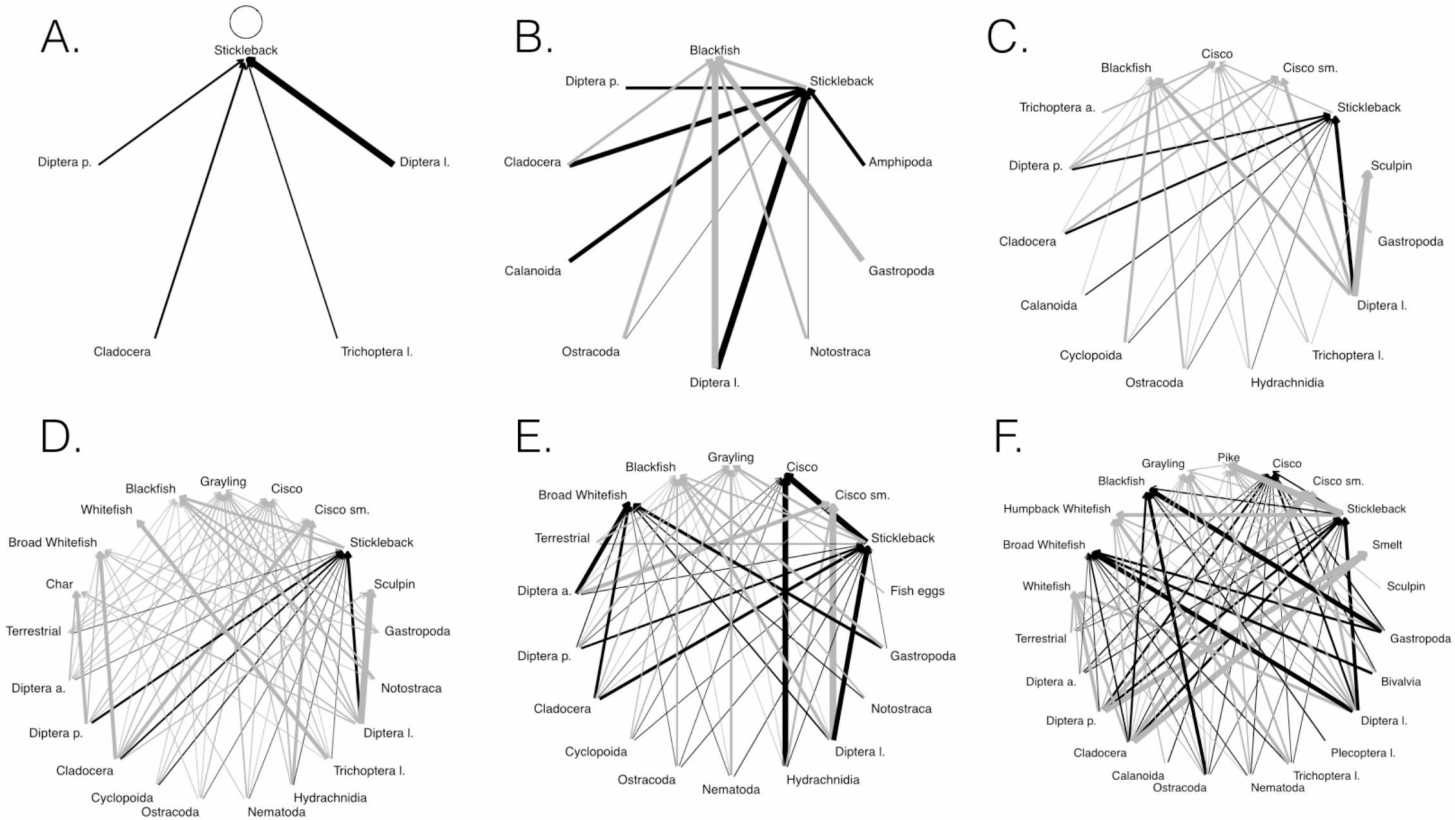

Figure 4.3. Example food web diagrams for fishes of the Arctic Coastal Plain, Alaska. Diagrams represent food webs from water bodies with differing surface water connections (A) ponds with ephemeral connections, (B) lakes with no connections, (C) lakes with ephemeral connections, (D) headwater lakes with one outflow, (E) lakes with a 1st order stream outflow, and (F) lakes with a 2nd order stream outflow. Links in black are shown for fish species that occurred in all lakes of that type, whereas links in gray are shown for species that occurred in at least one lake of that type. Fish are Stickleback = ninespine stickleback, Blackfish = Alaska blackfish, Cisco = least cisco ≥ 100 mm FL, Cisco sm. = least cisco < 100 mm FL, Sculpin = slimy sculpin, Whitefish = juvenile whitefish, Grayling = Arctic grayling, Smelt = rainbow smelt. For invertebrate prey: l = larva, p = pupa, and a = adult.

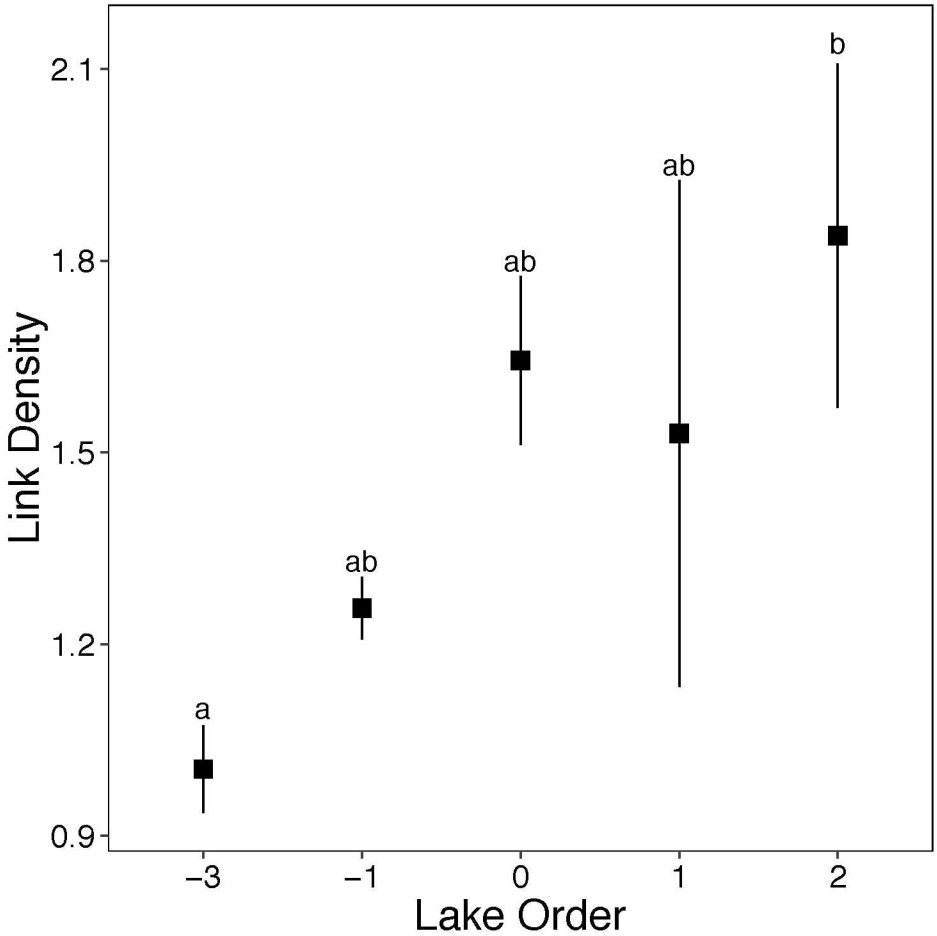

Figure 4.4. Mean (± 1 SE) link density, the number of links per taxa, across the range of local surface water connectivity, or lake order, for lakes at two locations on the Arctic Coastal Plain of Alaska. Lake orders, adopted from Riera et al. (2000), indicate a lake's relationship with the hydrologic network as either -3, isolated; -1, ephemerally connected; 0, headwater lake with outflow only; 1, first order lake with 1st order stream inflow; and 2, seconder order lake with a 2nd order stream outflow. Multiple comparisons are indicated with letters above each point, mean richness values that share a letter are not statistically different.

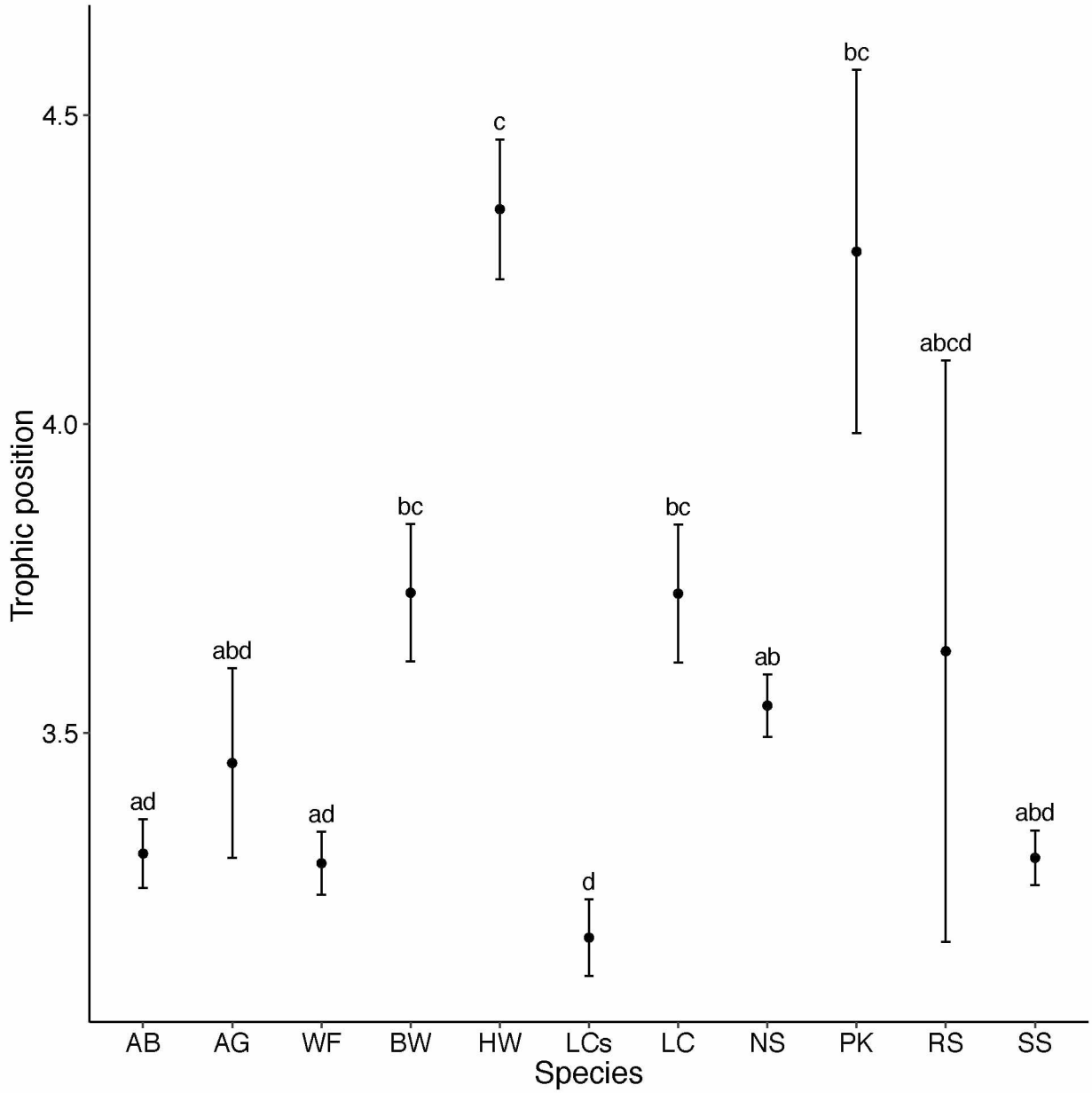

Figure 4.5. Mean (± 1 SE) trophic positions calculated as the difference in $\delta^{15}N$ between individual fish and the snail baseline for fish species captured in lakes at the northern location on the Arctic Coastal Plain, Alaska. Species are, AB = Alaska blackfish, AG = Arctic grayling, WF = juvenile whitefish, BW = broad whitefish, HW = humpback whitefish, LCs = least cisco < 100 mm FL, LC = least cisco ≥ 100 mm FL, NS = ninespine stickleback, PK = pike, RS = rainbow smelt, SS = slimy sculpin. Multiple comparisons are indicated with letters above each value.

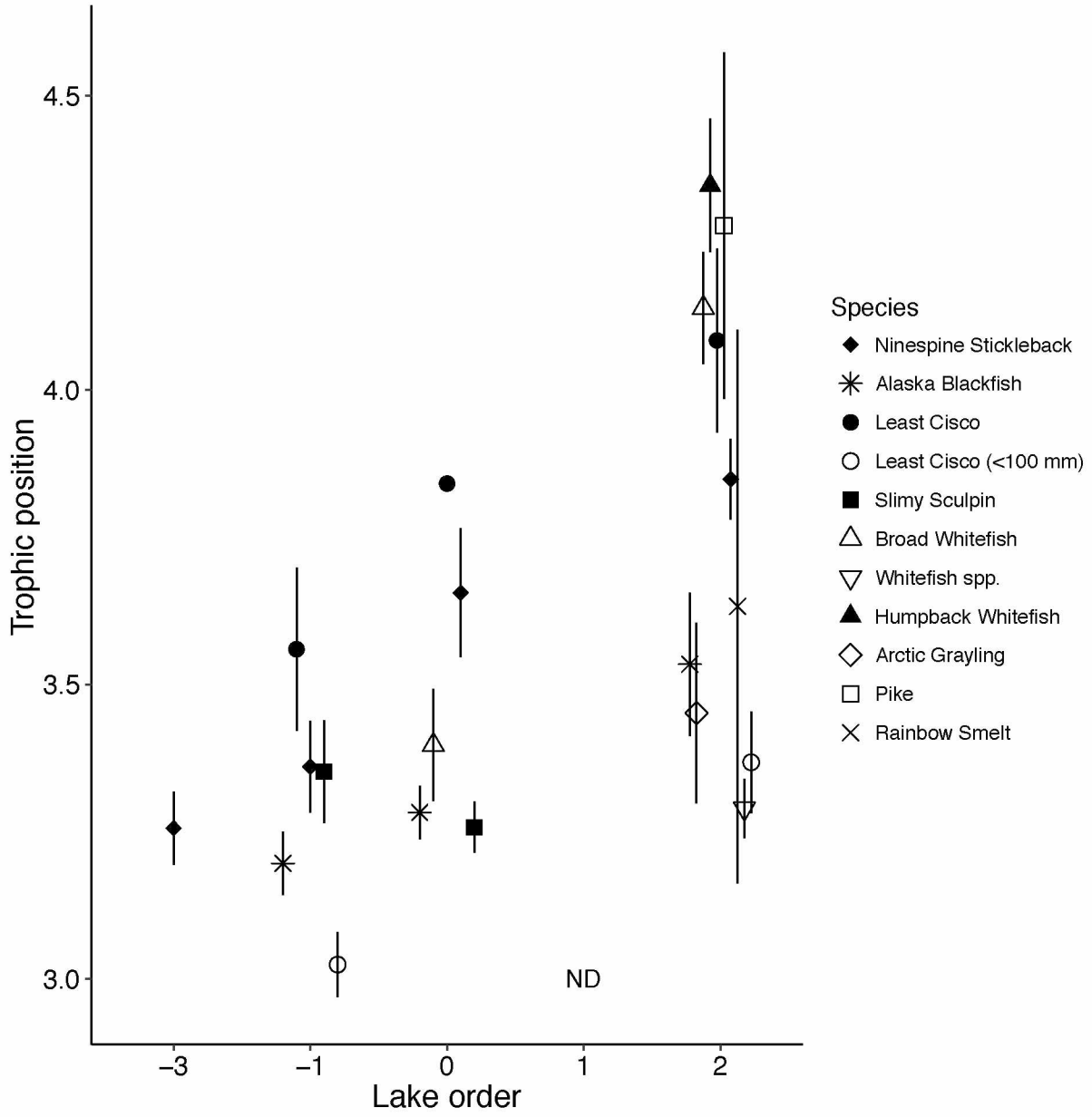

Figure 4.6. Mean (± 1 SE) of the trophic position, calculated as the difference in $\delta^{15}N$ between individual fish and the snail baseline, for fish species in lakes across the range of local surface water connectivity, or lake order, at two locations on the Arctic Coastal Plain of Alaska. Lake orders, adopted from Riera et al. (2000), indicate a lake's relationship with the hydrologic network as either -3, isolated; -1, ephemerally connected; 0, headwater lake with outflow only; 1, first order lake with 1st order stream inflow; and 2, seconder order lake with a 2nd order stream outflow. No data (ND) were available for 1st order lakes. Not all species are represented in this plot due to availability of data.

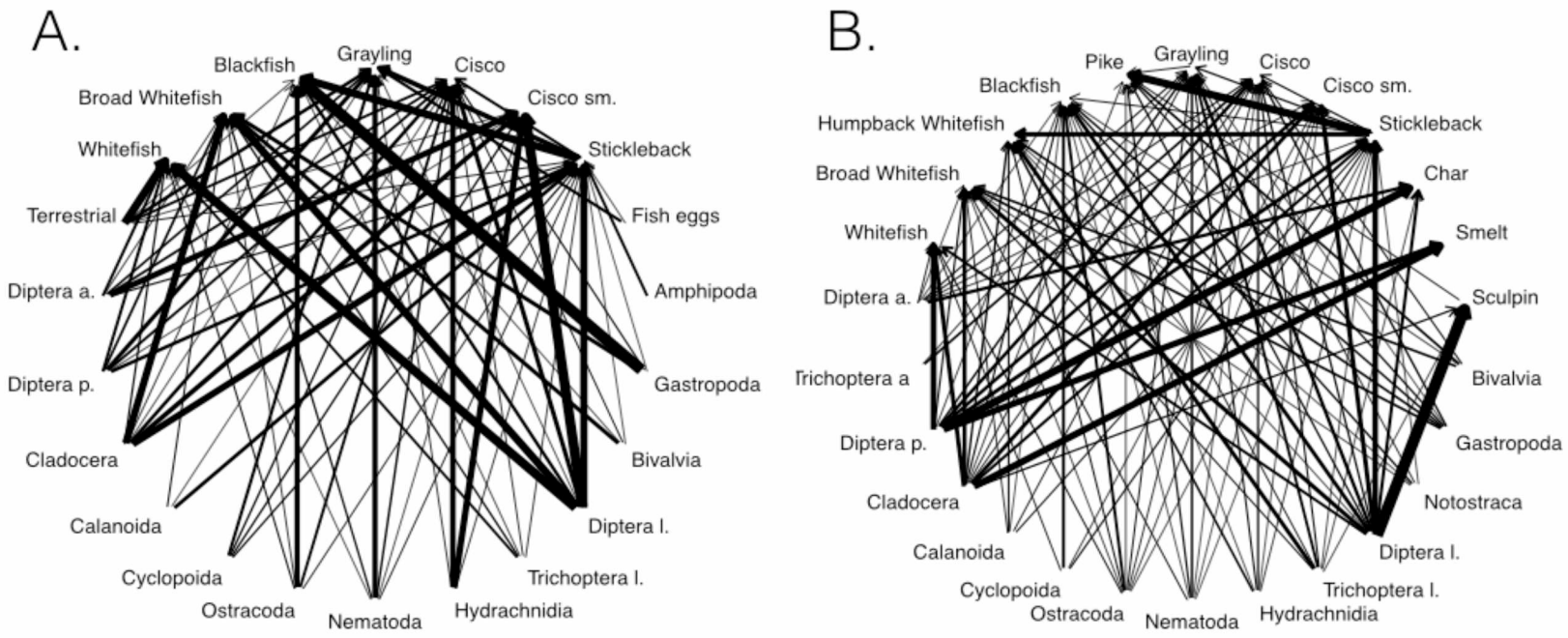

Figure 4.7. Meta-food web diagrams for lakes at the southern sampling location (A) and the northern sampling location (B) on the Arctic Coastal Plain, Alaska. Fish are Stickleback = Ninespine Stickleback, Blackfish = Alaska Blackfish, Cisco = Least Cisco ≥ 100 mm FL, Cisco sm. = Least Cisco < 100 mm FL, Sculpin = Slimy Sculpin, Whitefish = juvenile whitefish, Grayling = Arctic Grayling, Smelt = Rainbow Smelt. For invertebrate prey: l = larva, p = pupa, and a = adult.

Table 4.1. Number of ponds or lakes sampled (N) across the range of connectivity (lake order) found on the Arctic Coastal Plain, Alaska. Lake orders, adopted from Riera et al. (2000), indicate a lake's relationship with the hydrologic network as either -3, isolated; -1, ephemerally connected; 0, headwater lake with outflow only; 1, first order lake with 1st order stream inflow; and 2, seconder order lake with a 2nd order stream outflow. For each category, richness of fish species found and the assemblages in each grouping is given, along with the number of different food webs, the mean number of links (range), the average link density (standard deviation), and the maximum trophic position (MTP; standard deviation). No data (ND) were available for trophic positions in 1st order lakes. Fish are NS = Ninespine Stickleback, AB = Alaska blackfish, LC = least cisco, SS = slimy sculpin, BW = broad whitefish, AG = Arctic grayling, AC = Arctic char, BB = burbot, HW = humpback whitefish, PK = pike, and RS = rainbow smelt.

	Ponds		Lakes				
	Isolated	Ephemeral	Isolated	Ephemeral	Headwater	1st order	2nd order
Lake order	-3	-1	-3	-1	0	1	2
N	8	8	4	4	3	2	3
Richness	0	1	1 - 2	2 - 4	4	3 - 5	4 - 9
Assemblages	None	NS	NS	AB NS	AB LC NS BW	BW LC NS	AB BW LC NS
			AB NS	LC NS	AC AG NS SS	AB AG BW LC NS	AB AG BW LC NS
				AB LC NS SS			AB AG BB BW HW LC NS PK RS
N webs	Na	1	2	3	2	2	3
N links	Na	13 (6 - 21)	12 (9 - 18)	26 (16 - 35)	43 (33 - 51)	35 (17 - 52)	62 (41 - 99)
Link density	Na	0.93 (0.04)	1.00 (0.14)	1.22 (0.08)	1.64 (0.23)	1.53 (0.56)	1.84 (0.47)
MTP	Na	3.5 (0.5)	3.3 (0.2)	3.6 (0.3)	3.84 (-)	ND	4.3 (0.2)

Table 4.2. The number (n) of fish included in stomach content analysis (SCA) and stable isotope analysis (SIA). Also given, the number of lakes sampled and the mean number of trophic links (Links) with standard deviation (SD) for each of the fish species captured on the Arctic Coastal Plain, Alaska.

Species	n SCA	n SIA	n lakes	Links (SD)
Alaska blackfish	24	21	8	6.5 (3.6)
Arctic char	3	ND	1	4
Arctic grayling	20	13	3	15 (2.7)
Broad whitefish	15	18	4	10 (6.4)
Humpback whitefish	3	3	1	12
Least cisco (≥ 100 mm)	49	24	8	11.6 (6.5)
Least cisco (< 100 mm)	40	22	6	6 (1.9)
Ninespine stickleback	429	81	16	11.1 (1.9)
Pike	3	2	1	9
Rainbow smelt	3	2	1	3
Slimy sculpin	8	7	2	2.5 (0.7)
Whitefish spp.	38	12	4	4.8 (4.3)

Table 4.3. Trophic summary data for the southern and northern sampling locations on the Arctic Coastal Plain, Alaska, includes the number of water bodies (N), the fish assemblages, along with fish species richness, number of trophic links and link density, for both the meta-food web and the average food web. Values in parentheses are standard deviation of fish richness and link density, and the range of number of links. Fish are NS = ninespine stickleback, AB = Alaska blackfish, LC = least cisco, BW = broad whitefish, AG = Arctic grayling, AC = Arctic char, BB = burbot, HW = humpback whitefish, PK = pike, and RS = rainbow smelt, and SS = slimy sculpin.

		South		North	
		Ponds	Lakes	Ponds	Lakes
	N	4	8	4	8
	Assemblages	NS	AB AG BW LC NS	NS	AB AC AG BB BW HW LC NS PK RS SS
Meta-food web	Richness	1	5	1	11
	N links	22	77	17	143
	Link density	1	0.45	0.94	3.18
Average food web	Richness	1 (0)	2.8 (1.5)	1 (0)	3.9 (2.5)
	N links	16 (14 - 21)	26.88 (10 - 52)	10.25 (6 - 14)	40 (9 - 99)
	Link density	0.95 (0.03)	1.35 (0.42)	0.90 (0.03)	1.47 (0.40)

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GENERAL CONCLUSIONS

The function of fish communities and their food webs in lakes of the Arctic Coastal Plain required that several factors operate in favor of individual species: (1) presence in the regional species pool, (2) ability to colonize the patch given functional traits (e.g., swimming ability), (3) ability to colonize the patch given availability of resources (e.g., prey), (4) ability to persist in a patch given the environment (e.g., tolerate winter), and (5) ability to persist in the patch given predators (e.g., find refuge). Simply put, each fish must live in the area, be able to access a habitat, survive the extreme Arctic climate, have access to food, and avoid predators. I found that colonization factors played an important role, not only in the assemblage of fish communities, but also in the structuring of their food webs. Further, feeding habits of individual fish species and the generalist behaviors they demonstrated may bolster resilience to the extreme and variable climate of the Arctic Coastal Plain.

Surface water connectivity among lakes and across regions acted as a primary driver for

the distribution of individual fish species, and therefore, species richness, assemblage composition, and food web structure. Channel connectivity in the Arctic was a fundamental driver, or faunal filter (Tonn 1990), which structured fish assemblages across the landscape according to species' functional traits (i.e., life history or body morphology) and principles of metacommunity assembly (e.g., colonization rates). Dispersal abilities of fish, coupled with the arrangement or accessibility of available habitat had a strong influence over current distribution patterns (De Bie et al. 2012; LeCraw et al. 2014). This was true over regional and local spatial scales. Regionally, the availability of surface water influenced larger patterns of fish species richness and food web complexity – with wetter areas having more species and more complex meta-food webs. Locally, the physical presence of a channel provided an access point for individual fish to enter a lake; yet the strength and permanence of channel connections may play an important role in determining what species have access and when. In tandem, regional and local properties of hydrologic connectivity filtered species, resulting in the assemblage found in and across lake patches.

Lake communities are assembled not only by abiotic factors (e.g., surface water connectivity), but also by biotic factors (e.g., predation; Jackson et al. 2001). In lakes, pelagic fishes often exert strong top-down influence on their invertebrate prey (Carpenter et al. 1987). However, invertebrate responses in complex aquatic habitats are typically intractable (Batzer 2013), so the use of an experimental design in simple pond habitats provided an advantage for determining control of invertebrate prey by their fish predators. The response of invertebrates to Ninespine Stickleback in the experimental ponds was strong. Invertebrate taxonomic richness and biomass responded consistently with strong declines, and, to a lesser extent, invertebrate abundance and size. The patterns witnessed during the course of the experiment were related in

many ways to selective feeding and preference for specific taxa over others. Understanding the role of a ubiquitous predator provided information on the effects of top-down influence and predator foraging ecology on invertebrate prey, establishing a baseline for investigation of food webs in more complex or heterogeneous habitats.

Common Arctic Coastal Plain fishes employed generalist foraging strategies, which help fish take advantage of fluctuations in prey availability in space and time (Hayden et al. 2014). Variability in abundance of invertebrate prey has the potential to disrupt energy flow if predators lose access. Therefore, there is an advantage among fishes that can switch between prey resources – having the benefit of maintaining a supply of food and energy while allowing declining prey to rebound from predatory pressure (Rooney et al. 2006). The use of both benthic and pelagic prey by common Arctic Coastal Plain fishes not only stabilizes their individual species diets but the food web as a whole. Redundancy of trophic niches, even with high degree of individual variation in species diets, indicates similar or shared resource use that further contributes to the stability and resilience of food webs. In such an extreme environment, resilience of food web function would protect against perturbations or stochastic events, such as winterkill, spring flooding, summer droughts, and, potentially, climate change.

At small spatial scales, the generalist feeding habits of individual fish promoted stability within their food webs. Food webs were more complex in lakes with strong permanent channel connections, and more fish species, compared to food webs in lakes with no channel connections or ponds with ephemeral channel connections. At larger spatial scales, habitat complexity promoted species persistence and energy flow, thereby offering increased food web stability (Gravel et al. 2011; Bellmore et al. 2015). Complexity arose from aggregating the total number of food webs in a region into one meta-food web, where food webs are linked by predator and

prey movements between habitat patches, or in this case, lakes and ponds (Pillai et al. 2011). This contrasts with the average food web from each region, where complexity did not differ based on the mean representation of a region's food web. Therefore, it is the accumulation of different food webs from a variety of habitat patches and communities that likely promotes stability on the landscape.

Access to lake and pond habitats via surface water appears to be a critical component of aquatic ecosystem function on the Arctic Coastal Plain. Fish colonization potential relied heavily on the presence or absence of surface water connections or the abilities of fishes within a habitat to persist given their physical tolerances, abilities, and life history requirements. Access to habitats is likely to change with climate warming in the Arctic (Reist et al. 2006), and with it changes to fish species richness, composition, and food web structure. Effects of climate change may be dampened locally, through the resilience of food webs and foraging strategies of fish that stabilize webs and maintain energy flow if species are lost (Dunne et al. 2002; Beckerman et al. 2006). It is likely that across the broader landscape some communities and food webs will be restructured due to local changes in colonization potential. If the landscape dries, as projected (Martin et al. 2009), then many of the ephemeral or weak channel connections may be lost, leaving temporarily connected ponds and lakes and headwater lakes more vulnerable to change than other strongly connected habitats. In these systems, top predators may colonize less frequently or lose the ability to persist as winter conditions remain harsh, while spring and summer water conditions offer little to no recolonization potential. However, the diversity of freshwater lentic habitats, which cover a spectrum of size and surface water connectivity, may contain the necessary heterogeneity to maintain an array of fish species assemblages and local food webs to preserve ecosystem function and resilience in the face of climate change.

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Appendix A

IACUC approvals

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UNIVERSITY OF ALASKA FAIRBANKS

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

October 6, 2011

To:	Amanda Rosenberger, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[233290-3] Ecology and bioenergetics of fish in North Slope coastal and inland lakes

The IACUC reviewed and approved the Revision referenced below by Designated Member Review.

Received:	June 19, 2011
Approval Date:	October 6, 2011
Initial Approval Date:	October 6, 2011
Expiration Date:	October 6, 2012

This action is included on the October 31, 2011 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

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March 28, 2012

To:	Amanda Rosenberger, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[233290-4] Ecology and bioenergetics of fish in North Slope coastal and inland lakes

The IACUC reviewed and approved the Amendment/Modification referenced above by Designated Member Review.

Received:	March 20, 2012
Approval Date:	March 28, 2012
Initial Approval Date:	October 6, 2011
Expiration Date:	October 6, 2012

This action is included on the March 27, 2012 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.

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UNIVERSITY OF ALASKA FAIRBANKS

Institutional Animal Care and Use Committee

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March 27, 2013

To:	Mark Wipfli, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[233290-5] Ecology and bioenergetics of fish in North Slope coastal and inland lakes

The IACUC reviewed and approved the Reportable Event referenced above by Full Committee Review.

Received:	February 4, 2013
Approval Date:	March 21, 2013
Initial Approval Date:	October 6, 2011
Expiration Date:	October 6, 2012

This action is included on the March 21, 2013 IACUC Agenda.

The committee reviewed this submission and concurs that no violation has occurred as no work took place during the lapse in approval.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*