Pacific salmon in the Canadian Arctic: Indicators of change

By

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Abstract

The Arctic is rapidly changing. Warming temperatures are both facilitating new opportunities and threatening biodiversity. Despite a global effort to conserve biodiversity, and the recent acceleration of related conservation initiatives in Canada, species are already responding to a changing Arctic. However, our abilities to assess these changes, including shifting distributions and their impacts, are limited. Therefore, innovative approaches are necessary to focus the vastness of the Arctic to key habitats, the breadth of species diversity to key indicators of change, and to integrate knowledge in order to predict and manage a future Arctic. In this thesis, I establish Pacific salmon *Oncorhynchus* spp. as indicators of ecosystem-level change in the Canadian Arctic. More broadly, however, I have developed tools and strategies to help assess the impending biodiversity crisis in the Arctic. I developed a novel model to successfully apply citizen science to monitor rapidly shifting biodiversity in the Canadian Arctic and I extend the breadth of community-based monitoring across species and their habitats to encompass broad-scale areas and fine-scale assessments. By aligning thermal tolerances with thermal regimes at critical groundwater spring oases, I developed a novel model that predicts watersheds vulnerable to colonizations by salmon, and identifies the associated risk of competition with native char. I also use genetic tools to establish that chum salmon *O. keta* colonized the upper Mackenzie River at deglaciation, and that vagrants are currently accessing the Mackenzie River via coastal pathways. Together, I advance science regarding: 1) the application of citizen science to monitor biodiversity shifts in the Arctic; 2) predictions of distributional shifts to extreme environments; and 3) assessing the viability of the Arctic freshwater and marine environments as fish habitat over the past several thousand years. By

integrating the subsistence way-of-life with scientific approaches, we can better manage the development opportunities and predict the conservation impacts in a future Arctic.

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Chapter 1 - Introduction

The Arctic, defined here to include the area encompassing the Arctic Ocean and rivers draining to the Arctic Ocean, is inherently dynamic, seemingly isolated, exceedingly vast, and is experiencing rapid changes that have both local and global implications. Indeed, climate change is currently the most significant threat to biodiversity in the Arctic (CAFF 2013), as the north is perceived both as a global conservation haven for species shifting distributions northward (Yoon et al. 2015), and a potential global conservation hazard for cold-adapted species in a warming environment (Reist et al. 2006b). The importance of assessing biodiversity is rooted in reconciling the emerging potential of the Arctic with protection of its environment, species, and indigenous cultures. This is an international challenge as both the rate of environmental change in the north and the shift in political and economic attention northward appear more rapid than the pace of developing scientifically-based strategies to both conserve aquatic species and sustainably manage current and emerging opportunities. Recognition of this disparity is apparent as Arctic nations are currently negotiating a ban on fishing in the central Arctic Ocean until there is sufficient science and appropriate management in place (Arctic Five 2015), and international efforts are focused on conserving biodiversity through the development of protected areas under the Convention on Biological Diversity (Secretariat on the Convention of Biological Diversity 2014). The complexity of predicting the effects of climate change on species in the north is exacerbated by the dearth of knowledge regarding basic distributions and biology of many Arctic species and their habitats (Reist et al. 2006a). Preparing for a future Arctic therefore requires an innovative approach that focuses the vastness of the Arctic to key habitats and the breadth of species diversity to key indicators of change, and that integrates knowledge into a coordinated effort. By developing and embracing a collaborative approach that effectively connects the subsistence way of life with a scientific perspective, conservation and management initiatives align into a powerful platform to proactively prepare for a future Arctic.

Biologically, culturally and economically relevant indicator species provide information to assess ecosystem-level implications of on-going environmental changes in the Arctic, and guide the development of emerging opportunities. To be an effective indicator of a changing Arctic, however, species must be both sensitive to and reflective of environmental change within a defined period of time, detectable across a remote area and above ambient variability, scientifically based but not necessarily scientifically derived, and be relevant to the broader issues (DFO 2015). Pacific salmon *Oncorhynchus* spp. are ideal harbingers of change because they have been identified as indicators of ocean status (Irvine and Riddell 2007), are responding to changing environmental conditions (Grebmeier et al. 2006; Dunmall et al. 2013; Nielsen et al. 2013), and can be tracked at northern distributional extremes using an established community-based monitoring program (Dunmall et al. 2013). International attention is also now focused on assessing the impacts of environmental variability on abundances and habitats of salmon through an intensive, coordinated and concerted effort (International Year of the Salmon (IYS) Working Group 2016). The assumption that the distribution of salmon will shift in response to environmental variability is implicit to this initiative as IYS has developed a new term, salmosphere, which explicitly recognizes the current and future distribution of salmon in a changing world (Saunders et al. 2015). Salmon uniquely provide linkages among oceans, countries, cultures, economies, and ecosystems. Therefore, identifying salmon as indicators of a rapidly shifting Arctic recognizes their importance across their current distribution and potentially future role in a warming and vastly changed world.

The distributions of salmon can reflect shifting environmental conditions both directly because fish, as ectotherms, maintain thermal preferences through behavioral choice (Reist et al. 2006a) and indirectly through the link between increased productivity and prey availability for potentially colonizing species (Dunmall et al. 2013). Indeed, thermal tolerances of Pacific salmon in the marine environment have been used to model their ocean distributions (Myers et al. 2007) and predict northward shifts of species and habitats based on warming temperatures (Welch et al. 1995; Kaeriyama 2008; Abdul-Aziz et al. 2011; Yoon et al. 2015). Growth of juvenile pink *Oncorhynchus gorbuscha* and chum *O. keta* salmon captured in the Chukchi Sea in 2007 demonstrate not only presence in the Arctic but also the viability of the Arctic marine environment as habitat for growing Pacific salmon (Moss et al. 2009). As Pacific salmon feed on high energy-content prey, positive growth rates in Pacific salmon captured in the Chukchi Sea may indicate an increase in productivity of the lower trophic levels due to higher water temperatures and longer day lengths at higher latitudes, which is then propagated up the food chain (Moss et al. 2009). Increasing reports of adult Pacific salmon harvested as bycatch in subsistence nets in the Canadian Arctic indicate that distributional shifts of salmon are also occurring and can be effectively monitored in a community-based effort (Dunmall et al. 2013). Therefore, salmon may effectively integrate effects across trophic levels and distributional shifts may reflect ecosystem-level change in the Arctic marine ecosystem

While current increases in abundance and distribution of salmon in the Arctic may reflect broader-level changes, salmon are not new to the Arctic (reviewed in Nielsen et al. 2013). A cooling of the Arctic in the early Miocene 15-20 million years ago (MA) may have resulted in the divergence of *Oncorhynchus* from *Salmo* due to differing thermal tolerances (Stearley 1992), and speciation of Pacific salmon is likely related to the active geology during that same period

(Montgomery 2000). The different Pacific salmon species were likely derived during the major glacial events of the Pleistocene and have colonized, or established recurrently spawning populations in novel areas, to current distributions from multiple glacial refugia following the last glacial maximum (Waples et al. 2008). In the Arctic, the distribution of native Pacific salmon extends from small numbers of salmon in the Lena and Kolyma rivers in Chukotka (Berg 1949; Heard 1991; Salo 1991; Crawford and Muir 2008), to a potentially established population of chum salmon in the Mackenzie River in the North American Arctic (McPhail and Lindsey 1970; McLeod and O'Neil 1983; Stephenson 2006). This includes vagrants, or salmon present in non-natal rivers or those outside of known marine distributions, along the Alaskan North Slope, the Canadian Arctic and Greenland (Craig and Haldorson 1986; Stephenson 2006; George et al. 2009; Dunmall et al. 2013), as well as the UK (Telegraph 2015; BBC 2017a) and Ireland (BBC 2017b). Introduced pink salmon in the Russian Arctic have established spawning populations in the White and Barents seas (Gordeeva and Salmenkova 2011), and these are believed to have migrated to northern coastal rivers in Scandinavia, Scotland and Ireland (Welcomme 1988). Chum salmon that were similarly introduced in Russia are believed to have migrated to Finland (Welcomme 1988). Sockeye *O. nerka*, Chinook *O. tshawytscha* and coho *O. kisutch* salmon are rare in the Arctic and are considered vagrants (Hunter et al. 1974; Babaluk et al. 2000a, 2000b; Stephenson 2006; Crawford and Muir 2008; Dunmall et al. 2013).

While distributional changes are a ubiquitous and measurable response to environmental variability, biodiversity shifts due to warming temperatures require successful colonizations at northern range boundaries, or range contractions at southern boundaries, or both (Reist et al. 2006a; Alsos et al. 2007; Dunmall et al. 2016). Therefore while opportunistic colonizing fishes appear capable of accessing extreme freshwater environments as thermal barriers lessen with warming temperatures (Comte and Grenouillet 2013; Dunmall et al. 2013), establishment in these environments may depend on the relatively immobile early (i.e., egg, larva, fry) life stages that have narrow thermal tolerance windows and are more vulnerable to changes in temperature (Reist et al. 2006a; Pörtner and Farrell 2008). Indeed, the early colonization process in cold, freshwater environments appears to be influenced by species-specific thermal tolerances (Milner et al. 2008), which may also spatially stratify colonizing and native fish species within watersheds (McHugh and Budy 2005). Therefore, determining the likelihood for northward shifting vagrants to successfully colonize novel areas requires understanding of the thermal tolerances of critical life-stages and identification of critical habitats with those parameters (Dunmall et al. 2016). Viable freshwater habitat in many Arctic rivers during the winter is spatially limited to perennial groundwater spring areas due to the harsh conditions inherent to Arctic environments (Reist et al. 2006a). Owing to this inherent coupling, potentially suitable habitats for vagrant salmon may be in areas occupied by native, cold-tolerant riverine char such as Dolly Varden *Salvelinus malma* (Dunmall et al. 2016). Therefore, aligning the minimum thermal tolerances during critical early life stages with the thermal profiles of groundwater springs effectively narrows the geographic scope to key habitats, termed Arctic oases, and provides a strategy to predict both the potential for establishment of salmon in novel watersheds and the likelihood of competition between Dolly Varden and vagrant salmon for specific spawning sites (Dunmall et al. 2016). More broadly, this approach may provide strategies to assess ecosystem-level implications of on-going environmental changes, including assessing species interactions, the potential for disease transfer, and potential opportunities for emerging fisheries.

Thesis Outline

The overall goal of this thesis is to establish Pacific salmon in the Arctic as indicators of climate-driven shifts in freshwater and marine habitat availability, and assess the potential associated risk of competitive interactions with native substrate-spawning salmonids. The chapters collectively address the overarching hypotheses that salmon colonized the Mackenzie River during deglaciation, that vagrancies are increasing in the Arctic likely due to changing marine Arctic conditions, that establishment is possible in novel Arctic locations with suitable winter temperatures at groundwater springs, and that competition between colonizing salmon and native char may occur where spawning site-selection and species-specific thermal tolerances overlap. In Chapter 2, I introduce the Pacific Salmon Collection Program, called Arctic Salmon, as a community-based monitoring tool to track distribution and relative abundance changes for Pacific salmon across the Canadian Arctic. I then discuss the ecology of salmon in the context of changing environmental characteristics that may be contributing to the observed distribution and abundance changes for Pacific salmon across the Canadian Arctic. In Chapter 3, I develop a novel model to position citizen science as a community-based monitoring tool that bridges indigenous knowledge and scientific research. I then assess that model using Arctic Salmon and identify the importance of a mutual reporting step during data collections and continual communication among indigenous and scientific knowledge holders. In Chapter 4, I develop a reliable method to assess temporal and spatial variation in water temperatures that can effectively monitor key parameters year-round in critical habitats in remote dynamic streams. I also incorporate that method as part of a community-based monitoring effort. In Chapter 5, I use this method to align the thermal tolerances of salmon and Dolly Varden with the water temperatures at perennial groundwater springs to predict watersheds vulnerable to colonization by vagrant chum and pink salmon and assess the resulting risk of interaction with native cold-tolerant Dolly Varden. In Chapter 6, I use population genetic analyses to identify the historic and contemporary pathways by which chum salmon colonized the Mackenzie River. I then use a multi-disciplinary approach to reconstruct the history of chum salmon in the Mackenzie River from deglaciation in order to assess the viability of the Arctic to support projected distributional shifts given future climate warming. Finally, in Chapter 7, I integrate the current trends in salmon abundance and distributional change in the Arctic and discuss the shifting ecological and cultural role of salmon in a warming Arctic.

Chapter 2 - Pacific Salmon in the Arctic: Harbingers of Recent Changes

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Contributions of authors: I coordinated the Pacific Salmon Collection Program, which provided all Pacific salmon data from 2011 to 2013, with oversight by J. Reist and M. Docker. J. Reist implemented and has guided the program from 2000 to present. E. Carmack assisted with analyses of ocean circulation patterns influencing Pacific salmon abundances in the Canadian Arctic. J. Babaluk provided the kokanee salmon samples. M. Heide-Jørgensen provided the sample from Greenland. All data presented were analyzed by myself with the exception of the otolith microchemistry data, which was analysed by J. Babaluk. I wrote and submitted initial and final drafts of the manuscript. All co-authors assisted with revisions of drafts of the manuscript.

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Abstract

Pacific salmon appear to be expanding their range into Arctic ecosystems and may be acting as effective sentinels of climate change. Salmon harvests voluntarily reported through the Pacific Salmon Collection Program (PSCP) suggest recent increases in both the abundance and distribution of Pacific salmon in the Arctic over the past decade. In the Canadian western Arctic, chum salmon have been harvested annually since 1997 and more abundant harvests appear to have increased in frequency. Pink salmon harvest has increased from the sporadic catch of individual fish prior to 2003 to 41 pink salmon reported in 2004, 18 reported in 2008, three reported in 2011 and eight reported in 2012 (i.e., predominantly in even-numbered years). Recent reports also expand the known distribution of this species upstream in the Mackenzie River, eastward in the Beaufort Sea and one putative pink salmon was recorded off the east coast of Greenland. Since 2003, one kokanee, one coho, seven Chinook and ten sockeye salmon have also been reported in the Mackenzie River watershed. Multiple fish identified by local subsistence harvesters as “unusual” were captured near Arctic Bay, Nunavut in 2011 and 2012. Although abundance and distributional data obtained from voluntary harvest reports need to be interpreted with caution, Pacific salmon may be following thermally suitable habitat northward and benefiting from increased productivity in the Arctic. Reduced sea ice extent and longer durations of open water in the Arctic may also facilitate expanded marine migrations of juvenile and adult salmon. Efforts to document the harvest of Pacific salmon will continue. Pacific salmon may be demonstrating new marine pathways that facilitate the expansion of other similarly opportunistic species and, as such, may be harbingers highlighting major Arctic changes.

Introduction

Climate change is affecting the terrestrial, freshwater and marine ecosystems in the Arctic through changes to important physical, chemical and biological processes (Reist et al. 2006a; Prowse et al. 2009). In the marine ecosystem, warming temperatures and changes to other oceanographic variables such as sea ice, advection and turbulence influence vital biotic processes including growth rate, reproductive rate, phenology, swimming speed, mortality, recruitment and distribution (Drinkwater et al. 2010). Therefore, shifts in species' distributions, which are occurring in the Arctic as temperature barriers lessen due to climate warming (Vermeij and Roopnarine 2008; Post et al. 2009), may reflect ecosystem-level changes. Pacific salmon *Oncorhynchus* spp. may be effective biological indicators of these ecosystem changes (Irvine and Riddell 2007) because they appear to be naturally colonizing Arctic habitats as conditions become more favorable (Babaluk et al. 2000a; Grebmeier et al. 2006). Chum *Oncorhynchus keta* and pink *O. gorbuscha* salmon have a relatively small but historical presence in the Arctic and are the only species of Pacific salmon with natal populations in the Arctic (reviewed in Nielsen et al. 2013). Vagrant adult Chinook *O. tshawytscha*, coho *O. kisutch*, sockeye *O. nerka* and kokanee (i.e., freshwater-resident *O. nerka*) salmon have also been found in the Arctic, although rarely (reviewed in Nielsen et al. 2013). Although the marine migration routes of Pacific salmon harvested in the Arctic are not currently known, it is likely that these fish have either migrated from marine over-wintering habitat in the Pacific Ocean or have over-wintered in the Arctic Ocean. We hypothesize that the marine pathways facilitating expansion of salmon into the Arctic are related to increased temperatures contributing to expanded marine habitat availability, including surface water distributional shifts and potential deep water Arctic refugia, and increased marine productivity facilitating survival and growth of Pacific salmon in the Arctic Ocean.

As Pacific salmon in the offshore marine environment primarily use the upper portion of the water column (within the top 40-60 m; Walker et al. 2007), warming sea-surface temperatures (SST) are predicted to affect ocean distributions of salmon (Myers et al. 2007; Abdul-Aziz et al. 2011). The current conceptual model for Pacific salmon distribution in the open ocean, based primarily on pink, chum and sockeye salmon, posits that the salmon occupy the Bering Sea during the summer and fall feeding season, and migrate south and east for winter habitat (Myers et al. 2007). Pacific salmon actively change migration routes, timing and rates based on spring SST and follow the northwest progression of the 2^{o}C isotherm during open ocean migrations to summer habitat (Myers et al. 2007). The southern distributional limit of Pacific salmon in the open ocean is also related to species-specific thermal limits in SST; sockeye salmon have the coldest upper thermal limit (8.9^{o}C), followed by coho (9.4^{o}C) and chum and pink (10.4^{o}C) salmon (Welch et al. 1995, 1998). Future climatic projections of warming SST in the North Pacific Ocean and Bering Sea shift this southern thermal limit northward, potentially shrinking the availability of thermally suitable habitat (Welch et al. 1995, 1998). However, this same warming SST may similarly shift the northern thermal limit northward (Welch et al. 1998), perhaps into the Chukchi or Beaufort seas (Kaeriyama 2008). Warming climatic conditions producing warmer winters and earlier springs have resulted in the earlier return of mature salmon to spawning grounds and the earlier arrival of maturing salmon to the feeding grounds in the Bering Sea (Myers et al. 2007). Relatively high abundances of juvenile pink and chum salmon were caught in the Chukchi Sea in 2007 (Eisner et al. 2013) and demonstrated higher growth rates compared to those caught in the Bering Strait (Moss et al.

2009). This indicates northward shifting distributions in the marine environment coupled with increased productivity that would benefit colonizing species.

Feeding behavior and prey preference may also be contributing to the range extension of Pacific salmon into the Arctic because the availability of key prey species may be increasing in the Arctic with reductions in sea ice and the apparent associated increase in production (Moore and Laidre 2006; Moore and Huntington 2008). Sockeye salmon have the narrowest food spectrum of all Pacific salmon species in the marine environment, and feed primarily on crustaceans, including euphausiids, hyperiids and copepods, but also consume fish and squid (Karpenko et al. 2007). Pink salmon diet overlaps that of sockeye salmon, but also includes a wider variety of prey items (Karpenko et al. 2007). Chum salmon are the most flexible consumer (Karpenko et al. 2007) and can survive on large quantities of low calorie prey items (Gritsenko et al. 2000). The retreating sea ice supports a phytoplankton bloom (Perrette et al. 2011), which may contribute to increases in zooplankton and upper trophic level species at the ice-edge (Hunt et al. 2002). Strong phytoplankton blooms have been recorded in the Canadian archipelago and elsewhere in the Arctic (Perrette et al. 2011) and large under-ice phytoplankton blooms were also recently reported, presumably due to reductions in sea ice thickness and presence of melt ponds which allow sufficient light penetration (Arrigo et al. 2012). These shifts in productivity may increase feeding opportunity for Pacific salmon in the Arctic and are an example of ecosystem-level changes due to warming temperatures (Grebmeier et al. 2006).

Other sentinel species may also be opportunistically expanding northward due to increased feeding opportunity and suitable habitat conditions for longer periods of time in novel locations. Similar to Pacific salmon, bowhead whale *Balaena mysticetus* feed on zooplankton, especially euphausiids and copepods (Ashjian et al. 2010), and reductions in sea ice may be benefiting this species through increased feeding opportunities (Moore and Laidre 2006) and opportunities for dispersal (Heide-Jørgensen et al. 2012). Pacific-origin populations of bowhead whale migrate between the Bering Sea and the Canadian Arctic in the spring and fall, passing near Barrow, Alaska, where they form feeding aggregations (Moore et al. 2010). These aggregations may be indicating concentrations of prey that would be similarly suitable for Pacific salmon. Also, reductions in sea ice in the Northwest Passage are creating opportunities for increased movement of bowhead whale through this area and may eventually allow bowhead whale from populations originating in the Pacific and Atlantic oceans to travel between these different oceans (Heide-Jørgensen et al. 2012). Seasonally migrant whales may also benefit from reductions in sea ice, feeding on forage fish that also benefit from increased production resulting from reduced sea ice (Moore and Huntington 2008). Sections of the M'Clure Strait to Lancaster Sound support large populations of marine mammals and seabirds, suggesting higher productivity in these areas (McLaughlin et al. 2004). As Pacific salmon and certain species of ice-associated or seasonally migrant whale feed on similar prey items and undergo long seasonal marine migrations, it is possible that the benefits of reduced sea ice they experience are similarly experienced by Pacific salmon.

The warmer and more saline Atlantic layer, which occurs below 200 m in the Arctic (Carmack et al. 1989), may provide an over-wintering refuge for salmon in the Arctic Ocean (as reviewed in Irvine et al. 2009). Grey whale *Eschrichtius robustus* have been recorded over-wintering in the Beaufort Sea (Moore et al. 2006) and Arctic cod *Boreogadus saida* may use this habitat during winter as they prefer warmer temperatures (Crawford et al. 2012). Pacific salmon undergo daily vertical migrations to optimize growth and maturation by behavioral regulation of body temperature (Azumaya and Ishida 2005) and salinity (Quinn 2005), to optimize feeding on prey species that also migrate vertically (Walker et al. 2007) or as a mechanism for open-ocean orientation (Friedland et al. 2001). Sockeye salmon generally have the shallowest vertical distribution of all Pacific salmon species, typically less than 40 m, followed by pink, coho, chum and Chinook salmon, although there are exceptions (Walker et al. 2007). Chinook and chum salmon occasionally attain depths exceeding 300 m in the offshore marine environment and more consistently attained depths of up to 350 m daily during migrations in coastal waters during the fall, likely to avoid higher surface water temperatures (Tanaka et al. 2000; Walker et al. 2007). Chum salmon were found to experience a wide range of temperatures in the marine environment (-1 to 22 ^{o}C), likely coinciding with these vertical migrations (Walker et al. 2000). Therefore, it may be possible for Pacific salmon that make deep vertical migrations to adopt a strategy that allows them to benefit from thermoregulation in cold water while reducing the energetic costs of long migrations (Moore and Huntington 2008; Irvine et al. 2009).

Pacific salmon may be effective indicators of marine ecosystem changes associated with climate warming due to their expanding distribution and increased abundance in recent years. Thus, the objectives of this paper are to: 1) summarize the recent trends of relative abundance and the expansion of the known geographic distribution of Pacific salmon in the Canadian Arctic since previous reviews (Stephenson 2006; Nielsen et al. 2013); and 2) use the marine ecology of Pacific salmon (i.e., thermal preference, vertical distribution, swimming speed and prey preference), coupled with changes in oceanographic conditions resulting from warming temperatures, to discuss possible marine pathways facilitating this observed expansion. If the trends of warming ocean temperatures, sea ice retreat and associated changes in oceanographic conditions continue, Pacific salmon harvest throughout the Arctic may indicate marine pathways facilitating northward expansion of other opportunistic colonizing fauna.

Methods

The Pacific Salmon Collection Program (PSCP) was established by Fisheries and Oceans Canada, Central and Arctic Region, in 2000 to record the capture of salmon by aboriginal and non-aboriginal harvesters in the Northwest Territories (Babaluk et al. 2000a; Stephenson 2006). As Pacific salmon are not specifically targeted in the Northwest Territories, establishment of the PSCP did not affect fishing effort for Pacific salmon, but rather provided an incentive to report harvested Pacific salmon to more accurately document actual numbers and locations of harvested salmon and to verify species identification. All communities in the Mackenzie River watershed as well as coastal communities in the Beaufort Sea voluntarily participate in the PSCP. As Pacific salmon harvest had already been documented to occur throughout the Mackenzie River and in many Beaufort Sea communities (Stephenson 2006), the establishment of the PSCP did not increase the number of communities reporting harvest of Pacific salmon in the Mackenzie River watershed. Rather, it facilitated the documentation of more rarely harvested Pacific salmon species (i.e., pink, Chinook, coho, sockeye and kokanee salmon) in communities that regularly reported chum salmon harvest and allows observation of trends in year-to-year abundance and distribution of Pacific salmon harvested in Mackenzie River watershed and Beaufort Sea communities.

Reports of Pacific salmon harvested from 2004 to 2012 in the Canadian western Arctic and provided to Fisheries and Oceans Canada through the PSCP are provided herein. Species identification was verified from actual specimens using keys of morphological and meristic counts (e.g., Scott and Crossman 1973), except as otherwise noted. A kokanee captured in 2005 was initially identified using meristic character data from Scott and Crossman (1973), and the life-history form was confirmed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) analyses of the otolith to determine the pattern of strontium distribution (see methods in Swanson et al. 2010). In 2011, efforts to promote the PSCP increased and many local community organizations (i.e., Renewable Resource Councils, Hunters and Trappers Committees) became involved, which increased local communication and the convenience of reporting harvest. Through this program, it is possible to monitor overall trends in relative abundance of salmon (assuming effort remained stable), as well as document capture dates and locations by species.

These reports of Pacific salmon harvested between 2004 and 2012 are compared to the data provided in Stephenson (2006), who reviewed the total reported Pacific salmon harvest in the Canadian western Arctic to 2003. Trends in salmon abundance were estimated by comparing: 1) frequency of exceptional years, defined as when the reported chum salmon harvest in a single year is a minimum of five times higher than the reported harvest over each of the previous 10 non-exceptional years, and 2) total harvest reported per year, although different collection methods for harvests reported prior to 2003 and those reported after 2003 restrict interpretation regarding trends using absolute numbers. To determine harvest to 2003, Stephenson (2006) included the subsistence and commercial fisheries, salmon captured during non-directed research by consultants, government and university researchers, and salmon reported through the PSCP between 2000 and 2003. Total reported chum salmon harvest per year in Stephenson (2006) was tallied from 1931 to 2003. Where a range of harvest values were provided in Stephenson (2006), the maximum was used here and where a range of years of harvest was provided, the harvest was included in the latter year. The harvest reported by the PSCP was separated from the reported harvest through other methods included in Stephenson (2006), when overlap occurred (i.e., 2000 to 2003), to allow for a comparison of harvest trends to more recent years. Related recent information regarding Pacific salmon on the Alaskan North Slope is also summarized from information obtained from the literature.

The PSCP does not currently extend beyond the Northwest Territories. Therefore, no formal on-going collections are currently underway for Pacific salmon obtained from the subsistence fisheries in the Canadian eastern Arctic, and very little data exist regarding incidental harvest of Pacific salmon in Nunavut. However, observations of vagrant salmon or "unusual fish" elsewhere in the Arctic are reported. These fish were tentatively identified to species by sending out high resolution photographs without any associated harvest location information independently to up to eight researchers specializing in Pacific salmon *Oncorhynchus* spp. or char *Salvelinus* spp. These individuals provided their opinion regarding species using morphological information and/or meristic counts obtained from these photographs including criteria such as the size, shape and color of the fish, the length and pigment of the lower jaw, the presence or absence of spots, the shape and size of the eye, the size of the caudal peduncle, the number of fin rays and the number of scales above and below the lateral line. Unfortunately, actual specimens are not available to verify these species identification efforts.

Results

Canadian Western Arctic

Chum salmon abundance appears to have increased in the Mackenzie River over the past decade. Although chum salmon are historically known from the Canadian western Arctic, more abundant harvests have been reported more frequently in past years (Figure 2.1). Higher chum salmon harvest in the Canadian Arctic has been noted in 1978 to 1980, 1987, 1998 and in 2003 using total reported harvest by multiple activities including subsistence and commercial catch, incidental catch by government, university researchers and consultants, and those salmon reported to the PSCP (Figure 2.1). Since 2003, an exceptional year of chum salmon harvests occurred in 2011, when reported chum salmon harvest was more than five times higher than the low-level harvest over the prior 10 years (Figure 2.1). It is possible the years with lower harvest are simply due to lower incidence of reporting, not necessarily to a lower harvest of salmon, and it is possible that the years with higher harvest are simply due to increased incidence of reporting. However, due to the difference in harvest between exceptional and low-level harvest years, and because the reporting is consistent among communities across the Northwest Territories, the reporting of specimens to the Pacific Salmon Collection Program reflects subsistence harvest trends. Generally, as harvest increases, voluntary reports of harvests also increase.

Pink salmon have also become more common in the western Arctic, and they are being caught in more places in recent years. In the Canadian Arctic, pink salmon harvest increased from captures of mostly single specimens prior to 2003 to 41 pink salmon reported to the PSCP in 2004, 18 reported in 2008, three reported in 2011 and eight reported in 2012 (Figure 2.1). Four pink salmon were harvested at the confluence of the Arctic Red and Mackenzie rivers near Tsiigehtchic in 2004 and one was harvested in the Beaufort Sea near Paulatuk in 2012, expanding the known adult occurrences of this species upstream in the Mackenzie River and also eastward in the Beaufort Sea (Figure 2.2).

Kokanee, sockeye, coho and Chinook salmon have all been found in small numbers in the Canadian western Arctic (Babaluk et al. 2000a, 2000b, Stephenson 2006). Since 2004, one additional kokanee, likely from the Peace River, British Columbia/Alberta system, was captured in the Slave River near Fort Smith on October 5, 2005, bringing the total captured in the

Canadian Arctic to two fish (Figure 2.2). The strontium (Sr) profile for this 4+ year old salmon was indicative of freshwater residency, and was compared to a kokanee previously caught in the Mackenzie River watershed and a sockeye salmon previously harvested near Sachs Harbour (Figure 2.3; Babaluk et al. 2000b). The low, relatively flat Sr signal (~500 ppm) early in each fish's life (0 - ~500 microns) indicated that all three fish occupied a freshwater habitat during this period after which the sockeye salmon migrated to the sea where it spent the duration of its life, as indicated by the elevated Sr signal. Both kokanee remained in freshwater habitats for the duration of their lives, as indicated by the continuation of the low Sr signals. From 2004 to 2012, ten additional sockeye salmon have been reported from the subsistence fishery: seven were harvested in 2004, two were reported in 2005 and one was reported in 2011. These captures did not extend the known distribution of sockeye salmon in the Canadian western Arctic. A coho salmon was captured in the Canadian Arctic in 2011 near the confluence of the Arctic Red River and the Mackenzie River at Tsiigehtchic, bringing the total number of coho salmon captured and reported in the Canadian western Arctic to three fish. This capture did not extend the known distribution of coho salmon in the Mackenzie River watershed. Seven additional Chinook salmon have been captured in the Mackenzie River since 2003: five in 2004, one in 2005 and one in 2008. Likewise, these captures did not extend the known distribution of Chinook salmon.

Canadian Eastern Arctic

Although the Canadian eastern Arctic is not included in the PSCP, residents of Arctic Bay, Nunavut, reported harvest of an unknown number of “unusual fish” in 2011 and 2012 (Figures 2.2, 2.4). Several harvesters were catching these fish using gillnets in August to early September of each year, and the fish were all silver in color (i.e., non-spawning) when captured.

Unfortunately, species identification cannot be verified from actual specimens. Using a high resolution photograph of a representative specimen, these fish have been placed both in the genus *Oncorhynchus* by five scientists knowledgeable in Pacific salmon (n=2 suggest sockeye salmon, n=2 suggest chum salmon and n=1 said either sockeye or chum salmon), and in the genus *Salvelinus* (most likely Arctic char *Salvelinus alpinus*) by three scientists knowledgeable in char. Thus, the difficulties of correctly identifying a fish using a photograph are highlighted. However, the local subsistence harvesters in Arctic Bay have repeatedly captured fish over two years that they have independently self-identified as "unusual", suggesting that these fish were somehow different than the char normally harvested. Efforts to obtain actual samples of subsequent catches to identify these "unusual fish" to species will continue in future years.

Greenland

Researchers from the Greenland Institute of Natural Resources incidentally caught a pink salmon on the east coast of Greenland (70° 20' 53.11" N, 28° 9' 21.24" W) on August 24, 2012 (Figures 2.2, 2.4). While the specimen was not preserved, species was identified as a pink salmon from a high resolution photograph which clearly showed the development of a distinctive "humped-back" shape and the large black spots on the dorsal surface and on both lobes of the caudal fin (Figure 2.5). All scientists that viewed this photograph (n=7) independently agreed that this fish was a pink salmon. This record documents the first known pink salmon captured on the east coast of Greenland.

Discussion

In the past 10 years, the geographic occurrences and relative abundance of adult Pacific salmon in the Arctic has changed. The frequency of exceptional years of chum salmon harvest in the Mackenzie River watershed has increased and the harvest of pink salmon has changed from the sporadic capture of individuals to the reported capture of between eight and 41 pink salmon in several even years since 2004. The known geographic occurrences of adult Pacific salmon in the Arctic has also expanded with the pink salmon captured near Paulatuk, Northwest Territories, and the putative pink salmon captured on the east coast of Greenland (Figure 2.2). The presence of adult Pacific salmon in new locations, the increase in the number of species of Pacific salmon being harvested, and the increase in relative abundance of these species in subsistence harvests may be indicative of overall changes in the Arctic marine environment that facilitate increased survival and dispersal and highlight the importance of continuing to monitor Pacific salmon as sentinels of Arctic change.

Increases in the harvest of chum salmon in the Canadian Arctic may be attributed to increased survival of natal populations, increased vagrants from outside sources, or both as chum salmon is the only Pacific salmon species natal to the Canadian Arctic (Stephenson 2006; Irvine et al. 2009). On the Alaskan North Slope, evidence of spawning also exists for chum salmon in several drainages between Point Hope and Prudhoe Bay (Craig and Haldorson 1986; Johnson and Blanche 2011) and juvenile chum salmon have been captured in the Colville River (Moulton 2001 as reported in Fechhelm et al. 2009). Natal chum salmon may survive lethal low temperatures associated with Arctic marine winters by migrating to the North Pacific, over-wintering in the Beaufort Sea in the warm Atlantic layer, or behaving similar to other anadromous salmonids and finding suitable fresh or brackish water for over-wintering (as reviewed in Irvine et al. 2009). Vagrant chum salmon may be similarly following feeding opportunities into the Arctic and become entrained in currents (e.g., the Alaska coastal current) leading to the Mackenzie River. The increased frequency of exceptional chum salmon years since 2004 suggests that survival has increased in the freshwater, the marine environment or both. Changes to freshwater habitats resulting from warmer temperatures are apparent (Prowse et al. 2009) and could also contribute to the increased frequency of exceptional years of chum salmon in the Arctic (i.e., greater survival of the freshwater phase for fish of this species).

The larger harvests of pink salmon that have occurred in the Canadian Arctic in several even years since 2004 may be similarly reflecting changes facilitating increased dispersal and survival. Although robust self-sustaining spawning populations of pink salmon in the North American Arctic have not been confirmed through the capture of juveniles (Nielsen et al. 2013), directed efforts to capture juvenile pink salmon has not been conducted to our knowledge, and would be difficult due to the coincidental timing of outmigration and spring melt. Pink salmon have the highest straying rate of the Pacific salmon species, so the capture of vagrants is not uncommon (Hendry et al. 2004). On the Alaskan North Slope, pink salmon are now suspected to spawn in 11 drainages west of Point Barrow, Alaska (Woods and Carothers 2011), which has increased from the eight drainages suspected by Craig and Haldorson (1986). Their status east of Point Barrow is less well known although local knowledge suggests that pink salmon may spawn in the Ikpikpaq and Itkillik rivers (George et al. 2009). Pink salmon are regularly caught daily in the subsistence fishery at Elson Lagoon, Alaska, during summer (George et al. 2009). The pink salmon harvest on the Alaskan North Slope was exceptionally high in 2008: 19,531 pink salmon were harvested from Elson Lagoon (Woods and Carothers 2011) and catch-per-unit-effort information from a 26-year monitoring project at Prudhoe Bay shows a high catch of pink salmon in 2008 compared to other years (Fechhelm et al. 2009). Therefore, the possibility of a self-sustaining population of pink salmon along the Alaskan North Slope exists and warrants further investigation. If verified, the vagrant pink salmon captured in the Canadian Arctic may be sourced from established populations along the Alaskan North Slope. Alternatively, the pink salmon captured along the North Slope could be vagrants from populations further away in North America or Russia. These fish presumably follow the current conceptual model for open ocean distribution and migrate to summer feeding grounds in the Bering Sea (Myers et al. 2007), and then follow similar marine pathways as other marine species to feeding opportunities in the Arctic.

The appearance of the pink salmon on the east coast of Greenland is an interesting anomaly, not only because this is the first record of a Pacific salmon captured on the east coast of Greenland, but also because the potential origin and migration routes of this pink salmon suggest significant changes have occurred in the Arctic. Confidence in identifying this fish as a pink salmon is high, albeit from a photograph, because of the distinct morphological characteristics present and because the fish was beginning to develop secondary sexual characteristics, making those distinguishing characteristics more pronounced (Figure 2.5). Presumably, the captured pink salmon was entrained in the transpolar current, a Pacific origin water mass moving across the polar cap and extending south past the east coast of Greenland through the Denmark Strait (Figure 2.4). The lowest sea ice extent ever recorded was in 2012 and a section of sea ice connecting the polar ice cap to the Severnaya Zemlya islands melted for the first time (National Snow and Ice Data Center 2012; Figure 2.4). This may have provided opportunity for pink salmon to follow this transpolar current from small natal runs in the Lena River or further east, skirting and perhaps actively feeding at the ice edge to east Greenland (approximately 2500 nautical miles, NM; Figure 2.4). Assuming pink salmon are approximately 0.5 m in length, and travel at 1 body length per second (Drenner et al. 2012), a pink salmon would travel at 23.3 NM/day and take approximately 107 days to reach the capture site. Presumably entrained in the transpolar current, which moves ice between 5 and 20 cm/sec (2.3 to 9.3 NM/day) toward Fram Strait (Polyak et al. 2010), this fish would have reached the capture site in approximately 10 to 30 fewer days. Therefore, active swimming following retreating ice coupled with passive movement while entrained in ocean currents may have resulted in this possible extension to the geographic occurrences of adult Pacific salmon in the Arctic.

Alternative origin and migration route options are also possible, although less likely. The pink salmon captured in east Greenland may have originated from the self-sustaining odd-year population of introduced pink salmon to the Kola Peninsula (Gordeeva and Salmenkova 2011, ICES 2013). However, the pink salmon captured in east Greenland was indicating signs of gonad maturation by developing a dorsal “hump” and darkening color in 2012, an even year. Also, prevailing Atlantic currents would have moved the pink salmon eastward away from the capture location, making it an unlikely origin. Pink salmon were also introduced into Norway from the 1960s to the late 1970s (Bjerknes and Vaag 1980), which produced self-sustaining populations in 11 rivers in Finnmark, northern Norway (Hesthagen and Sandlund 2007), and pink salmon are also caught occasionally in Finland (ICES 2013). However, the prevailing Atlantic currents moving eastward again reduce the likelihood of a Scandinavian origin for the pink salmon caught in east Greenland. Pink salmon have also been caught annually in low numbers (5 to 30 per year) in Icelandic rivers since the 1960s (ICES 2013); however, these fish are likely strays from northern Russian populations (Icelandic Ministry of Fisheries and Agriculture 2013). There are also pink salmon in the Great Lakes following a single introduction of fry into Lake Superior in

1956 but it is thought that these pink salmon are not anadromous (Kwain 1982) and hence are an unlikely origin for the pink salmon caught in east Greenland. Several attempts have been made to stock pink salmon in the western North Atlantic, with little long-term success (Dempson 1980; Randall 1984). However, Dempson (1980) suggests that small naturally occurring populations of pink salmon in Newfoundland remain a possibility. Pink salmon were artificially maintained in Maine from 1906 to 1925, but returns diminished by 1927 (as reviewed in Dempson 1980) and pink salmon were planted in Maine once again in 1982 (Randall 1984). Pink salmon from British Columbia were transplanted to Newfoundland starting in 1959 (Lear 1975), but returns had diminished by 1976 (Dempson 1980). Pink salmon have been captured on the east coast of Canada in northern Labrador and in Newfoundland up to the late 1970s (Dempson 1980), and in New Brunswick in 1983 (Randal 1984) and also in Nova Scotia (Crossman 1991). However, no reports of pink salmon have been found for the western North Atlantic for 30 years (ICES 2013) and therefore it is an unlikely source for the pink salmon captured on the east coast of Greenland. If the pink salmon captured in east Greenland originated on the west coast of North America, estimated travel distance following the prevailing currents moving east and north is approximately 3750 NM from Point Hope, Alaska and it would take the pink salmon approximately 157 days to reach the capture location. A routing through the M’Clure Strait is likely more feasible than via the Davis Strait because of reduced ice-cover and evidence that the Northwest Passage (via M’Clure Strait) has already been used as an ice-free corridor to connect individuals from two populations of bowhead whales originating in the Atlantic and Pacific oceans (Heide-Jørgensen et al. 2012). Although pink salmon are unlikely to over-winter in the Arctic due to their shallow vertical distribution, they can eat a variety of prey items (Karpenko et al. 2007), suggesting this possibility cannot be ruled out. If additional specimens are captured in future years, we hope that they will be provided for further analyses to allow for a more thorough discussion of possible origins and migration routes.

The capture of a second kokanee in the Mackenzie River watershed in 2005, 14 years after the capture of the first kokanee in 1991, suggests the pathways facilitating dispersal of this species to the Mackenzie River drainage remain open. Babaluk et al. (2000b) summarize possible origins for the kokanee captured in 1991, including stocking efforts in Saskatchewan, Alberta and British Columbia, as well as native populations in the Arctic and Thutade lakes at the headwaters of the Peace River system. Babaluk et al. (2000b) concluded that the most likely origin of the kokanee captured in 1991 was the nearest known native populations in the Peace River system. Although stocking efforts for kokanee continue in British Columbia, as the kokanee captured in 2005 was age 4+ (i.e., hatched in 2001) and provincial stocking reports show that only 100 kokanee total were stocked in 2001, it is unlikely to have originated from this stocking program. No other stocking efforts for kokanee from any province into this system are known. Therefore, the kokanee captured in the Mackenzie River drainage in 2005 likely originated from the native populations in the Peace River system, similar to the kokanee captured in 1991.

There are many opportunities in researching dynamic Pacific salmon; however, the challenges of working with these rare species in the vast geographic area of the Arctic must be addressed. Relying on voluntary reporting of Pacific salmon is necessary due to their relative low abundance in the vast geographic area. However, identifying the distribution of Pacific salmon using this method is a reflection of the locations of subsistence fisheries or other research projects and our ability to access information from these harvests. Therefore, this information can be used to identify trends in relative abundance and to document harvest locations, but is not a reflection of the actual number of Pacific salmon in the Arctic or the overall extent of their geographic distribution. Often, there are issues with correctly identifying species because of the rarity of Pacific salmon in subsistence fisheries. Increased communication with local communities and other research projects operating in the Arctic may increase reporting. An additional challenge in using this method is that the only certainty is the harvest location; the possible origins of vagrant salmon and routes of colonization are largely inferred from information regarding oceanographic conditions, ecology of the species, and locations of other self-sustaining populations. Compounding this, the Arctic marine ecosystem is undergoing substantial changes, and the overall effect of these changes on aquatic species is largely unknown. Also, vagrants to the Arctic may be escapees from aquaculture efforts. As records of aquaculture for Pacific salmon species have not been found for Norway, Iceland or eastern Canada, and Russian efforts are largely unknown, we assume that, if present, escapees would originate from western North American or Japanese aquaculture efforts and therefore follow similar marine pathways to the Arctic as vagrants from natal populations in these areas.

The future of Pacific salmon in the Arctic looks promising; geographic occurrences are expanding and trends suggest higher abundances. However, in order for vagrant salmon to become self-sustaining populations, viable freshwater habitat must be found, the timing of spawning and emergence must be correct to allow for survival of the juvenile fish, and the juvenile salmon must survive the harsh marine environment and return as adults. Future work using genetic analyses to more clearly identify origin of Pacific salmon harvested, similar to mixed-stock fishery analyses (e.g., Beacham et al. 2009b, Flannery et al. 2010), would provide information on the origin and source populations of salmon in the Canadian Arctic. Verifying successful spawning in the Arctic is necessary to identify potential sources for vagrants and the habitat conditions necessary for successful spawning and egg incubation for salmon at the northern extent of their range. Clearly, Pacific salmon provide an opportunity to monitor significant changes to the Arctic perhaps as a result of climate warming, and may be indicating pathways used by other similar opportunistic marine species. The challenges of researching such rare and colonizing species are matched by the opportunities they present.

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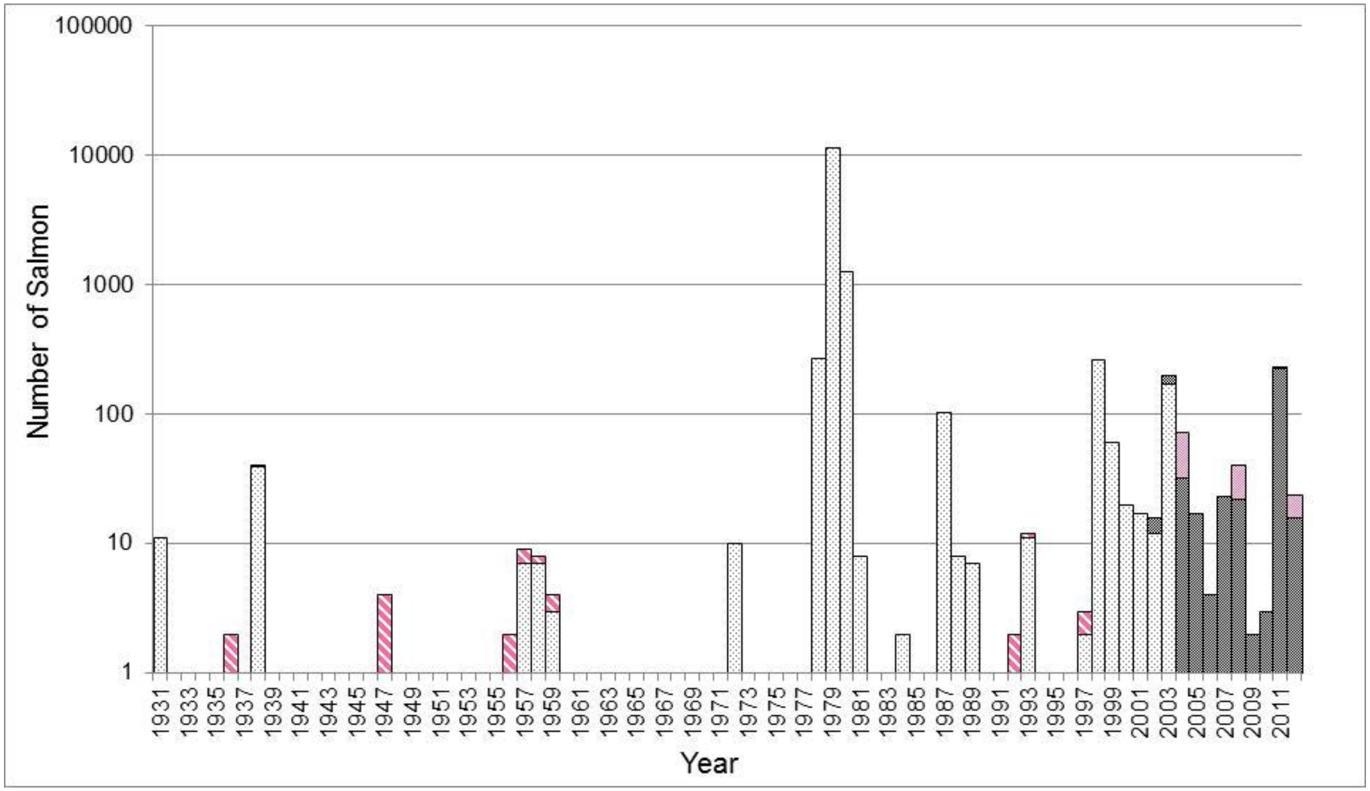

Figure 2.1:Data prior to 2003 were compiled by Stephenson (2006) from the literature and Fisheries and Oceans Canada (DFO) catch records (chum salmon = white bars; pink salmon = pink striped bars); those from 2004 and onwards (inclusive) are from the Pacific Salmon Collection Program (PSCP) (chum salmon = cross-hatch bars, pink salmon = pink cross-hatch bars), conducted by DFO. In 2002 and 2003, the reported chum salmon harvest obtained from the PSCP is indicated separately from the harvest reported by other methods included in Stephenson (2006). No salmon were obtained from the PSCP in 2000 and 2001.

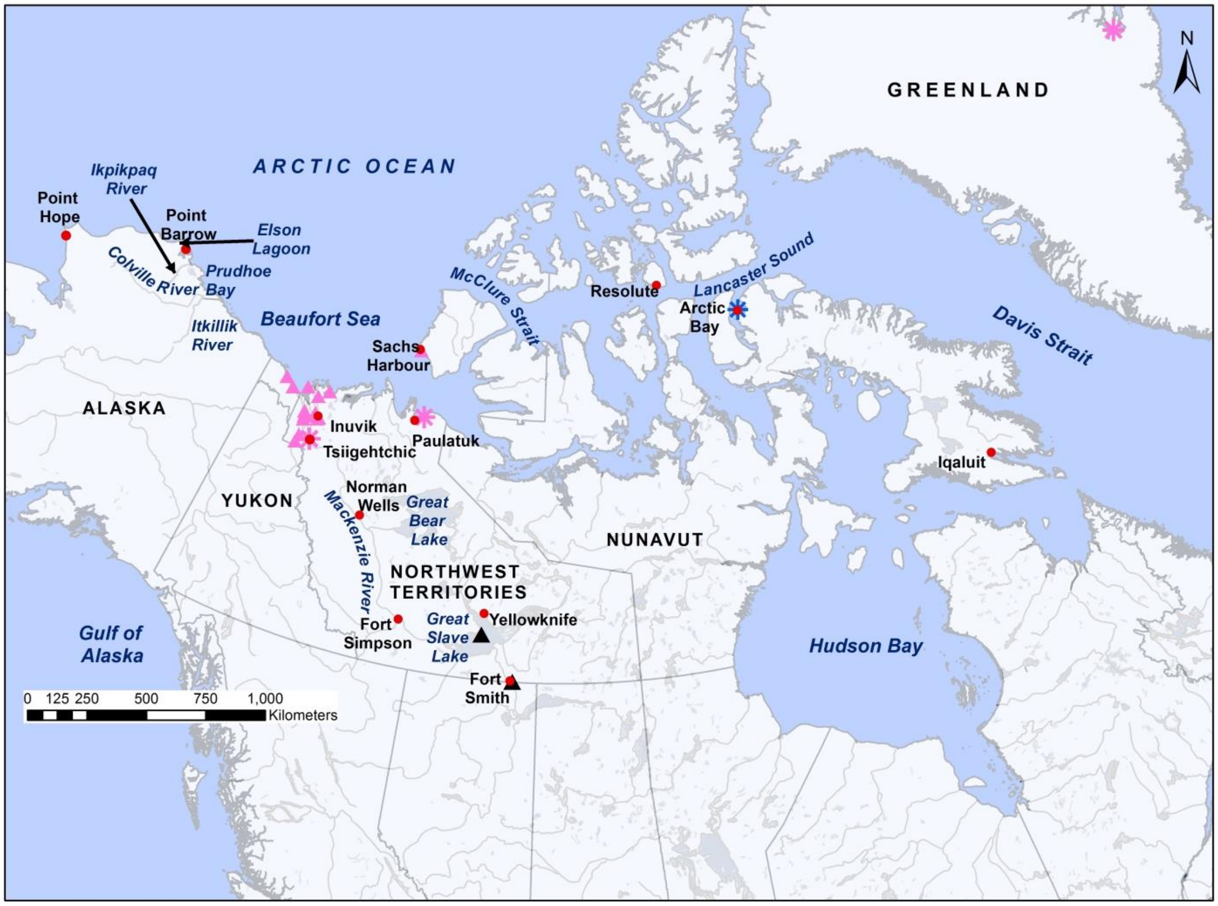

Figure 2.2: Overview of the Arctic showing the place names included in the text and the harvest locations of Pacific salmon species that have expanded their distribution since 2003. Historic pink salmon harvest locations (pink triangles) are shown and each symbol may represent the capture of more than one fish over several years. New capture sites (pink stars near Tsiigehtchic and Paulatuk, Northwest Territories, and east Greenland) for pink salmon are also included. Kokanee salmon harvest is represented by black triangles. The "unusual fish" (blue star) were harvested at Arctic Bay, Nunavut in 2011 and 2012.

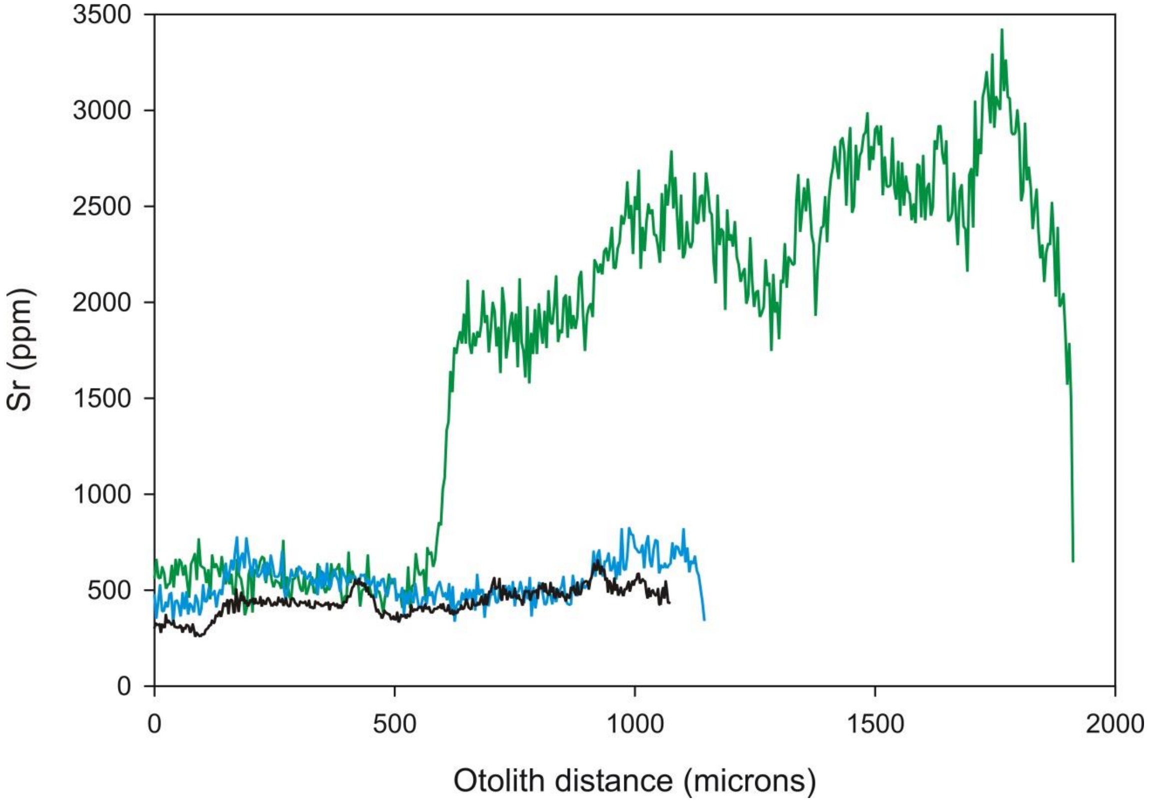

Figure 2.3: Strontium distributions from line-scans of otoliths from a sockeye salmon captured at Sachs Harbour, Northwest Territories, in late August, 1993 (green line, scanning proton micro-probe analysis), a kokanee captured in Great Slave Lake, Northwest Territories, on August 11, 1991 (blue line, scanning proton micro-probe analysis), and a kokanee captured in the Slave River at Fort Smith, Northwest Territories, on October 5, 2005 (black line, LA-ICP-MS analysis).

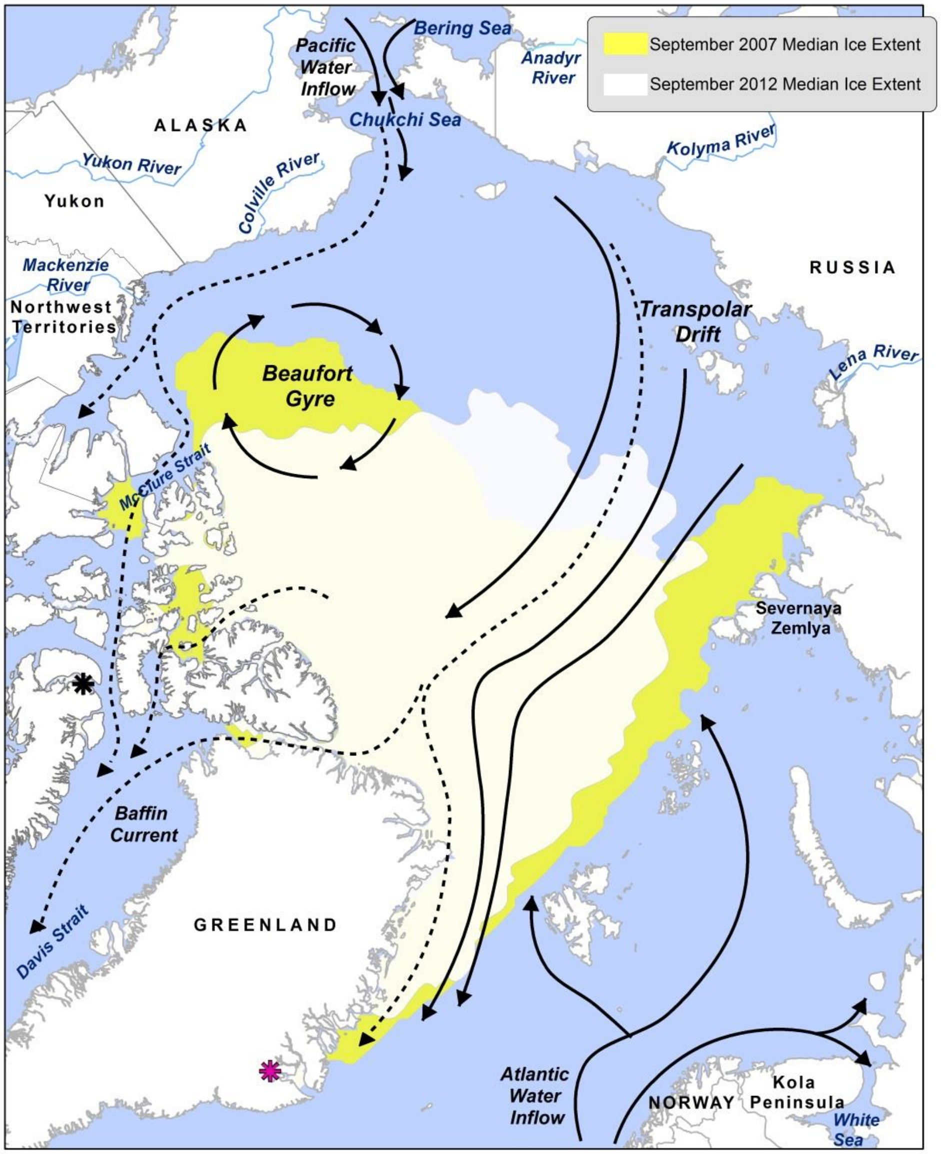

Figure 2.4: Schematic of the Pacific upper-water current and Atlantic deep water current inflows in the Arctic Ocean, and the median sea ice extent in September 2007 and 2012. The solid lines depict ice drift and surface currents, while the dotted lines are pathways for Pacific origin waters within and exiting the Arctic Ocean. The harvest location of the pink salmon on the east coast of Greenland (pink star) and the “unusual fish” at Arctic Bay, Nunavut (black star), are shown.

Figure 2.5: Photograph of the pink salmon captured on the east coast of Greenland on August 24, 2012. Photo credit: Mads Peter Heide-Jørgensen

Chapter 3 - A framework for citizen science applications in the Arctic

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Contributions of authors: Under the oversight of J. Reist, I developed the model, and wrote and submitted initial and final drafts of the manuscript. J. Reist reviewed drafts of the manuscript.

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Abstract

Assessing biodiversity in a rapidly changing Arctic is a key challenge inherent to international initiatives focused on conserving biodiversity. Integrating local knowledge with scientific research would facilitate these assessments; however, this integration is rare in the Arctic. Applying citizen science as a community-based monitoring tool may effectively bridge indigenous and scientific knowledge due to the commonality of using specific and easily documented indicators to assess environmental change in both knowledge systems. Here we have developed a novel framework to effectively apply citizen science in the Canadian Arctic, and then assessed the framework using Arctic Salmon, which is a current example of a citizen science project using occurrences and distributional shifts of Pacific salmon to monitor environmental change in the Canadian Arctic. While the overarching citizen science framework remains similar to other applications, the fundamental differences unique to bridging indigenous and scientific knowledges stem from the addition of a mutual reporting step during data collection, and from constant communication and input between both knowledge systems. The mutual sharing of individual observations among participants is critical to the development of a communication network which increases the value in reporting observations. This may lead to increased participation and also allows an on-going evaluation of the data collection processes. While broadly appealing as a tool to assess environmental change, citizen science must be carefully applied to ensure the collaborative production and integration of knowledge, which will provide critical information necessary to predict impacts and opportunities associated with biodiversity shifts in the Arctic.

Keywords: citizen science, co-management, climate change, environmental monitoring, indigenous knowledge, scientific knowledge

Introduction

Biodiversity in the Arctic is changing. Assessing these changes, however, is challenging because of the lack of basic information about species and their habitats (Reist et al. 2006b), and the inherent harsh, cold, dynamic, and often inaccessible environment. Arctic biodiversity is irrevocably linked to the culture of Indigenous peoples in the north and their perceptions of change are rooted in their dependence on the environment and social values to protect subsistence opportunities (Meltofte 2013). Indeed, the dearth of scientific information about species and their habitats in the Arctic is contrasted with the breadth of local and traditional knowledge about the environment. Integrating this local knowledge with scientific research in the north, however, is rare. While there are many examples of effective community-based monitoring in the Arctic (e.g., Berkes et al. 2007; Tremblay et al. 2008; Brook et al. 2009; Gofman 2010) and employing community members as research assistants is also common, these efforts do not necessarily translate to effective collaboration or inclusion of local knowledge (Armitage et al. 2011). The challenge facing scientists and Indigenous peoples alike is the difficulty in protecting biodiversity in a rapidly changing Arctic. Innovatively creating the opportunity to collaboratively produce and integrate indigenous knowledge and scientific research provides a powerful approach to assess these changes, and provides critical information necessary to predict impacts and opportunities associated with biodiversity shifts in the Arctic.

Citizen science is a growing form of community-based monitoring (Gofman 2010; Newman et al. 2012) that, by definition, integrates local knowledge and observations into scientific research. Although the concept of citizen science is not new, it has been facilitated by relatively recent technological advances including websites, smartphone apps and social networking, which have increased the rate of information transfer, broadened the geographic scale of coordinated data collections, and engaged interested citizens that may otherwise not have been involved (Dickinson et al. 2012; Newman et al. 2012). Citizen science seems ideally suited to applications in the Arctic because it fosters active partnerships between scientists and non-scientists (Bonney et al. 2009) and links institutions and user groups across jurisdictional levels and communities across geographic space using networks (Whitelaw et al. 2003; Dickinson et al. 2012). From a researcher perspective, the benefits of citizen science include the ability to document ecological changes occurring at a rapid rate across a vast geographic area including remote locations at potentially lower cost (Gofman 2010; Dickinson et al. 2012). From a management perspective, citizen science provides the opportunity for mutual information sharing and collaboration among decision-makers in the co-management process. From a community perspective, however, motivation to participate in citizen science projects may be low due to lack of knowledge about the project and interest in other opportunities (Gofman 2010) or conflicts with other subsistence activities. Participation may also fail due to a perception of low value and relevance, perhaps due to a lack of connection to the project and a lack of trust (Pandya 2012). In the Arctic, citizen science projects appear to be less common compared to methods primarily targeting social (i.e., hosting meetings, completing population surveys) or ecological systems (i.e., participatory research, recording observations) (Huntington et al. 2011). If applied collaboratively and under a common priority, however, citizen science projects can facilitate the integration of knowledge in the co-management process.

The commonality of using specific and easily documented indicators to assess environmental change in both indigenous and scientific knowledge systems provides the foundation for citizen science in the Canadian Arctic. The contemporary knowledge obtained by monitoring the environment through indicators can be translated to developing baseline data and quantitatively monitoring ecological changes at both fine- and broad-spatial scales. Although the broad suite of indicators usually gathered by indigenous knowledge is often different than the specific indicators used in scientific research, both of these monitoring methods can highlight similar ecosystem-level changes (Riedlinger and Berkes 2001; Berkes et al. 2007; Tremblay et al. 2008). Thus, focusing observations on specific indicators and employing protocols to transition these data into information is critical to a novel approach using citizen science to better inform the co-management process. The objectives here are to: 1) develop a novel model framework using citizen science to bridge indigenous and scientific knowledge systems related to monitoring environmental change; and 2) evaluate this model using a current citizen science project, called Arctic Salmon, which quantitatively monitors rare, perhaps colonizing salmon species across a vast and remote geographic area (Dunmall et al. 2013). In this manner, citizen science is developed as a tool to integrate information from social and ecological systems. The approach is assessed by its success in engaging northern community members in monitoring opportunistic northward colonizing species, a timely issue that is critical to effectively managing risks and opportunities in a changing Arctic.

Methods

An approach to facilitate knowledge co-production related to monitoring environmental change using citizen science was developed by applying the general framework for engaging diverse communities in citizen science projects (Pandya 2012) to a general integrative model for citizen science project development (Bonney et al. 2009). The resulting model depicts a constant flow of information between scientific and indigenous knowledge systems. This progression also highlights how different approaches within the these knowledge systems can contribute equally at each step, formalizes on-going evaluations at each step, and emphasizes that the adaptive process of developing citizen science as a tool to monitor environmental change is itself a goal (i.e., Carlsson and Berkes 2005).

The approach was then applied to a current citizen science example, a project called Arctic Salmon (Dunmall et al. 2013), to understand its success at monitoring environmental change across a remote geographic area, and ultimately discern how citizen science can effectively contribute to co-management in the Arctic. As the model is rooted in effective communication, it was evaluated to assess yearly scope using metrics of reach and engagement from both scientific and Indigenous stakeholders using insights data from the Arctic Salmon Facebook page (www.facebook.com/arcticsalmon). These metrics included the number (#) of likes, the average reach of the page each September from 2015-2017, and the average # of people that engaged in the page each September from 2015-2017. Page reach is defined as the # of unique users who have seen any content associated with the Page, and page engagement is the # of unique users who have interacted with (e.g., liked, commented on, and shared) a post. The month of September was chosen to compare among years because it is the peak of the annual salmon migration and therefore is representative of the most consistent effort on outreach and engagement related to the citizen science project. The model was also evaluated using the # of requests received annually from scientific and indigenous groups for outreach related to Arctic Salmon (e.g., posters and presentations), and requests received from scientific or Indigenous groups for collaborations to develop new projects related to salmon in the Canadian Arctic.

Results and Discussion

Citizen science spans indigenous and scientific knowledge systems to facilitate knowledge co-production and effectively monitor environmental change as a common priority in the Canadian Arctic (Figure 3.1). Applying the general model for citizen science (Bonney et al. 2009) to derive information from multiple knowledge systems (i.e., Indigenous and scientific knowledge) requires input from each knowledge system at each step. Modelling this input visually as information flowing from each knowledge system to each step in the citizen science approach, and then back to each knowledge system before proceeding to the next step emphasizes the integration of information, and thus allows for knowledge co-production. The derivation of information within each knowledge system may differ; however, the integration of this information at each step within the process allows for continual communication and evaluation. This fosters collaborative processes, which are integral to delivery of citizen science in the Canadian Arctic.

As developing citizen science as a tool to monitor environmental change in the Arctic is itself a goal (Carlsson and Berkes 2005), the steps involved are a product of the adaptive process. Therefore, the steps are a result of applying the general framework for engaging diverse communities in citizen science projects (Pandya 2012) to a general integrative model for citizen science project development (Bonney et al. 2009). Together, this resulted in the development of a citizen science model for the Canadian Arctic. Each step in the model is described in the following.

Define indicator:

Indicators of environmental change critically provide the commonality between indigenous and scientific knowledge systems. Although aligning the indigenous and scientific knowledge systems to a specific indicator may seem challenging, the holistic approach of indigenous knowledge parallels the ecosystem-level approach to science. Ideal indicators monitor the cumulative impacts of change (Holt and Miller 2011), which are applicable to both knowledge systems. As the data collection in citizen science projects is done primarily by non-scientists, an appropriate indicator identified from indigenous knowledge that reflects the cumulative impacts of change on the environment as a whole, and has a clear correlate in the scientific knowledge system, would be highly-valued by both knowledge systems and would effectively engage those collecting the information. Community ‘buy-in’ regarding citizen science projects can be challenging, especially in under-represented groups (Pandya 2012); however, appropriately defining and agreeing to a particular indicator using input from both knowledge systems provides an opportunity to increase interest in the project and motivation to collect the information. Also, choosing an indicator that can be observed as part of regular activities, such as during subsistence harvest efforts, while at traditional camps, or during regular travel among communities, may enhance participation because the connection to the individual observer is tangible, little extra effort is required to document observations, and participation can be done with minimally added tools. Unifying the indicator makes the value of observations and resultant information apparent to those involved in both knowledge systems.

Record:

Although the qualitative and semi-quantitative (i.e., relative change) focus of indigenous knowledge differs from the quantitative nature of scientific knowledge during data collection, recording the information in a standardized manner delineates common approaches and identifies common language critical to accurate recording. Data collection protocols, which often include simple but standardized data forms, ensure that the information identified as important by both knowledge systems is collected in a manner that is transferrable and repeatable so that it can be collected over a long timeframe and wide geographic space. Thus, protocols effectively connect each observation, and, by doing so, elevate personal perspectives to aggregated trends (Huntington et al. 2004). Training of participatory citizens may be appropriate to consistently allow for the linkage of observations into data and then information, and training approaches would benefit from input from each knowledge system regarding the appropriate method and implementation. Training may be passive and simply involve a set of stepwise instructions, or active training may be required, including in-person or virtual training sessions, depending on need and the intricacy of the observations or data being recorded. The development and use of specific training tools may also facilitate the recording process by standardizing the information and focusing observations on the defined indicator. These training tools may include species identification guides, which are maximally beneficial in this context when wording is minimized and specific key features that quickly and easily allow differentiation among species are highlighted using full-color, accurate illustrations of phenotypes present in the area of interest (e.g., Fisheries and Oceans Canada 2015). Creating these guides so they are easily portable by using laminated cards or printing on water resistant paper increases use by helping to ensure they are available as the observation is recorded.

Report:

This step critically creates an opportunity for communication between knowledge systems during data collection and before analyses and evaluation. As effective communication is essential but methods to communicate differ between knowledge systems, this novel step adds an opportunity to integrate observations and information and evaluate the process as data are being collected. Technology facilitates engaging non-scientists and scientists at this step. The constant accessibility via cell phones combined with the widening cellular network and associated widespread presence of cell-phone cameras create the opportunity for immediate information transfer between citizens and scientists. Moreover, employing social media as a communication tool expands this opportunity for information transfer to others who are virtually connected through a common interest. This creates a sense of community, which reinforces participation, and contributes to a positive feedback loop of non-scientists providing information that engages other non-scientists in observations and data collections. This loop may be virtual, without geographic boundaries, or may develop within a community through in-person communications. Similarly, scientists may engage in the reporting of information as it is derived in citizen science projects by assembling information and distributing it using visual references such as photos or maps, which can begin or enhance this positive feedback loop to further engage non-scientists to collect data. Rather than formalizing the information into structured scientific reports, this integrated reporting step allows mutual information transfer to foster further data collections and community support within the citizen science project.

Analyze:

Each knowledge system analyzes the data derived from citizen science projects using a different emphasis, which together contribute to a more informed product. Indigenous knowledge systems contribute a historic perspective, which is invaluable when assessing the magnitude of observed contemporary changes. Scientific knowledge systems may be integrating the information as part of a risk assessment, which has a predictive component and thus futuristic perspective. Providing the opportunity to share these analyses using terms that are mutually understood contributes to knowledge co-production.

Evaluate:

Interpretation and communication of the data derived by citizen science projects are combined into an evaluation step by each knowledge system. As interpretation adds meaning to the data, this step will differ within each knowledge system because meaning is derived from experience within indigenous knowing and from connecting cause-and-effect relationships within scientific knowledge. Interpretation of the data using perspectives from both knowledge systems therefore adds to knowledge co-production and a more complete product. Evaluation of the indicator can also occur after analysis to assess, for each knowledge system, whether the indicator was appropriate for monitoring the intended aspects of change (e.g., the cumulative impacts of environmental change in the example below), if it contributed to the hypotheses and objectives derived from the scientific knowledge system, and if it adequately represented the traditional or cultural values within the indigenous knowledge system.

A case study: Arctic Salmon

Given the vast geographic area of the Arctic, the rapid rate of ecological changes that are occurring, high costs of comprehensive monitoring therein, the associated need for long-term monitoring across this wide geographic space, and the co-management networks inherent to the north, citizen science monitoring projects have merit in addressing key data deficiencies in a dynamic Arctic ecosystem.

The occurrences and variations in local abundances of various species of Pacific salmon in the Canadian Arctic were identified as indicators of the cumulative impacts of environmental changes through indigenous knowledge, and also as an ecosystem-level indicator of environmental change by scientists. Subsistence harvesters were reporting increased harvests of Pacific salmon *Oncorhynchus* spp. and there was local interest in determining why this was occurring, and if there could be impacts to native fishes like char *Salvelinus* spp. Thus, critically, the indicator was identified through communication between indigenous and scientific knowledge holders, and there was interest from both non-scientists and scientists in monitoring occurrences of Pacific salmon as an indicator of environmental change. The utility of Pacific salmon as an indicator was assessed by having traditional knowledge of historical harvest available, which assisted in identifying trends, and also by having local knowledge of consistent but low level harvests of Pacific salmon, which ensured the harvest remains relatively novel but frequent enough to allow assessments of change (Holt and Miller 2011), and thus harvests were a useful parameter to monitor.

Data were collected through the organized sharing of information using a standardized data form and a network of agencies and interested individuals across the Canadian Arctic. The data form was kept minimal; it only contained the critical information necessary to place a single observation into the broader ecological context (Figure 3.2). A mixture of quantitative and qualitative questions allowed information to be gained from both knowledge systems, and suggested categories for qualitative answers assisted in transferring qualitative information into quantitative trends. A species identification guide was developed using illustrations that highlighted key morphological differences among species, was printed on water resistant paper to increase the potential for use during subsistence activities, and included the data form to facilitate immediate information transfer (Supplementary Appendix A, Fisheries and Oceans Canada 2015). Prior to the start of the fishing season, sampling kits were distributed to the network of agencies and community organizations that agreed to accept salmon from community harvesters. These sampling kits included a letter with a brief summary of the project and instructions for filling out the data forms, storing the salmon frozen, and contact information to arrange shipments of salmon to the project office at Fisheries and Oceans Canada, Freshwater Institute, at the end of the fishing season. The sampling kits also contained data forms, string, fish bags, rewards and a form to track salmon handed in through the program. In this manner, the network extended from the individual harvester through the co-management framework and was inclusive to all interested organizations, agencies and individuals. In addition, the distribution of rewards at the community-level increased participation due to the increased convenience of reporting, the immediate receipt of the reward, and the shift to a more community-focused project through increased buy-in, local advertising and greater acceptance.

Critically, the process of conducting citizen science in the Canadian Arctic highlighted that the value of data differs between non-scientists and scientists. While monetary incentives were offered to non-scientists to increase value in providing single observations (i.e., during the recording step), unsolicited value was fostered by communicating the connection of single observation to other similar data (i.e., from feedback during the reporting step). Conversely, scientists emphasized the record step because acquiring standardized data is often challenging. However, shifting the focus to increased reporting indirectly led to increased recording.

Communication and outreach was vital to the success of the Arctic Salmon project. Providing information about recorded data regularly allowed continual evaluation of the data collection process. This reporting also provided the opportunity to informally share information to foster interest, which appeared to lead to increased reporting of similar observations, and thus increased participation in the process. Media interactions were used as a tool to facilitate communication to a targeted northern audience to facilitate this communication of information about in-season salmon returns. Interest in the project by non-scientists, which was used as a proxy for potential participation, was evaluated by the number of unsolicited requests for information sharing received to the Arctic Salmon project from media outlets (e.g., newspaper, radio, online articles) and community groups, which increased from three in 2015 to 19 in 2017 (Figure 3.3). Interest in the project by scientists was evaluated by tallying both the number of unsolicited requests received yearly for outreach in the form of presentations at scientific conferences, which increased from zero in 2015 to five in 2017, and the number of unsolicited requests for collaborations for new projects, which increased from zero in 2015 to five in 2017.

Networking tools, including online social networking (www.facebook.com/arcticsalmon), were developed to facilitate information sharing, which provided greater involvement in the citizen science process, and led to contextual or historical information shared by Indigenous or local knowledge holders. Facebook page interactions (e.g., page likes or followers) were used as a gauge of interest in the Arctic Salmon project, and rose by approximately 150 people per year to 856 total "likes" and 869 total "followers" by October 21, 2017 (Figure 3.3). The sharing of information by scientists to non-scientists was also important during data recording; however, the type of information shared by scientists at this step mattered. The most effective reporting during data recording, based on resulting interactions with non-scientists, was the distribution of single observations, without interpretation, to a broader audience. By replacing words with maps, photos, and video, this information was quickly understood, and deemed relevant by the recipients. Facebook page engagements (e.g., comments, reactions, and shares) and page reach (the total number of unique users who have seen any content associated with the page) during each September from 2015-2017 were used to assess the effectiveness of reporting during data recording and participation in the citizen science project. Page engagements increased from 82 people during September 2015 to 1013 people during September 2017, and organic (i.e., unpaid) page reach increased from 751 people in September 2015 to 9,192 people in September 2017 (Figure 3.3). Therefore the reach of the page extends far beyond the number of people that "like" it, making Facebook a powerful communications tool.

Virtual video calling applications (i.e., FaceTime) were also used to increase personal connections to the project, and as a training tool that allowed interactive visual demonstrations and information sharing among Indigenous and scientific knowledge holders. Also, by associating the citizen science project with a consistent brand name (i.e., Arctic Salmon) and logo (Figure 3.4), the project and resulting information were easily recognizable. Consistency in reporting using this brand name created a sense of trust and community regarding the project. By fostering this information-sharing loop during data collections, scientists benefited from the opportunity to assess the on-going data collection process and non-scientists gained a sense of inclusion by meaningfully participating in the process and directly seeing the results of their collection efforts. These benefits were independent of the means used to initially enhance participation (i.e., monetary rewards for samples).

By including indigenous and scientific information in data analyses, the associated contextual depth expanded and the resulting information can be effectively applied by all decision-makers. Reporting after data analyses was important, and information transfer between knowledge systems was most effective when done orally and in-person using common terms and visual aids to depict the historical context, the current situation, and the predictive trends. Reporting the progression of data analyses from the single observations to the broader understanding highlighted the integration of indigenous and scientific knowledge, and emphasized knowledge co-production. This reporting and communication can also lead to an evaluation of the process, the outcomes, and ultimately the indicator itself to ensure that the goals from each knowledge system were achieved, and to make the process more effective for future monitoring efforts.

Conclusions

A directed and inclusive approach to citizen science provides a novel model to implement community-based monitoring using existing collaborative networks, and is an effective tool at bridging indigenous and scientific knowledge systems under a co-management framework. Using protocols that collect both quantitative and qualitative information, this approach develops local observations into data to examine scientific hypotheses and address indigenous questions, while facilitating an adaptive process through constant reciprocal reporting and evaluation. This approach goes beyond aligning scientists and non-scientists on a common priority (Pandya 2012) by also unifying indigenous and scientific knowledge systems around a common easily tracked indicator to monitor environmental change. Including additional reciprocal reporting during data collections adds an innovative step to increase inclusion, participation, and develop a sense of community regarding the monitoring project. Similarly, linking each step in the approach back to the specific knowledge system is a unique process to develop networking pathways that facilitate information transfer and collaborations, which leads to increased participation in a positive feedback loop. Reinforcing the value of information from both indigenous and scientific knowledge throughout the process using these networks can lead to knowledge co-production and ultimately more informed decisions under a co-management framework.

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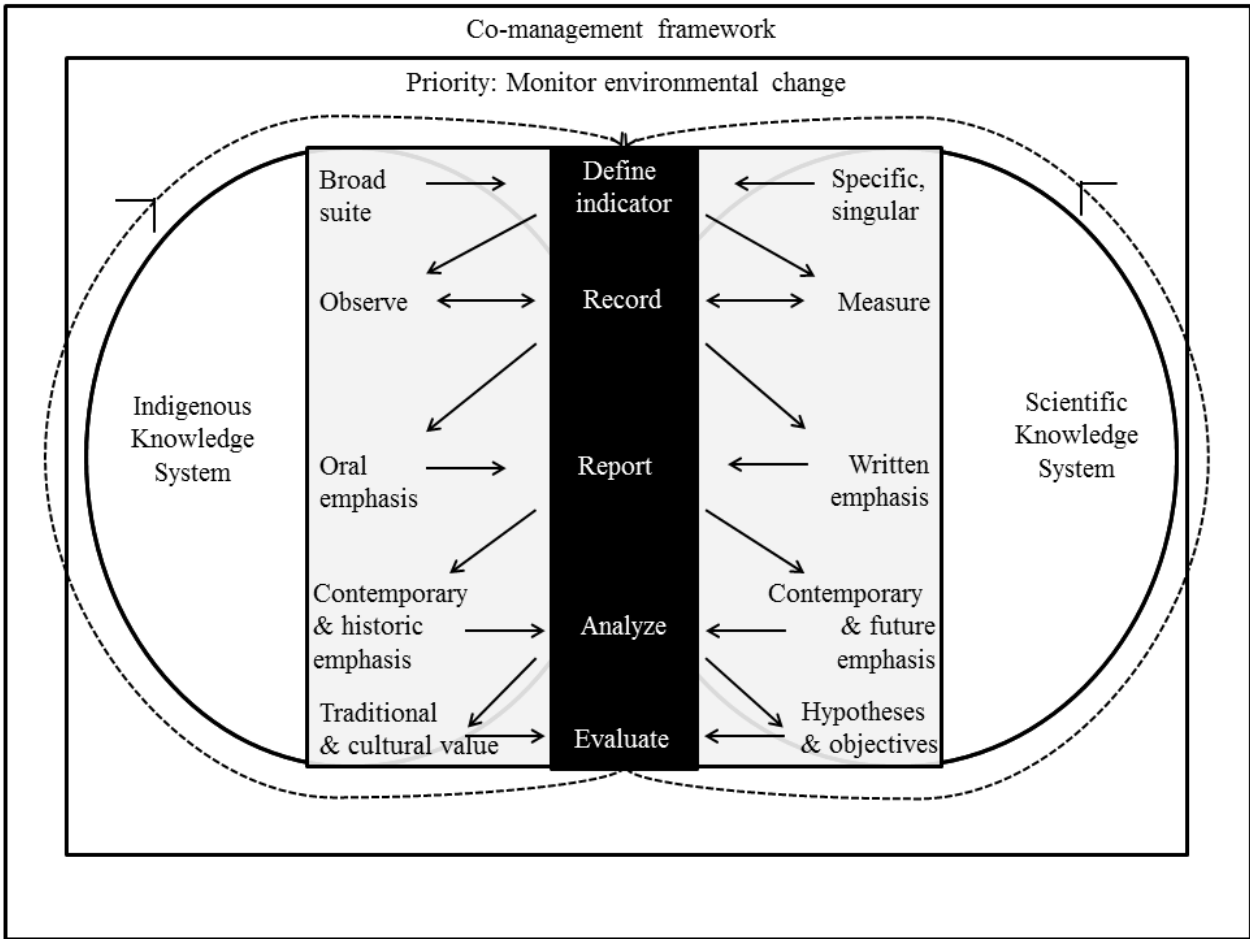

Figure 3.1: A model for citizen science to monitor a changing Canadian Arctic. Under a common priority of monitoring environmental change, citizen science (grey square) can bridge Indigenous and scientific knowledge systems (white circles). The arrows depict the contributory flow of information from the general citizen science framework (black box) out to each knowledge system and back to the framework at each step in the process, which equalizes the value of information derived from indigenous knowing and scientific knowledge and contributes to knowledge co-production.

What kind of salmon? (circle one)
Chum / Pink / Coho / Chinook / Sockeye / Atlantic / unknown
Date Caught (dd/mm/yyyy): ______________________________
Location Caught (be specific): ____________________________
Nearest Community: ____________________________________
Gillnet mesh size: ______________________________________
How many hours was the net set? _________________________
If you squeeze gently, does eggs/milt come out? Y or N
How many other fish (all species) were also in the net? _______
(please turn over)

Have you caught salmon before? Y or N
How many salmon do you catch / season? _________________
Has that increased, decreased or remained the same over time?
Have you seen salmon spawning? ________________________
Where? ____
Name & address: _______________________________________
Email or phone: ____
Would you like more information about this project? Y or N
Gift card received? Y or N
(please turn over)

Figure 3.2: The data collection form used by the Arctic Salmon citizen science project. The combination of qualitative and quantitative information links local and scientific knowledge and the categorical responses allow information to be compared across geographic areas.

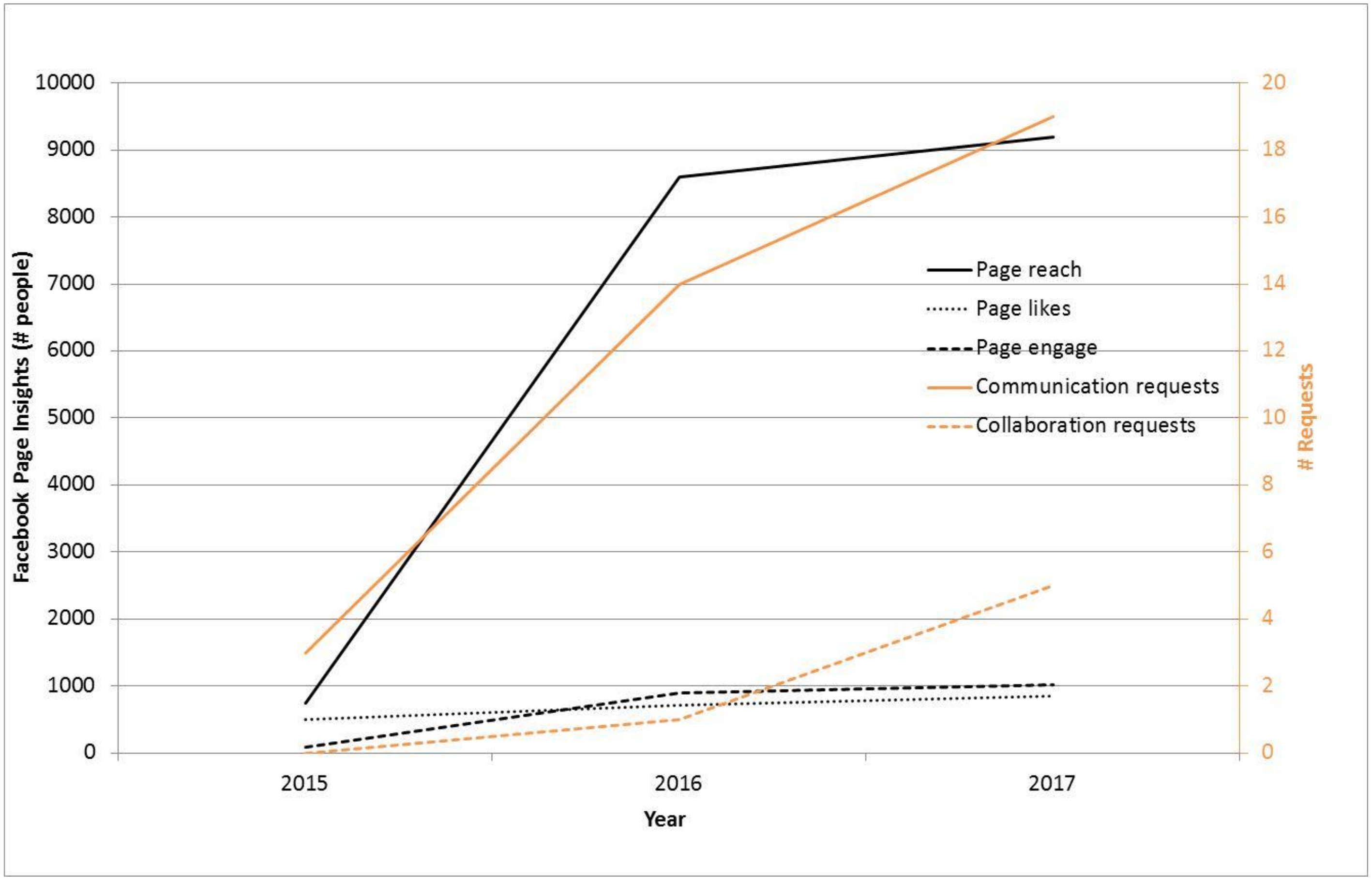

Figure 3.3: The effectiveness of the communication and outreach by the Arctic Salmon citizen science project was evaluated using the Arctic Salmon Facebook page (www.facebook.com/arcticsalmon) metrics of engagement (e.g., likes, reactions, shares, and comments) and interaction (e.g., the number of unique users who saw the page, termed reach), during each September 2015-2017, as well as the annual number of unsolicited requests for outreach (i.e., communication requests) and collaborations (i.e., collaboration requests).

Figure 3.4: The Arctic Salmon logo is used on all reporting outputs to increase rapid public recognition and connection to the citizen science project.

Chapter 4 - Monitoring water temperature to assess fish habitat in high elevation and high latitude streams

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Contributions of Authors:

Under the oversight of J. Reist and with guidance from N. Mochnacz, I identified monitoring locations in essential fish habitats. T. Kroeker and I designed the probes, and N. Mochnacz and I installed the probes. I analyzed the data and wrote the initial and final drafts of the manuscript. All co-authors commented on earlier drafts of the manuscript.

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Abstract

Warming temperatures have added urgency to characterizing the thermalscapes and thermal tolerances of cold-adapted fishes in order to effectively manage and conserve such species. This is especially relevant at high latitude and high elevation streams, which are experiencing rapid environmental changes, yet are data-poor, remote, and difficult to access. I have developed a reliable method to assess temporal and spatial variation in water temperatures that can be effectively deployed to remain year-round in remote dynamic streams, and incorporated into community-based monitoring programs. By using this method to compare Dolly Varden *Salvelinus malma* spawning sites in a Yukon North Slope river, I demonstrate inter-annual variation in the viability of spawning habitat within a spawning location, and spatial variation in temperatures and developmental rates within a spawning location and among spawning sites within a river. Characterizing and quantifying the amount of viable thermal habitat for cold-adapted species improves predictions of how warming may affect high latitude and high elevation stream ecosystems. This information can then be used by managers to identify the thermal refugia that are essential for conservation of native species, and assess risks associated with distributional shifts by native and potentially colonizing species.

Introduction

Stream fishes are strongly influenced by their thermal environment due to the critical linkages between environmental temperatures and physiological processes (Pörtner and Farrell 2008). Predicting the vulnerability and response of stream fishes to warming temperatures therefore requires an understanding of the thermalscapes, or thermal regimes of essential habitats, and the thermal tolerances of these fish at key life-stages (Isaak et al. 2015; Dunmall et al. 2016). Cold-adapted fishes, like salmon and char, may be particularly vulnerable to warming temperatures because they occupy high elevations and high latitudes (Isaak et al. 2015). These systems also often have low water flows, which translates to low resiliency to changes in temperature and therefore these changes are transferred to the biota. In these extreme environments, these fish rely on thermal refugia created by perennial groundwater springs to survive warmer summer and harsh winter conditions (Power et al. 1999). At a finer-scale, site selection by these substrate-spawning salmonids is also influenced by temperature, as well as dissolved oxygen and conductivity, which can vary greatly at small spatial scales (Baxter and Hauer 2000; Geist et al. 2002) and sites may also differ between surface conditions and interstitial habitats (Zimmerman and Finn 2012). Therefore, identifying these refugia and monitoring their key environmental parameters is essential to determine the availability of critical habitat for cold-tolerant fish in extreme environments, and can also be used to predict potential distributional shifts for native fishes, as well as opportunistic colonizing species (Isaak et al. 2015; Dunmall et al. 2016).

Monitoring environmental parameters to assess fish habitat is common; however, many approaches may not be applicable to extreme environments. Typically, water temperature can be predicted from air temperatures (Meisner et al. 1988), or can be monitored using data logging devices that are either adhered to boulders to assess stream temperatures (Isaak et al. 2013) or buried in the substrate to assess hyporheic temperatures (Zimmerman and Finn 2012). Within-site variation can be significant along latitudinal and elevation gradients (Graae 2012; Snyder et al. 2015), however, making it difficult to broadly predict conditions. Also, the inherent dynamic nature of these streams, including the potentially catastrophic seasonal break-up of river ice (Power 2002), poses challenges unique to year-round monitoring in extreme environments and may impact retention or recovery of monitoring devices. Here I describe a reliable method to continuously monitor hyporheic and instream temperatures in dynamic remote streams and demonstrate its utility by comparing temperature data collected from Dolly Varden *Salvelinus malma* spawning locations along the Yukon North Slope. Importantly, this method can also be applied as part of a community-based monitoring approach to allow consistent and relatively low-cost monitoring in remote areas that are currently data-poor but are critical to predicting ecosystem-level responses to continued warming trends.

Methods

Design, installation and removal of probe

The overall design consists of a steel probe with a threaded steel cap at the top and a pointed end at the bottom with holes drilled in the sides at the bottom to allow water to continuously flow through the pipe at a particular depth (Figure 4.1). The 5 cm diameter pipe was welded to a section of 2.5 cm diameter pipe, which was threaded onto steel machine-pointed tips. Triangle “wings” (5 cm x 11 cm) were welded onto the pipe to prevent it from spinning in the substrate when the threaded cap was removed upon data retrieval. A series of 36 holes, 3 mm in diameter, were drilled into the pipe along the lower portion to allow water flow but maintain structural integrity and prevent gravel from filling the pipe upon installation. A 4.76 mm hole was drilled into the center of the threaded steel cap, and a 45 cm piece of 3.18 mm diameter plastic coated aircraft cable was threaded through the hole. Three aluminum sleeves were threaded onto the cable, two under the cap, and one over the cap. Calibrated temperature loggers (HOBO U22, Onset Computer Corporation, Massachusetts, USA) were attached to either end of the cable using aluminum sleeves so that the logger inside the pipe would hang at the level of the holes. The extra sleeve was crimped just under the cap so that the temperature logger installed in the pipe could not be pulled above the top row of drilled holes, and sufficient excess cable was provided outside the cap so the logger on top of the cap could be cable-tied to the pipe after installation. The excess cable was removed. These loggers were set to record water temperature at hourly intervals. This maximized data while conserving memory space and battery life so that the temperature loggers would continue to record hourly water temperatures for up to five years.

A post pounder was constructed to facilitate installation of the probes. The post pounder was made out of a 60 cm long section of 38.1 mm outer diameter steel pipe. One end of the pipe was threaded and a cap was screwed on and then welded to the upper end. Handles were constructed out of dual 20 cm long x 2.54 cm wide pieces of steel at 6.35 mm thickness that were moulded to fit around the pipe. These were welded together to the pipe approximately 18 cm below the top of the cap.

To install the probes, a 122 cm section of 31.75 mm diameter solid stock steel was placed in a capless probe. The post pounder slid over the exposed end of the solid stock and the probe was pounded into the substrate until the holes in the pipe were in the substrate at the depth of interest for monitoring. Approximately 5 to 10 cm of the probe should remain above the level of the substrate. Occasionally, a greater force was necessary to install the probe due to mixed cobble substrate. In these instances, the post pounder was left on the solid stock to protect the end of the solid stock from flaring, and a sledge hammer was used to pound in the probe by hitting it onto the top of the post pounder. Once installed at the desired depth, the solid stock was removed and air was blown into the probe to evacuate any sediments using a 1 m section of rubber tubing. The cap with the two temperature loggers attached was then hand-tightened onto the top of the probe and the temperature logger on top of the cap was cable-tied to the pipe so that it faced down-stream. This prevented the instream logger from being frozen into the ice, and also protected it during dynamic river break-ups. The location was recorded and a piece of flagging tape was placed in nearby vegetation on the river bank.

To retrieve the data, the approximate area of the temperature probes was located first using the known coordinates and a hand-held GPS (Garmin GPSMAP 64), and then using a metal detector (Schonstedt GA-72Cd Magnetic Locator) to pinpoint the exact location. This method allowed retrieval of data when water clarity or the presence of snow and ice prevented visual location of the exact location of the probe. Once the probe was located, the cap was removed and replaced with a new cap if need be. The temperature loggers were then downloaded using a waterproof shuttle (HOBO U-DTW-1, Onset Computer Corporations, Massachusetts, USA), relaunched, sediment was blown out of the pipe, and the instream logger was redeployed.

To remove the pipe once data is no longer needed from that particular location, a 121.92 cm Hi-lift All-Cast truck jack (Hi-Lift Jack Company, Bloomfield, USA) was placed in the stream next to the pipe. If needed, a section of wood was placed under the foot of the jack to stabilize it in the stream gravel. A 46 cm section of 7.94 mm chain fitted with a grab hook on one end was wrapped around the pipe below the cap and was hooked into a circle, which was looped over the jack runner. The pipe was then slowly jacked straight up and out of the substrate, similar to a post-pulling exercise.

Monitoring temperature in Dolly Varden spawning habitat

Using the above method, fine-scale differences in hyporheic and surface water temperatures were assessed within and among two Dolly Varden spawning sites on Fish Hole Creek, a tributary of the Babbage River, Yukon North Slope (YT, Figure 4.2). At the upper site, three probes were installed September 13, 2013 side-by-side, approximately 1.5 m apart, one mid-stream (68.6, -138.73425, Upper_1), one at the bank (68.6, -138.73439, Upper_3), and one in-between (68.6, -138.73428, Upper_2). The mid-stream and bank probes were installed at the immediate downstream edge of Dolly Varden spawning redds, whereas the probe in-between was installed where there was no redd at the time of installation. At the lower site, seven probes were installed on September 11, 2013 in a grid as a cross-type pattern, and all probes were installed at the immediate downstream edge of Dolly Varden spawning redds and were situated so that the probes were approximately 1.5 m apart. From the furthest downstream site (68.60019, -138.73523, Lower_1) to the furthest upstream site (68.60016, -138.73508, Lower_7) there were a total of five probes every 1.5 m. Of these, the second furthest upstream probe (68.60014, -138.73512, Lower_4) was the middle of the cross, with a probe approximately 1.5 m to the east (68.60011, -138.73515, Lower_6) and another probe approximately 1.5 m to the west (68.60017, -138.73520, Lower_5). All probes remained in place until they were removed using the described method on February 20, 2016. Data loggers simultaneously recorded surface and hyporheic water temperature at hourly intervals, which were summarized as mean estimates per calendar day (daily mean). The data loggers were downloaded at least once per year. Daily means were categorized into spawning (September 15 to October 15) or incubation (October 16 to March 1) timeframes to allow temperature comparisons among life-stage events, probes, sites, and years. The potential for development of eggs and alevins (i.e., with yolk sac still attached) was compared among sites using Accumulated Thermal Units (ATU), which is the cumulative daily water temperature in degrees Celsius (°C), from spawning to emergence. This was calculated separately for both hyporheic and surface temperatures at each probe.

Statistical analyses were conducted using R software and a maximum alpha significance level of 0.05 (R Core Team 2015). At each probe in both the upper and lower sites, the hyporheic and surface temperatures were compared using paired t-tests. As the hyporheic temperatures and surface temperatures were significantly different at most probes, these temperatures were subsequently analyzed separately for the incubation and spawning timeframes. For each location, daily mean surface and hyporheic temperatures for the spawning and incubation timeframes were compared using an ANOVA. As the water temperatures during spawning were significantly different from those during incubation at each location, these data were subsequently analyzed separately. Daily mean hyporheic and surface temperatures for each of the spawning and incubation timeframes among sites and years were compared using a two-way ANOVA and TukeyHSD multiple comparison tests were completed to assess significant main effects using a Bonferroni p value adjustment. To compare ATU values for both hyporheic and surface temperatures among years and sites, the ATU values on March 31 were treated as count data and were compared using a Chi-squared goodness of fit test, where the frequency distribution of ATU counts was assumed to be equal among all probes and for all ATU values. To assess significant main effects, one-way proportion tests with Yates continuity correction were used to determine whether the observed ATU value was equal to the expected ATU frequency distribution for each location.

Results

The described method successfully recorded year-round hyporheic and surface water temperatures over multiple years immediately adjacent to active Dolly Varden redds in a remote, dynamic high latitude stream. This allowed both broad- and fine-scale thermal characterization of Dolly Varden spawning habitat, a comparison of the thermal potential for developmental rates within and among aggregations of spawning redds, and an assessment of interannual variability in habitat viability in this area. During spawning, the hyporheic and surface water temperatures at each probe were significantly different among all probes at the lower site except at Lower_2 in 2013, Lower_3 and Lower_5 in 2014, and Lower_5, Lower_6 and Lower_7 in 2015 (Table 4.1). During spawning, the hyporheic and surface water temperatures were significantly different among all probes at the upper site except in 2013 and in 2014 at the mid-stream probe, and in 2014 and 2015 at the probe near the bank (Table 4.1). During incubation, these temperatures were significantly different at each probe at the upper site except in 2014 at the probe near the bank (Upper_3) and for all probes at the lower site except in 2014 at the second to the last probe downstream in the grid (Lower_2), and the probe at the eastern arm of the cross (Lower_6), and in 2013 at the probe in the middle of the cross (Lower_4) (Table 4.1). Due to these differences, surface and hyporheic temperatures were analyzed separately. During the spawning timeframe, surface and hyporheic water temperatures were not significantly different among locations; however, they were significantly warmer in 2013 than in 2014 and 2015 for both surface (ANOVA, F=105.08, df= (2, 834), $P<0.01$; Tukey, $P<0.01$), and hyporheic (ANOVA, F=111.89, df= (2, 894), $P<0.01$; Tukey, $P<0.01$) temperatures (Figure 4.3). During incubation, there was a significant interaction effect of location and year for both the surface (ANOVA, F=52.07, df= (16, 4141), $P<0.01$) and hyporheic (ANOVA, F=1.65, df= (16, 4453), $P=0.04$) temperatures. The surface temperatures in 2013 were significantly colder than in 2014 and 2015 (Tukey, $P<0.01$) and hyporheic temperatures in 2015 were significantly warmer than in 2014 and 2013 (Tukey, $P<0.01$, Figure 4.4). Comparing among locations within the incubation period revealed that the hyporheic temperatures at the upper site were generally significantly warmer than those at the lower site, except that the in-between upper site (Upper_2) was not significantly different from the upper most probe in the lower site (Lower_7, Figure 4.4). Within each site, however, there were few significant differences except that the probe at the bank in the upper site (Upper_3) recorded significantly colder temperatures than were recorded at all other locations for both surface (Tukey test, $P<0.01$) and hyporheic (Tukey tests, $P<0.01$) temperatures (Figure 4.4). The surface water temperatures were more variable; however, those at the mid-stream probe in the upper site (Upper_1) remained significantly warmer at the surface than did those at the two most downstream probes in the lower site (Lower_1, Lower_2), and the eastern most probe in the lower site (Tukey, $P <0.01$, Lower_6).

Despite these temperature differences within and among sites, years, life-stage event timeframes, and between surface and hyporheic temperatures, however, the temperature-inferred developmental rates remained similar for both hyporheic and surface temperatures at all locations. There were no significant differences in ATUs among probe locations in 2014 at both the surface and hyporheic levels, and no significant differences in ATUs among probe locations in 2013 at the hyporheic level. A comparison of ATUs derived using surface water temperatures among locations in 2013 was significant ($\mathbf{X}^2=94.99$, df=9, $P< 0.001$), and the probe near the bank at the upper site (Upper_3) produced significantly fewer ATUs ($\mathbf{X}^2$=92.79, df=1, $P < 0.001$) and the probe mid-stream recorded significantly more ATUs at the surface (Upper_2, $\mathbf{X}^2$=4.51, df=1, $P < 0.05$) than did all other probes (Figure 4.5). Generally the mid-stream (Upper_2) and in-between (Upper_1) probes in the upper site recorded slightly warmer temperatures and thus produced slightly higher ATUs than did the lower site, whereas the probe at the bank (Upper_3) recorded colder temperatures (Figure 4.5).

Discussion

Warming temperatures have resulted in predictions of colonizations northward in latitude or upward in elevation for organisms tracking their thermal niches (Sunday et al. 2012). These warming temperatures have also identified the need to characterize thermal refugia for native species at high latitudes and elevations to facilitate conservation efforts (Isaak et al. 2015; Dunmall et al. 2016). However, those extreme environments that are experiencing the fastest rates of change (Corell 2006) are also data-poor (Reist et al. 2006b), remote, and highly variable with respect to environmental parameters, and are also difficult and expensive to access. I have described a reliable method to monitor surface and hyporheic temperatures in a remote aquatic systems over a long period that requires little or no maintenance, can be installed in critical habitats with minimal impact as part of a community-based monitoring program, and the data can be downloaded opportunistically and easily. Using data collected through this method, I characterize the thermal environment at three different scales: individual redds, within Dolly Varden spawning sites, and among spawning sites for both the surface and hyporheic temperatures in Fish Hole Creek, a tributary of Babbage River on the Yukon North Slope. I found there was significant temporal and spatial variation in surface and hyporheic water temperatures during both the spawning and incubation timeframes, which is important as thermal regimes are known to influence developmental rates (Beacham and Murray 1986). However, despite these differences, there were few significant differences in ATUs, and none for ATUs derived using hyporheic water temperatures. Importantly, this revealed that the redds near the outer edges of spawning locations may experience colder surface temperatures but experience no significant difference in the ATUs at the hyporheic level. This highlights the importance of monitoring water temperatures at the level where the eggs are developing, rather than simply the surface level, in order to accurately characterize and quantify critical habitats, and the interannual variability in those habitats for viable spawning and egg incubation. To quantify changes in water levels year-round, a continuously logging water level logger (HOBO U20-001-04, Onset Computer Corporations, Massachusetts, USA) may be placed inside the probe instead of a water temperature data logger using the same method.

A reliable method to continuously monitor habitat at varying spatial scales is necessary as part of a full assessment of spawning habitat (Baxter and Hauer 2000). Within a stream, environmental parameters such as hyporheic exchange, dissolved oxygen, and temperature may vary at relatively broad, reach-level scales, and also at fine scales within spawning sites (Baxter and Hauer 2000; Dunmall et al. 2016). These parameters can also vary at individual redds when comparing surface and hyporheic zones (Zimmerman and Finn 2012). At most individual Dolly Varden redds monitored, the paired surface and hyporheic temperatures were significantly different; however, the derived ATUs were not, with two exceptions. This suggests that these statistical differences were not biologically significant at most redds in this stream reach, and may reflect the relatively stable winter flow patterns at most sites (Mochnacz et al. 2010). Those exceptions, however, also show that spatial and interannual differences can occur, which may affect the viability of spawning habitats. Therefore, monitoring surface and hyporheic temperatures using this method allows characterization of temporal and spatial variability in viable spawning habitat, and also allows redundancy in data collection efforts, thus increasing confidence in the accuracy of the individual loggers and the probability of successful data collection if one logger fails at a given redd site.

I have used this method to install more than 50 probes over three years in streams throughout the Northwest Territories in habitats thought to be relevant for both Dolly Varden and bull trout *Salvelinus confluentus*. While the installation of these probes can be arduous, the high retention rate despite dynamic ice break-ups, river scouring, and dynamic systems has proven effective in remote systems as most probes that were installed remained in place until removed. I have lost only two probes, one was installed in loose gravel at the downstream edge of a pool and was washed away after two years, and another was installed in an area that was subsequently under several layers of ice and was presumably scoured out during a dynamic break-up. Several other probes have been found using the metal detector but were inaccessible during opportunistic attempts to download the data due to shifting channel morphologies. Subsequent recovery efforts were successful in most cases, as the stream shifted back to its earlier morphology, or gravel was physically removed when eggs were not incubating until the lid was reached. This method is also limited to streams that are less than 1 m deep due to the requirement to hand tighten the lid onto the pipes, although this step could be done using scuba or snorkelling gear if water currents allowed. As most substrate-spawning fish that inhabit high elevations and latitudes select spawning sites that are less than 1 m in water depth (Stewart et al. 2007; Stewart et al. 2009; Mochnacz et al. 2010), this method is widely applicable in extreme environments.

Understanding the broad and fine-scale thermalscapes at high latitudes and elevations will become increasingly important in order to conserve native species as air temperatures continue to rise (Isaak et al. 2015) and to predict areas vulnerable to colonizations by opportunistic species (Dunmall et al. 2016). Establishing year-round present baseline thermal profiles will characterize thermal inputs from groundwater springs as well as provide the basis for studies of thermal tolerances of key fish species, allowing subsequent assessments of the effects of change. Implementing these efforts as part of a community-based monitoring program also increases capacity to participate in monitoring efforts, allows community representatives to choose sites for monitoring based on local or traditional knowledge, and leads to increased opportunities to download the data. Therefore, this method provides a cost-effective, long-term solution to monitoring key environmental parameters in extreme environments, which will aid in re-dressing data gaps and assist in predicting species and ecosystem-level responses to continued warming.

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Sahtú Renewable Resources Board. K.M.D. gratefully acknowledges support from an NSERC Canada Graduate Scholarship, a W. Garfield Weston Foundation Award for Northern Research (PhD), and the 2014 American Fisheries Society J. Frances Allen Scholarship.

Table 4.1. The surface and hyporheic water temperatures at each of the probe locations were assessed for significant differences during both the spawning (September 15-October 15) and incubation (October 16-March 1) timeframes each year using paired t-tests. Location places are referenced in Figure 4.2.

Location	Year	timeframe	df	*P*-value
Upper_1	2013	spawning	30	<0.001
Upper_1	2013	incubation	166	<0.001
Upper_1	2014	spawning	30	<0.001
Upper_1	2014	incubation	137	0.09
Upper_1	2015	spawning	n/a	n/a
Upper_1	2015	incubation	n/a	n/a
Upper_2	2013	spawning	30	0.11
Upper_2	2013	incubation	166	<0.001
Upper_2	2014	spawning	30	0.84
Upper_2	2014	incubation	166	<0.001
Upper_2	2015	spawning	30	0.087
Upper_2	2015	incubation	127	<0.001
Upper_3	2013	spawning	30	<0.05
Upper_3	2013	incubation	166	<0.001
Upper_3	2014	spawning	30	0.95
Upper_3	2014	incubation	166	0.12
Upper_3	2015	spawning	30	0.079
Upper_3	2015	incubation	127	<0.001

Lower_1	2013	spawning	30	<0.001
Lower_1	2013	incubation	166	<0.001
Lower_1	2014	spawning	30	<0.001
Lower_1	2014	incubation	166	<0.001
Lower_1	2015	spawning	30	<0.01
Lower_1	2015	incubation	127	<0.001
Lower_2	2013	spawning	30	0.79
Lower_2	2013	incubation	166	0.02
Lower_2	2014	spawning	30	<0.001
Lower_2	2014	incubation	166	0.676
Lower_2	2015	spawning	30	<0.001
Lower_2	2015	incubation	127	<0.001
Lower_3	2013	spawning	30	<0.001
Lower_3	2013	incubation	166	<0.001
Lower_3	2014	spawning	30	0.75
Lower_3	2014	incubation	166	<0.01
Lower_3	2015	spawning	30	0.016
Lower_3	2015	incubation	127	<0.001
Lower_4	2013	spawning	30	<0.001
Lower_4	2013	incubation	166	0.069
Lower_4	2014	spawning	30	0.05
Lower_4	2014	incubation	137	<0.01
Lower_4	2015	spawning	n/a	n/a

Lower_4	2015	incubation	n/a	n/a
Lower_5	2013	spawning	30	<0.001
Lower_5	2013	incubation	166	<0.001
Lower_5	2014	spawning	30	0.092
Lower_5	2014	incubation	166	<0.001
Lower_5	2015	spawning	30	0.20
Lower_5	2015	incubation	127	<0.05
Lower_6	2013	spawning	30	<0.001
Lower_6	2013	incubation	166	<0.001
Lower_6	2014	spawning	24	0.001
Lower_6	2014	incubation	29	0.22
Lower_6	2015	spawning	30	0.10
Lower_6	2015	incubation	127	<0.001
Lower_7	2013	spawning	30	0.036
Lower_7	2013	incubation	166	<0.001
Lower_7	2014	spawning	30	<0.001
Lower_7	2014	incubation	166	<0.001
Lower_7	2015	spawning	30	0.86
Lower_7	2015	incubation	127	0.05

Figure 4.1: A photograph of the post pounder, probe and cap.

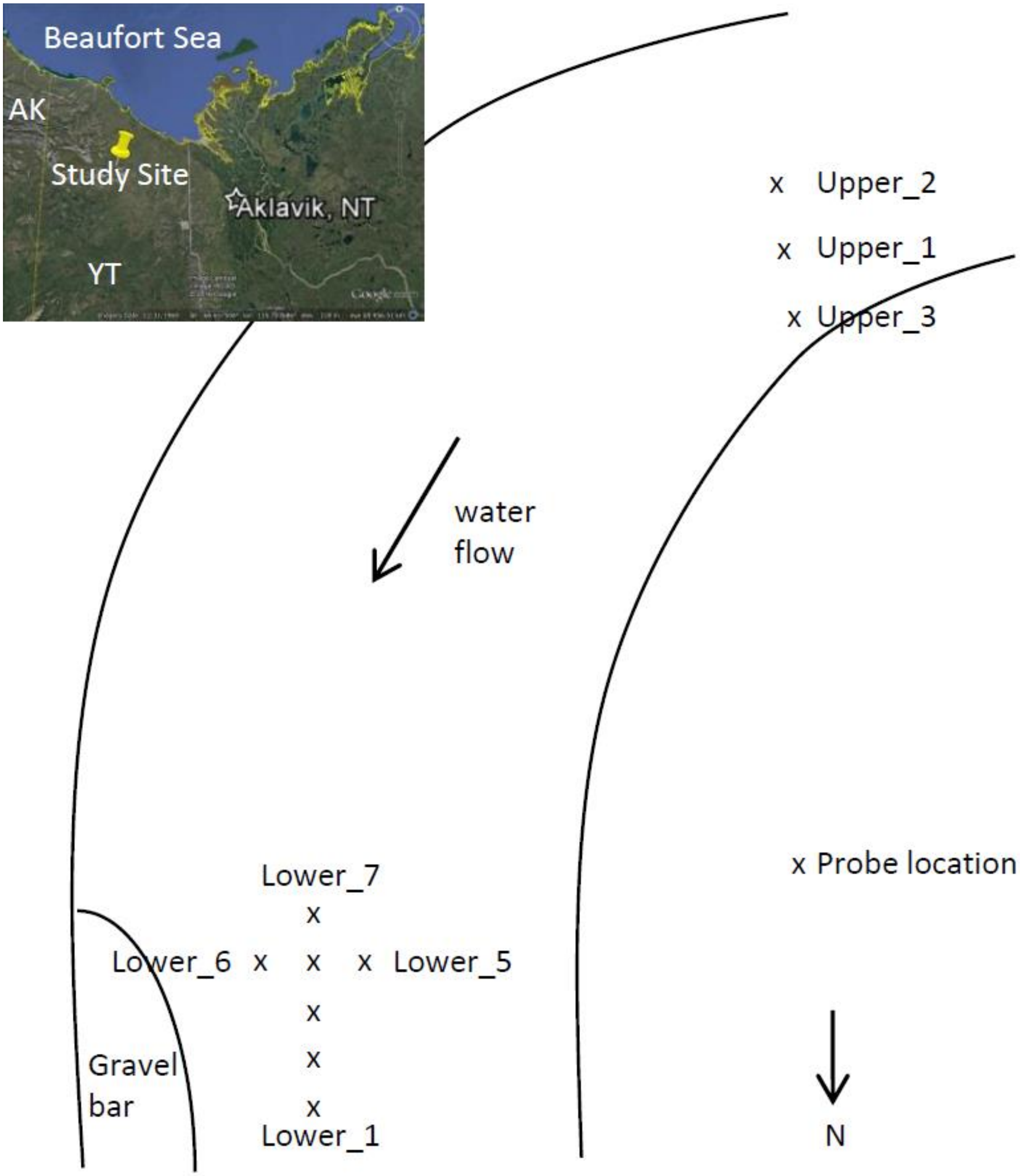

Figure 4.2: A schematic of the study site, which is located on a reach of Fish Hole Creek, a tributary of Babbage River, Yukon North Slope.

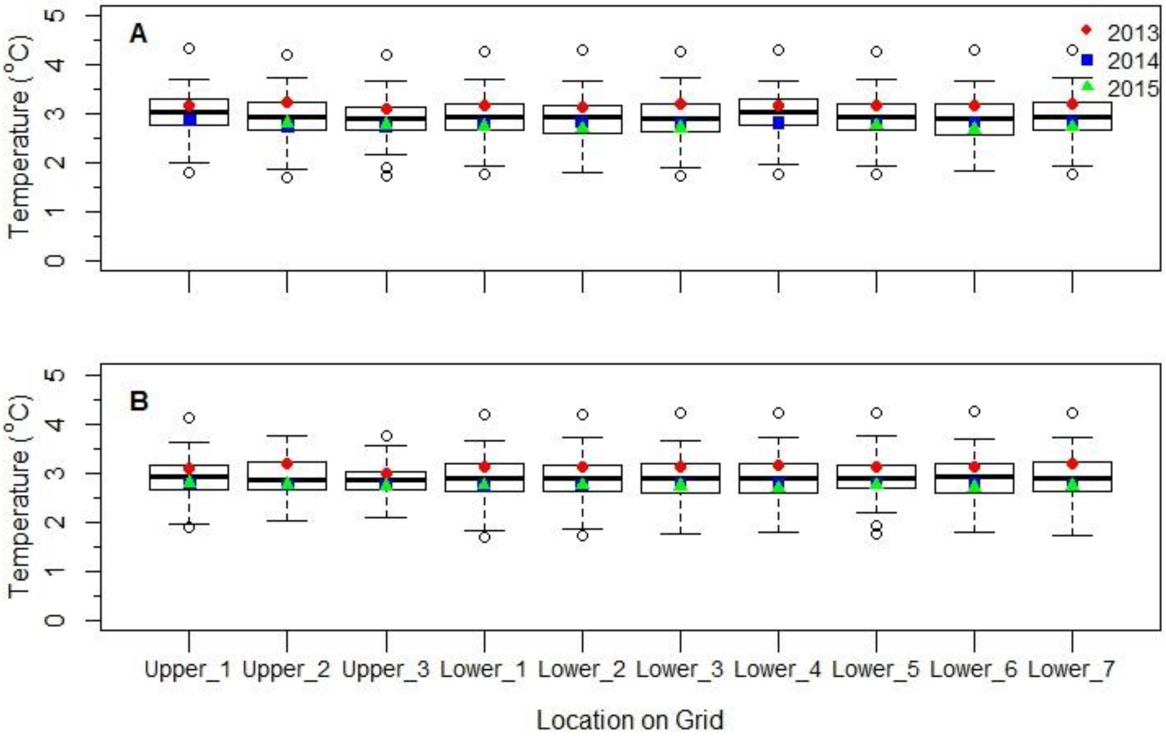

Figure 4.3: Boxplots (with the mid-line at the median value, box ends at upper and lower quartiles, highest and lowest values at the extreme lines, and outliers shown with open circles) of average daily water temperature combined for all years during the spawning timeframe (September 15-October 15) for the (A) surface and (B) hyporheic levels for the three probes at the upper site and the seven probes at the lower site on Fish Hole Creek (Babbage River, YT). The mean water temperature per year, site and level is also included as points to show the variability in temperatures among years.

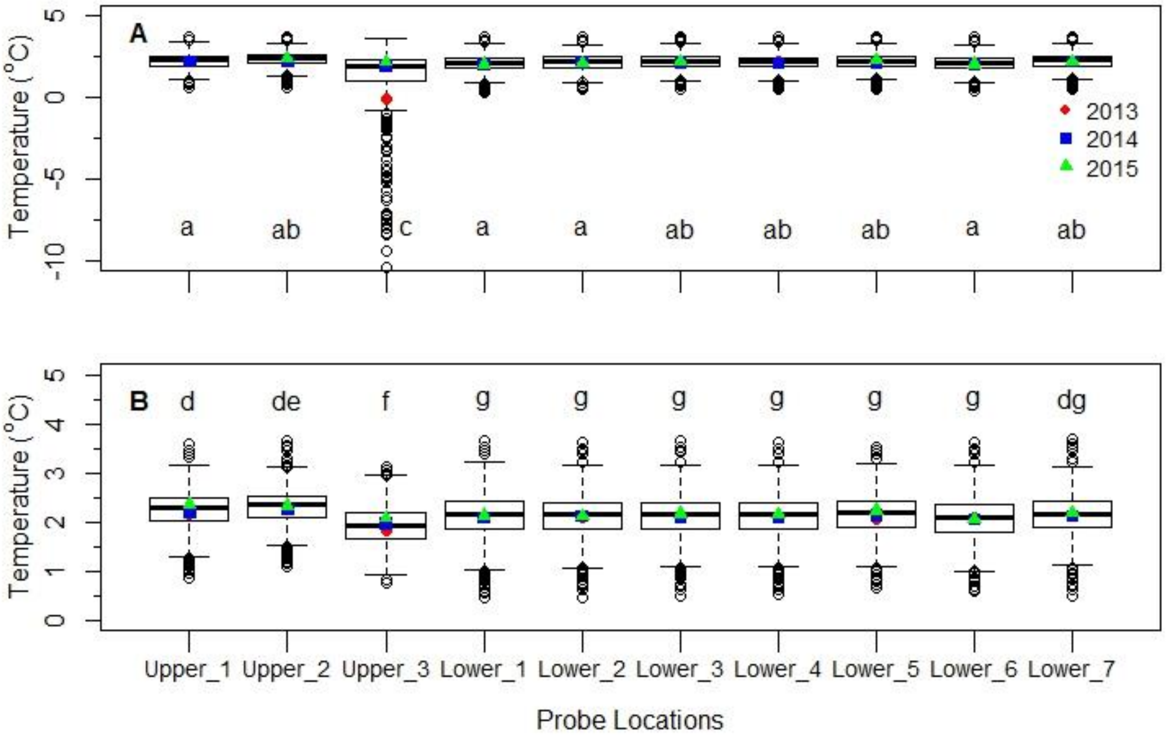

Figure 4.4: Boxplots (with the mid-line at the median value, box ends at upper and lower quartiles, highest and lowest values at the extreme lines, and outliers shown with open circles) of average daily water temperature combined for all years during the incubation timeframe (October 16-March 31) for the (A) surface and (B) hyporheic levels for the three probes at the upper site and the seven probes at the lower site on Fish Hole Creek (Babbage River, YT). The mean water temperature per year, site and level is also included as points to show the variability in temperatures among years. Significant differences (*P*<0.05) are denoted by different letters.

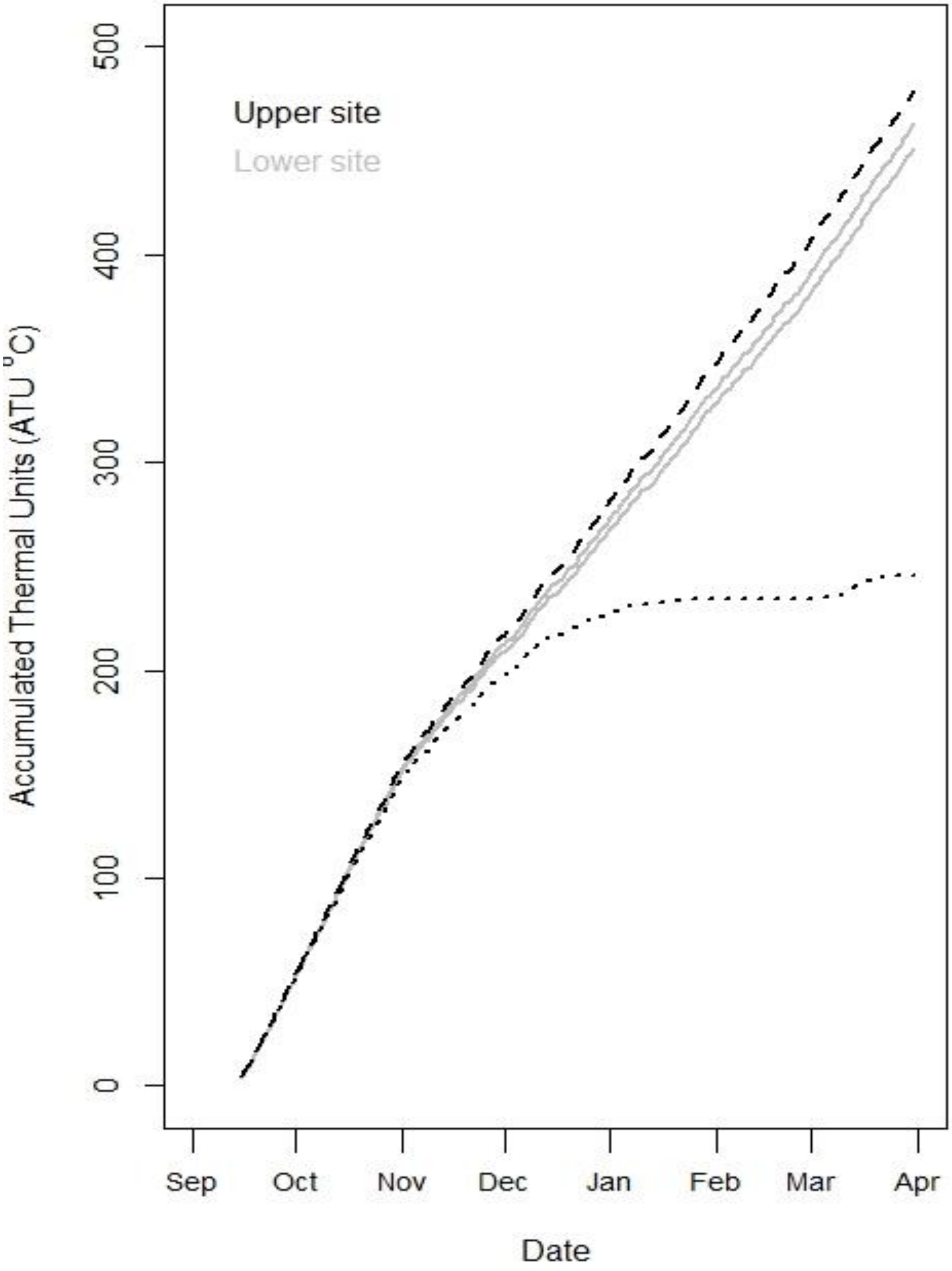
Upper site
Lower site
Accumulated Thermal Units (ATU °C)
0
100
200
300
400
500
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Date

Figure 4.5: The maximum and minimum accumulated thermal units (ATU °C) are shown for each of the upper (black) and lower (grey) sites for all years they were monitored on Fish Hole Creek (Babbage River, YT). ATUs were calculated by starting on a hypothetical spawn date of September 15 and continuing until March 31. Significant differences ($P<0.05$) are denoted by different line types; the thermal profile for surface temperature in 2013/14 at the upstream most probe at the lower site (Lower_7, maximum) and surface temperature in 2014/15 at the downstream most probe at the lower site (Lower_1, minimum) are represented by solid lines, the thermal profile for surface temperature in 2013/14 at the midstream probe in the upper site (Upper_2) is a dashed line, the thermal profile for surface temperature in 2013/14 at the probe near the bank at the upper site (Upper_3) is a dotted line.

Chapter 5 - Using thermal limits to assess establishment of fish dispersing to high latitude and high elevation watersheds

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Contributions of Authors:

This paper investigates C. Lean's hypothesis that temperature preferences between Pacific salmon and Dolly Varden allows for spatial segregation during spawning within rivers in Norton Sound, Alaska. Under the guidance of J. Reist and C. Zimmerman, I developed a monitoring plan to assess temperatures of essential fish habitat, installed data loggers, completed the data analyses, and wrote the initial and final drafts of the paper. N. Mochnacz identified critical habitats for Dolly Varden, assisted in installing the temperature loggers, and provided resources for the GIS analyses. All authors reviewed prior drafts of the manuscript.

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Abstract

Distributional shifts of biota to higher latitudes and elevations are presumably influenced by species-specific physiological tolerances related to warming temperatures. However, it is establishment rather than dispersal that may be limiting colonizations in these cold frontier areas. In freshwater ecosystems, perennial groundwater springs provide critical winter thermal refugia in these extreme environments. By reconciling the thermal characteristics of these refugia with the minimum thermal tolerances of life-stages critical for establishment, I develop a strategy to focus broad projections of northward and upward range shifts to the specific habitats that are likely for establishments. I evaluate this strategy using chum salmon *Oncorhynchus keta* and pink salmon *O. gorbuscha* that seem poised to colonize Arctic watersheds. Stream habitats with a minimum temperature of 4 °C during spawning and temperatures above 2 °C during egg incubation were most vulnerable to establishments by chum and pink salmon. This strategy will improve modelling forecasts of range shifts to cold freshwater habitats and focus proactive efforts to conserve both newly emerging fisheries and native species at northern and upper distributional extremes.

Introduction

The rapid rate of environmental change experienced by terrestrial (Diffenbaugh et al. 2013) and marine (Hoegh-Guldberg and Bruno 2010) ecosystems is also mirrored in freshwater ecosystems (Isaak and Rieman 2013). Marine and terrestrial ectotherms have shifted distributions northward in latitude and upward in elevation in response to climate warming (Sunday et al. 2012), and many taxa seem capable of tracking climate velocities (Diffenbaugh et al. 2013; Pinsky et al. 2015). In fresh water, stream fishes are similarly shifting in response to warming temperatures, but at a slower pace (Comte and Grenouillet 2013). Ectotherms in freshwater ecosystems may be particularly vulnerable to the effects of climate change because of the influence of temperature on physiological processes (Pörtner and Farrell 2008), and the potential for habitat fragmentation, which limits the potential to track thermally suitable habitat (Isaak and Rieman 2013). At high latitudes and elevations, these considerations are amplified and ectotherms experience cold, harsh conditions and dynamic flows (Power 2002), vast sections of rivers that may be frozen to the bottom in winter, and freshwater temperatures that are spatially and temporally heterogeneous (Power et al. 1999; Reist et al. 2006a). Freshwater cold-tolerant species are well-adapted to these extreme conditions (Power 2002), but at a cost of narrowing the thermal tolerance window (Pörtner and Farrell 2008), a trade-off that may be detrimental with the projected increase in temperatures (Reist et al. 2006a). Opportunistic colonizing fishes appear capable of accessing these extreme freshwater environments as thermal barriers lessen with warming temperatures (Comte and Grenouillet 2013; Dunmall et al. 2013). Establishment, however, may depend on the relatively immobile early (i.e., egg, larval, fry) life-stages that have narrow thermal tolerance windows and are vulnerable to changes in temperature (Reist et al. 2006a; Pörtner and Farrell 2008). Early life-stage survival due to thermal limits is also considered a population bottleneck for plants (Shevtsova et al. 2009), marine invertebrates (Byrne 2012), and may similarly limit invasions of introduced fishes to high elevations (e.g., McHugh and Budy 2005). Thus, due to the harsh conditions and limited viable habitat in cold frontier areas, it is establishment by these early-life stages, rather than dispersal, that may be limiting colonizations (McHugh and Budy 2005; Alsos et al. 2007). Species-specific thermal tolerances are an important determinant during this establishment phase of colonizations to cold freshwater environments (Milner et al. 2008). Specifically, minimum thermal tolerances at early life-stages may present a colonization bottleneck for stream fishes in extreme environments (McHugh and Budy 2005).

Perennial groundwater springs critically link thermal tolerances to thermal refugia by maintaining stability in highly variable systems, providing cold-water refugia during the summer and warm-water refugia during the winter (Meisner et al. 1988; Power et al. 1999). Cold-tolerant species have adapted to select areas with perennial groundwater springs for successful development during critical life-stages, a strategy that facilitated post-glacial Arctic colonizations (Power 2002). Successful establishment of contemporary colonizers could similarly occur if vagrants found appropriate habitat (i.e., niche tracking), or adapted to novel conditions (i.e., niche evolution). There is a reduced capacity, however, to adapt to colder temperatures and thermal tolerances are further narrowed during reproduction and early development (Pörtner and Farrell 2008). In these extreme environments, it is the predicted increase in groundwater temperatures (Meisner et al. 1988; Power et al. 1999) that will influence aquatic biota by potentially shifting thermal refugia, resulting in cascading effects on cold-tolerant species already sensitive to impacts of climate change (Reist et al. 2006a), and potentially facilitating the establishment of colonizing species in cold freshwater environments.

Variation in groundwater temperature across latitudes and elevations can be broadly predicted from air temperatures (Meisner et al. 1988); however, within-site variation in temperature can be significant along latitudinal and elevation gradients (Graae 2012; Snyder et al. 2015). Thus, the characterization and monitoring of these thermal refugia to determine baseline values and assess change is critical to translating the effects of warming air temperatures on groundwater temperatures at perennial springs and their associated dependent aquatic organisms in extreme freshwater environments. As well, relating the minimum winter temperatures in these thermal refugia with the lower thermal limits during critical early life-stages for both native and potentially colonizing fish species contributes to better informed models predicting viable fish habitat under climate change scenarios (Mohseni et al. 2003). Coupled, this information would have considerable impact on anticipating conservation concerns for cold-tolerant native fish species that may be unable to track thermal habitats further northward or upstream due to lack of connectivity, and predicting the likelihood of establishments by colonizing species opportunistically dispersing to high latitudes and elevations.

Temperature is therefore proposed as the fundamental predictive factor to anticipate watersheds likely to be established by dispersing aquatic ectotherms in extreme freshwater habitats. It is a pivotal abiotic parameter for fishes (Pörtner and Farrell 2008), influencing range limits (Sunday et al. 2012; Isaak et al. 2015), and also specifically driving adaptations at species-specific and even population-specific levels (Pörtner and Farrell 2008). Species-specific thermal tolerances can influence distributions within watersheds (Fausch et al. 1994; McHugh and Budy 2005), and other abiotic and biotic factors also influence the distribution of species at local and regional spatial scales (Fausch et al. 1994). Behavioral thermoregulation to remain within tolerances using thermal refugia, however, is critical to the vulnerability of ectotherms to warming temperatures (Sunday et al. 2014). Coupling these characteristics with the spatial distribution of thermal refugia as potential habitats for colonizing species would greatly inform predictions of leading edge range shifts in stream fishes to extreme habitats (Comte et al. 2014).

Therefore, under the overall goal of better understanding and predicting the risks associated with colonizations to extreme environments, my objective is to propose a strategy that aligns the thermal tolerances of fishes, especially during the critical early life-stages, with temperature profiles in thermal refugia to predict watersheds vulnerable to establishments by colonizing species. I then investigate the effectiveness of this strategy using the relevant and timely example of Pacific salmon *Oncorhynchus* spp., which appear to be responding to changing environmental conditions by distributing northward (Grebmeier et al. 2006; Dunmall et al. 2013; Nielsen et al. 2013). Due to the inherent coupling of groundwater springs with viable habitat for fall-spawning riverine fish species in the Arctic, potentially suitable habitats for vagrant salmon may be in areas occupied by native cold-tolerant riverine char such as Dolly Varden *Salvelinus malma*. These cold-tolerant char share similar general spawning habitat requirements with salmon except that Dolly Varden spawn in water temperatures as low as 3 °C (Stewart et al. 2009), whereas the lower thermal limit for spawning in chum and pink salmon is approximately 4 °C (Bailey and Evans 1971; Raymond 1981). I hypothesize that aligning the minimum thermal tolerances during critical early life-stages with the thermal profiles of groundwater springs will allow predictions regarding both the potential for establishment of salmon in novel watersheds and the likelihood of competition between Dolly Varden and vagrant salmon for specific spawning sites.

Methods

The thermal suitability of watersheds for establishment by vagrant salmon was assessed by summarizing point measurements of water temperatures during the potential spawning (September 15 to October 15) and incubation (October 16 to March 1) timeframes at known groundwater sources along the North American North Slope, and by conducting year-round monitoring at six known Dolly Varden spawning locations in the Canadian Western Arctic. Point measurements of water temperatures were summarized from the primary literature and agency reports (Table 5.1). The continuous year-round thermal monitoring at Dolly Varden spawning sites also allowed an assessment of both the annual thermal variation at specific groundwater springs and the fine-scale spawning site selection for vagrant salmon in relation to proximity to groundwater source. The thermal gradient present downstream of the groundwater springs and the species-specific differences in thermal tolerances were used to predict the risk of competition for specific spawning sites.

The six year-round monitoring locations are described as follows: 1) three locations (upper site at 68°35’51.04N, 138°44’06.0W; mid site at 68°36’25.2N, 138°44’09.6W; lower site at 68°36’17.4N, 138°43’56.3W) were in Fish Hole Creek, a tributary of the Babbage River, Yukon Territory (YT); 2) one location in Little Fish Creek (at 68°17’45.6N, 136°21’39.6W), a tributary of the Big Fish River, Northwest Territories (NT); 3) two locations in Fish Creek (upper site at 67°54’18.5N, 136°31’04.4W; lower site at 67°49’30.0N, 136°17’06.0W), a tributary of the Rat River, NT (Figure 5.1). Water temperature was monitored in each of these locations, except the Upper Fish Hole Creek and Upper Fish Creek sites, using temperature loggers (HOBO U22, Onset Computer Corporation, Massachusetts, USA) attached to a steel pipe driven into the river bottom. Water temperature was monitored from March 6, 2013 to November 15, 2014 in Lower

Fish Creek, from March 6, 2013 to March 2, 2015 in the Lower Fish Hole Creek site, and from March 7, 2013 to March 3, 2015 in Little Fish Creek. Surface water temperature was also monitored from September 15, 2012 to March 2, 2015 in the Upper Fish Hole Creek site and from September 15, 2013 to March 1, 2014 in the Upper Fish Creek site using a temperature logger (StowAway Tidbit, Onset Computer Corporation, Massachusetts, USA) that was epoxied onto a boulder at each location (Isaak et al. 2013). Loggers recorded water temperature at hourly intervals, which were summarized as daily mean estimates. These daily means were categorized into spawning (September 15 to October 15) or incubation (October 16 to March 1) timeframes to allow temperature comparisons among life-stage events, locations, and years. Conductivity measurements were collected at the four sites where the temperature monitoring occurred using a handheld conductivity meter (ECTestr 11 Plus, Oakton Instruments, Illinois, USA) and were used to indicate water source. Conductivity levels <500 microsiemens/centimeter (µS/cm) were considered to indicate karst-type water sources and thus of non-mineral origins.

Comparing potential egg developmental rates among sites allows predictions of viable site-selection by both native and colonizing fishes. Development was compared among sites using Accumulated Thermal Units (ATU), the cumulative daily water temperature in degrees Celsius (°C), from spawning to emergence. Assuming that spawning takes place in mid-September, the lower thermal thresholds for viable habitat was assessed using the species-specific minimum thermal tolerances during spawning of 4 °C (Bailey and Evans 1971; Raymond 1981), minimum incubation temperatures during early development (i.e., embryos) of 2.5 °C or 3.5 °C for chum salmon or pink salmon, respectively, and a minimum incubation temperature of 2.0 °C during later development (i.e., alevins) (Beacham and Murray 1990). The derived ATU values at emergence were then compared to the range of ATU values at emergence for chum salmon in the Noatak River, Alaska, which represents the northernmost chum salmon populations with known instream ATU information (ranged from 650 to 1440 ATU, Merritt and Raymond 1983) and to chum salmon in the Tanana River, AK near Fairbanks, which is the northernmost chum salmon population with ATU information obtained from a hatchery setting (range 700 to 900 ATU, Raymond 1981).

Statistical analyses were conducted using R software and an alpha significance level of 0.05 (R Core Team 2015). For each location, daily mean temperatures for the spawning and incubation timeframes were compared using an ANOVA. As the water temperatures during spawning were significantly different from those during incubation at each location, the data were subsequently analyzed separately. Daily mean temperatures for each of the spawning and incubation timeframes among sites and years were compared using a two-way ANOVA. As there was a significant interaction effect of location and year during the spawning timeframe, significant differences among years were assessed using independent t-tests for each site except Lower Fish Hole Creek, where data were only collected for 2013, and Upper Fish Hole Creek, where data were collected for 2012-2014. An ANOVA was used to compare among years within the Upper Fish Hole Creek site, and TukeyHSD multiple comparison tests were completed to assess significant main effects using a Bonferroni p value adjustment. An ANOVA was used to compare among locations during spawning using data from 2013 only because it was the only year monitored where each location was represented. As there was no significant effect of year for the incubation timeframe, data were pooled across years for each site. An ANOVA was used to compare among locations during incubation, and TukeyHSD multiple comparison tests were completed to assess significant main effects using a Bonferroni p value adjustment. To compare ATU values among sites, the ATU values on March 1 were treated as count data and were compared among locations using a Chi-squared goodness of fit test, where the frequency distribution of ATU counts was assumed to be equal among all locations. Where ATU data were available for multiple years within a location (i.e., Upper Fish Hole Creek and Mid Fish Hole Creek sites), the average ATU value on March 1 per location was used for the analyses. To assess significant main effects, one-way proportion tests with Yates continuity correction were used to determine whether the observed ATU value was equal to the expected ATU frequency distribution for each location.

Results

The strategy of aligning the thermal tolerances of potentially colonizing species with the spatial distribution of thermal refugia for critical life-stages successfully highlights watersheds vulnerable to establishments in extreme environments and pinpoints specific groundwater springs to focus detailed assessments. As groundwater springs at the northern extent of continental North America experience annual winter temporal stability but spatial variability (Table 5.1), this strategy was used to develop a regional model that predicts watersheds vulnerable to colonizations by chum and pink salmon (Figure 5.1). Based on point measurements of groundwater spring temperatures, several watersheds along the North American North Slope contain warm-water thermal refugia within the critical early life-stage thermal tolerance limits of chum and pink salmon (>4 °C during September or >2 °C during October to April and <500 µS/cm, Figure 5.1). At a finer scale, continuous thermal monitoring at Dolly Varden spawning sites allowed predictions of the thermal viability of the sites for colonizing salmon, and therefore the likelihood of competition between native char and colonizing salmon for specific spawning sites.

During spawning, the mean water temperature was more variable than during incubation (Figure 5.2). There was a significant interaction effect of location and year during spawning (ANOVA, F=2.326, df= (4, 391), $P=0.05$), and comparisons among years within each site indicated that temperatures during spawning were significantly warmer in 2013 than in 2014 at Little Fish Creek (t-test, t=2.62, df=79, $P=0.01$), Upper Fish Creek (t-test, t=9.01, df=59, $P<0.01$), and Mid Fish Hole Creek (t-test, t=3.28, df=46, $P<0.01$; Figure 5.2). Temperatures during spawning were significantly warmer in 2012 than in 2014 at the Upper Fish Hole Creek site (ANOVA, F=4.29, df= (2, 90), $P<0.01$; Figure 5.2). Temperatures were significantly different among sites (ANOVA, F=51.18, df= (5, 180), $P<0.01$; Figure 5.2), and specifically, the Little Fish Creek and the Upper Fish Creek sites were significantly warmer during spawning than all other locations and the Lower Fish Creek site was significantly colder than the Upper Fish Hole Creek site but not the Mid or Lower Fish Hole Creek sites (Tukey, $P<0.01$; Figure 5.2), demonstrating that water cools with distance from the groundwater spring source at a fine-scale.

During the incubation timeframe, there were significant differences in temperature comparisons among all sites except the Upper Fish Creek site was similar to the Upper Fish Hole Creek site (ANOVA, F=580.38, df= (5, 1224), $P<0.01$; Figure 5.2). The Little Fish Creek site, which is geothermally heated, was significantly warmer than the other sites, followed by Upper Fish Creek and Upper Fish Hole Creek, which were similar, and then Mid Fish Hole Creek, Lower Fish Hole Creek and the Lower Fish Creek site was the coldest (Tukey, $P<0.01$; Figure 5.2). A comparison of ATU during incubation revealed that the ATU values among sites were significantly different (Chi-squared test, $\mathbf{X}^2=779.59$, df=5, $P<0.01$) and more specifically, proportional comparisons suggested that the ATU values from all locations except the Upper Fish Hole Creek and Upper Fish Creek sites were significantly different (Little Fish Creek:

χ^2=604.72, df=1, P<0.01; Lower Fish Creek: χ^2=217.40, df=1, P<0.01; Mid Fish Hole Creek: χ^2=13.62, df=1, P<0.01; Lower Fish Hole Creek: χ^2=85.48, df=1, P<0.01; Figure 5.3). This suggests that slight but consistent differences in water temperatures along a temperature gradient within a watershed (i.e., the Upper, Mid, and Lower Fish Hole Creek sites) can significantly impact the thermal viability of the habitat (Figure 5.2; Figure 5.3). Although the Upper Fish Hole Creek and Upper Fish Creek ATU values were not significantly different by March 1, the Upper Fish Creek site initially accumulated thermal units at a faster rate than the Upper Fish Hole Creek site due to the persistence of warmer surface water temperatures into the winter months (Figure 5.3). While the Little Fish Creek site produced ATU values that would be thermally suitable for development in comparison to other northern chum salmon populations, the conductivity levels associated with the thermal spring would pose additional challenges for establishment (Table 5.1). Also, water temperatures occasionally dipped below 2.0 °C at the Upper Fish Creek and Upper Fish Hole Creek sites, which may negatively impact the survival of developing salmon if they were in those locations (Figure 5.2). The incubation temperatures at the Mid and Lower Fish Hole Creek and Lower Fish Creek sites were likely too cold to be viable habitat for chum and pink salmon (Figure 2).

Discussion

Whereas the distribution of marine ectotherms has been shown to be shifting predictably in response to warming temperatures (i.e., with species' ranges corresponding to their limits of thermal tolerance; Sunday et al. 2012), for freshwater species, there is little information to help predict what habitats are likely to be established by dispersing species or to understand the effects of warming air temperatures on thermal refugia at high latitudes and elevations. I have proposed a strategy to focus broad projections of range shifts to specific habitats and have evaluated that strategy using a timely example of salmon species that are dispersing northward and seem poised to colonize rivers currently occupied by cold-tolerant char species. I found that predictions of establishments in novel watersheds can be linked to broad-scale differences in thermal profiles among groundwater spring sources, fine-scale spatial differences in thermal suitability related to proximity to the groundwater source, species-specific thermal tolerances particularly for early life-stages, and the potential for adaptation by colonizing fishes to lower water temperatures. Integrating this information with both predictions of warming temperature trends (e.g., Prowse et al. 2006b) and identified thermal refugia for native stream fishes delineated through temperature networks (e.g., Isaak et al. 2015) will contribute to better understanding of dynamic ecosystems influenced by climate warming. While the mechanisms underlying distributional shifts remain complex, this strategy contributes to an overall framework for predicting changes in biodiversity resulting from warming temperatures and determining the resulting ecosystem-level impacts (Comte et al. 2014).

While this study provides a strategy for predicting systems with higher likelihood of colonizations, assessing colonization success remains difficult (Lockwood et al. 2007). Developmental rates may provide some insight into potential incubation success; however, a general lack of information regarding developmental rates at low incubation temperatures restricts the applicability of using developmental rates to assess colonization success. This is exacerbated by the often unknown population-level origins of colonizers coupled with the variation among populations in the developmental rates (Beacham and Murray 1990), and the tendency of models to overestimate developmental times when applied at low incubation temperatures (Alderdice and Velsen 1978). However, the projected rapid rate of temperature increases, especially during the autumn at high latitudes (Prowse et al. 2006b), will likely contribute to the success of opportunistic colonizers both by increasing the developmental rate during the critical early stages due to generally warmer freshwater temperatures and maintaining a higher developmental rate later into the incubation timeframe due to the persistence of those warmer temperatures later in the autumn and into winter. These warmer temperatures may also facilitate establishments by allowing adult fish to access novel habitats earlier in the season, increasing the time available for the development of deposited eggs. In addition, this earlier shift also means that vagrants to high latitude habitats would encounter plumes of warmer fresh water carried by northward flowing rivers (Prowse et al. 2006a) earlier in the season, which would increase their opportunity to ripen prior to spawning. Warmer temperatures, however, may be detrimental to native species adapted to colder thermal regimes (Reist et al. 2006b). Continuous thermal monitoring at these critical habitats would therefore provide information about maximum and minimum critical temperatures, thermal conditions for the development of native and potentially colonizing species, and the influence of groundwater springs as potential cold-water thermal refugia. Thermal monitoring along the temperature gradient present downstream from groundwater springs may also contribute to assessments of fine-scale site selection for colonizing species and allow predictions of spatial segregation of native and colonizing species for specific spawning sites based on species-specific thermal tolerances. This highlights the importance of continuous thermal monitoring in order to more fully understand the thermal regimes experienced by native and colonizing species and, in turn, be able to predict shifts in suitable thermal habitats and associated species-level responses at broad and fine scales to future warming scenarios.

The paucity of information about cold tolerances, especially during early life-stages, is an obvious data gap that hinders projections of successful establishments (Reist et al. 2006b). Despite generally warming temperatures, the winter extreme temperatures remain cold and conditions remain harsh at high latitude and elevation systems. Therefore, using groundwater springs as warm-water thermal refugia for over-wintering and egg incubation habitat remains necessary for both native and potentially colonizing species. While these groundwater springs are predicted to warm with increasing temperatures, their responses may be delayed or muted compared to ambient levels depending on the depth of the spring source, the amount of snow cover, and other microhabitat factors (Meisner et al. 1988; Kurylyk et al. 2014). This association is exacerbated in the Arctic due to the presence of permafrost and the large recharge zones for many of the groundwater springs (Kane et al. 2013; Utting et al. 2013). Indeed, the water supplying many of the groundwater springs on the Alaskan North Slope can originate on the south side of the Brooks Range, travel through limestone aquifers and under the permafrost, where it may be subjected to geothermal heat sources, and emerge at springs on the north side of the Brooks Range, with an estimated travel time of 1,000-1,500 years (Kane et al. 2013). Thus, water temperature at these Arctic springs may be more a reflection of proximity to geothermal heat sources and distance from recharge areas (Kane et al. 2013) than increases in air temperature. This emphasizes the need to better understand the minimum thermal thresholds at critical life-stages and variation in developmental rates at low temperatures for species opportunistically dispersing to novel watersheds at high elevations and latitudes in order to predict successful colonizations.

While outlining potential costs and benefits of unknown colonizations is premature, and because much depends on the abundance of vagrants in novel watersheds and their success at establishing, insights into the effects of opportunistic species colonizing novel locations can be gained by assessing locations where the colonizing and native species currently co-occur. In western Alaskan rivers, where Dolly Varden and salmon species currently reside, chum salmon spawning generally occurs in the lower and mid-sections of the river whereas Dolly Varden spawning generally occurs further upstream, in the higher reaches, in close proximity to groundwater sources (DeCicco 1985) and presumably in generally colder waters. Dolly Varden benefit salmon by feeding on the dead salmon eggs that may otherwise negatively impact survival of viable salmon eggs and juveniles in the gravel, and salmon benefit Dolly Varden by providing additional nutrients to the system and food in the form of eggs and carcasses of spawned salmon in the fresh water, as well as juvenile salmon in both the fresh water (Behnke 2002) and in the estuaries. As pink and chum salmon adults generally do not feed once in fresh water and their juveniles migrate downstream to estuaries and marine nearshore ecosystems soon after emergence, the likelihood for competition among native Dolly Varden and potentially colonizing pink and chum salmon for food resources in Arctic watersheds is presumably low. However, the required coupling of groundwater sources and viable spawning habitat at higher latitudes may restrict availability of viable spawning habitat for both native riverine char and colonizing salmon, increasing the risk of competition for potentially limited viable spawning habitat. In a more general, risk-management approach to range shifts, the benefits of distributional shifts by colonizing species tracking thermal niches may be balanced by the costs of ecosystem-level changes associated with environmental change for native species.

The unique characteristics of groundwater springs as thermal refugia may also link terrestrial and aquatic ecosystems and extend the applicability of this trait-based predictive strategy to assess establishments beyond aquatic ectotherms. Broadly drawing parallels between winter Arctic and arid ecosystems seems appropriate as similarly vast areas of unsuitable habitats are interspersed with ecological refugia at perennial groundwater springs (Davis et al. 2013). Locating these thermal refugia, however, may be challenging due to their rarity in vast and remote environments. Groves of balsam poplar *Populus balsamifera* are frequently associated with the presence of perennial groundwater springs in the Arctic (Childers et al. 1973; Craig and McCart 1974; Bockheim et al. 2003) and may be a visual cue to focus efforts. As these springs also contribute to an increase in the depth of the active soil layer (Bockheim et al. 2003), balsam poplar may also be a useful indicator of potentially viable habitat for opportunistic terrestrial as well as aquatic species. Landscape features such as aufeis areas could also be employed to visually identify perennial groundwater flow due to the build-up of layers of ice (Kane et al. 2013), and are apparent in satellite images (Yoshikawa et al. 2007). While simple trait-based approaches to identify mechanisms of range shifts have not been generally successful (Comte et al. 2014), focusing on life stage-specific traits influencing establishment within the colonization process provides a realistic strategy to identify likelihoods. With continued warming temperatures and associated predictions of range shifts, the importance of thermal refugia for both colonizing and native species in extreme environments is apparent. Aligning thermal tolerances to the characteristics of these groundwater springs provides a simple strategy to better inform predictions of successful colonizations by dispersing fishes and aid conservation and management efforts for sensitive native species in a changing environment.

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Table 5.1. Temperature, conductivity, and location of groundwater springs on North American North Slope where data were collected between September and April.

No.	Name	Date	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)	Temp. (°C)	Conductivity (µS/cm)	Reference
1	Lupine River	April 23, 1982	68.9228	-148.3498	2.2	300*	Bendock 1983
2	Saviukviayak River	April 23, 1982	68.9616	-148.1390	12.2	220*	Bendock 1983
3	Saviukviayak Spring	April 20, 1975	68.9389	-147.9792	6.5	247	Childers et al. 1977
4	Flood Creek	April 20, 1975	68.9777	-147.8583	7.2	222	Childers et al. 1977
5	Echooka River	November 4, 1971	69.2668	-147.3852	2.8	<322	Craig and McCart 1975
5	Echooka River	April 5, 1972	69.2668	-147.3852	2.8	<322	Craig and McCart 1975
5	Echooka River	November 1, 1972	69.2668	-147.3852	5.0	N/A	Craig and McCart 1974
6	Kavik River	November 5, 1972	69.5000	-146.6167	0.0	284	Craig and McCart 1974
7	Canning River	November 3, 1972	69.4500	-146.2333	0.5	294	Craig and McCart 1974
8	Shublik Spring	November 4, 1972	69.4500	-146.1830	3.5	252	Craig and McCart 1974
9	Canning River	November 3, 1972	69.3500	-146.0833	0.5	300	Craig and McCart 1974
10	Red Hill Spring	April 28, 1975	69.6269	-146.0272	33.0	1000	Childers et al. 1977

11	Canning River	November 5, 1972	69.1000	-145.9833	4.5	247	Craig and McCart 1974
12	Eagle Creek	November 4, 1972	69.4167	-145.8833	0.0	273	Craig and McCart 1974
13	Katakturuk River	April 28, 1975	69.6950	-145.1092	1.0	245	Childers et al. 1977
14	Sadlerochit Spring	April 14, 1972	69.6583	-144.4000	13.0	<540	Craig and McCart 1975
14	Sadlerochit Spring	April 6, 1972	69.6583	-144.4000	13.3	N/A	McCart 1974
14	Sadlerochit Spring	April 27, 1975	69.6583	-144.4000	13.0	410	Childers et al. 1977
15	Hulahula River	April 28, 1975	69.7608	-144.1542	1.0	240	Childers et al. 1977
15	Hulahula River	November 26, 1975	69.7608	-144.1542	1.0	225	Childers et al. 1977
16	Okerokovik River	November 24, 1975	69.7183	-143.2403	1.0	300	Childers et al., 1977
17	Aichikik River Spring	April 27, 1975	69.5183	-143.0333	3.6	338	Childers et al. 1977
18	Ekaluakat River	April 22, 1975	69.5908	-142.3000	6.4	350	Childers et al. 1977
19	Kongakut River Spring	April 27, 1975	69.5433	-141.8272	1.0	276	Childers et al. 1977
20	Kongakut Delta Spring	April 27, 1975	69.7267	-141.7686	1.0	215	Childers et al. 1977
21	Clarence River Spring	November 18, 1975	69.5122	-141.1936	0.0	250	Childers et al. 1977
22	Joe Creek	November 9, 1972	68.9333	-140.9500	4.0	235	Craig and McCart 1974
23	Firth River	November 9, 1972	68.6333	-140.9333	1.5	322	Craig and McCart 1974

24	Craig River	October 9, 1975	69.5746	-140.9068	2.0	250	Jones 1977
25	Fish Creek	November 8, 1972	69.4500	-140.2833	3.0	321	Craig and McCart 1974
25	Fish Creek	April 18, 1973	69.4500	-140.2833	2.0	311	Craig and McCart 1974
26	Fish Creek	September 10, 1975	69.59528	-140.1292	5.0	271	Jones 1977
27	Malcolm River	September 9, 1975	69.5248	-139.7978	5.0	237	Jones 1977
28	Firth River	November 9, 1972	69.4833	-139.7167	2.5	540	Craig and McCart 1974
28	Firth River	April 18, 1973	69.4833	-139.7167	2.0	454	Craig and McCart 1974
28	Firth River	September 9, 1975	69.4833	-139.7167	1.0	325	Jones 1977
29	Firth River	September 10, 1975	69.4770	-139.4821	5.0	29	Jones 1977
30	Babbage River	November 10, 1972	68.6500	-139.3333	4.5	283	Craig and McCart 1974
31	Spring River	April 16, 1973	69.2000	-138.9167	0.5	171	Craig and McCart 1974
32	Fish Hole Creek	November 10, 1972	68.6000	-138.7167	4.0	265	Craig and McCart 1974
32	Fish Hole Creek	study site (upper)	68.5975	-138.7350	2.3[†]		present study
32	Fish Hole Creek	study site (upper)	68.5975	-138.7350	2.2[‡]		present study
32	Fish Hole Creek	study site (upper)	68.5975	-138.7350	2.2[§]	436	present study
32	Fish Hole Creek	study site (mid)	68.6069	-138.7358	1.5[‡]		present study

32	Fish Hole Creek	study site (mid)	68.6069	-138.7358	1.8[§]		present study
32	Fish Hole Creek	study site (lower)	68.6048	-138.7323	0.9[‡]		present study
33	Crow River	April 16, 1973	69.1333	-138.4333	2.0	277	Craig and McCart 1974
33	Crow River	September 9, 1975	69.1333	-138.4333	2.0	271	Jones 1977
34	Little Fish Creek	November 11, 1972	68.2833	-136.3500	15.5	4546	Craig and McCart 1975
34	Little Fish Creek	April 19, 1973	68.2833	-136.3500	15.0	4531	Craig and McCart 1974
34	Little Fish Creek	study site	68.2961	-136.3610	5.2[§]	2980	present study
35	Upper Fish Creek	study site	67.9047	-136.5170	2.1[‡]	376	present study
35	Lower Fish Creek	study site	67.8250	-136.2844	-0.5[‡]	360	present study

[*] Conductivity was taken at an over-wintering site slightly downstream of the spring origin; temperature was collected at the spring origin.

[†] Average surface water temperature monitored from October 15, 2012 to March 1, 2013

[‡] Average surface water temperature monitored from October 15, 2013 to March 1, 2014

[§] Average surface water temperature monitored from October 15, 2014 to March 1, 2015

Note: Study sites were at Dolly Varden spawning locations in Canadian Western Arctic. Site numbers correspond to locations in Figure 5.1.

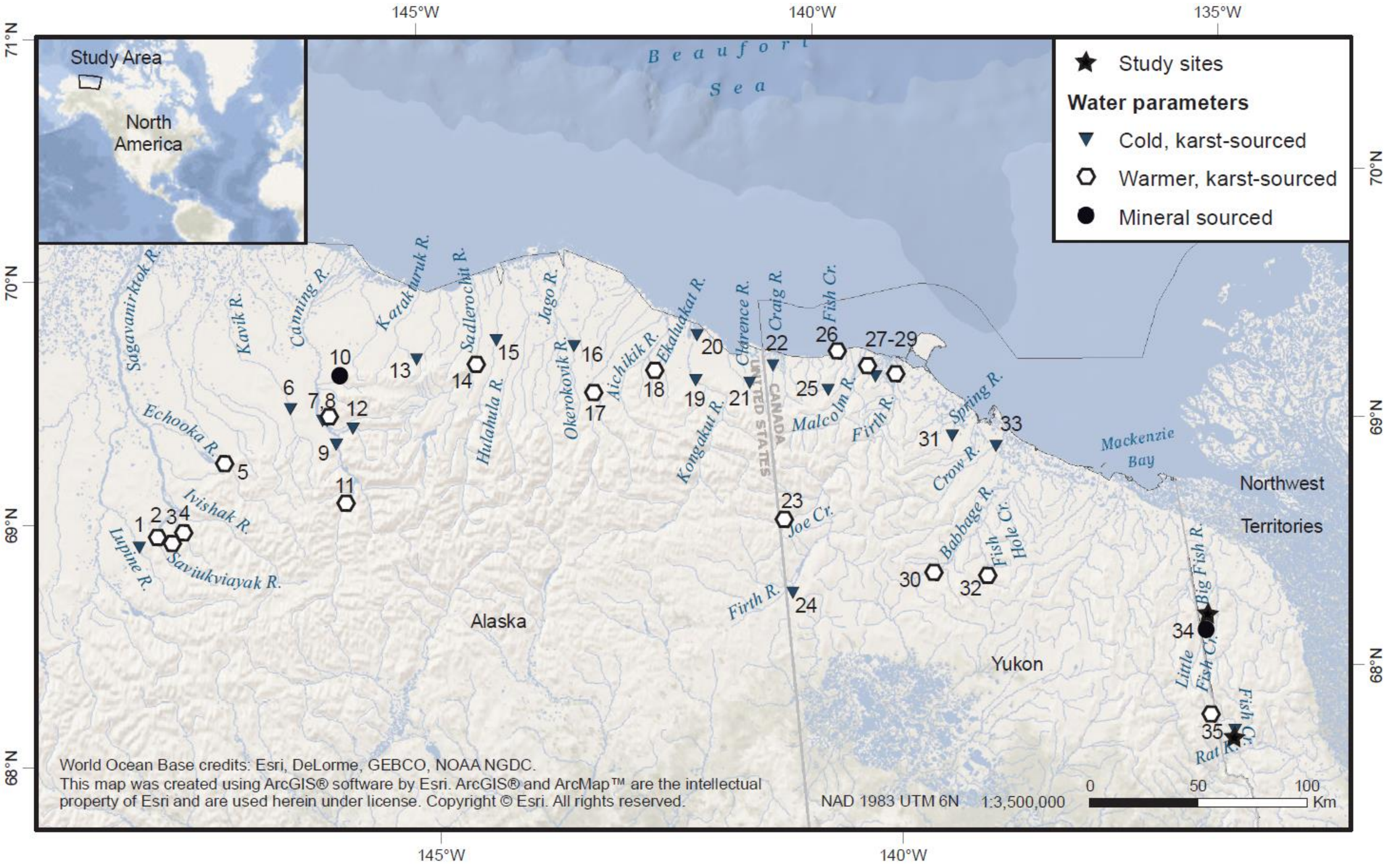

Figure 5.1: Locations of groundwater springs along the Alaska North Slope, Yukon, and Northwest Territories with water temperature data as identified from the literature, agency reports, and the present study (references in Table 5.1). Using water temperatures and

conductivity values collected during September to April, groundwater springs were categorized as: cold (<4 °C during September or <2 °C during October to April, filled triangles), warmer, karst-sourced (>4 °C during September or >2 °C during October to April and <500 µS/cm, open circles) and thermal, mineral-sourced (>500 µS/cm, filled circles). Locations of study sites for year-round thermal monitoring from the present study (stars) are also indicated. The numbers beside each symbol correspond to the locations in Table 5.1.

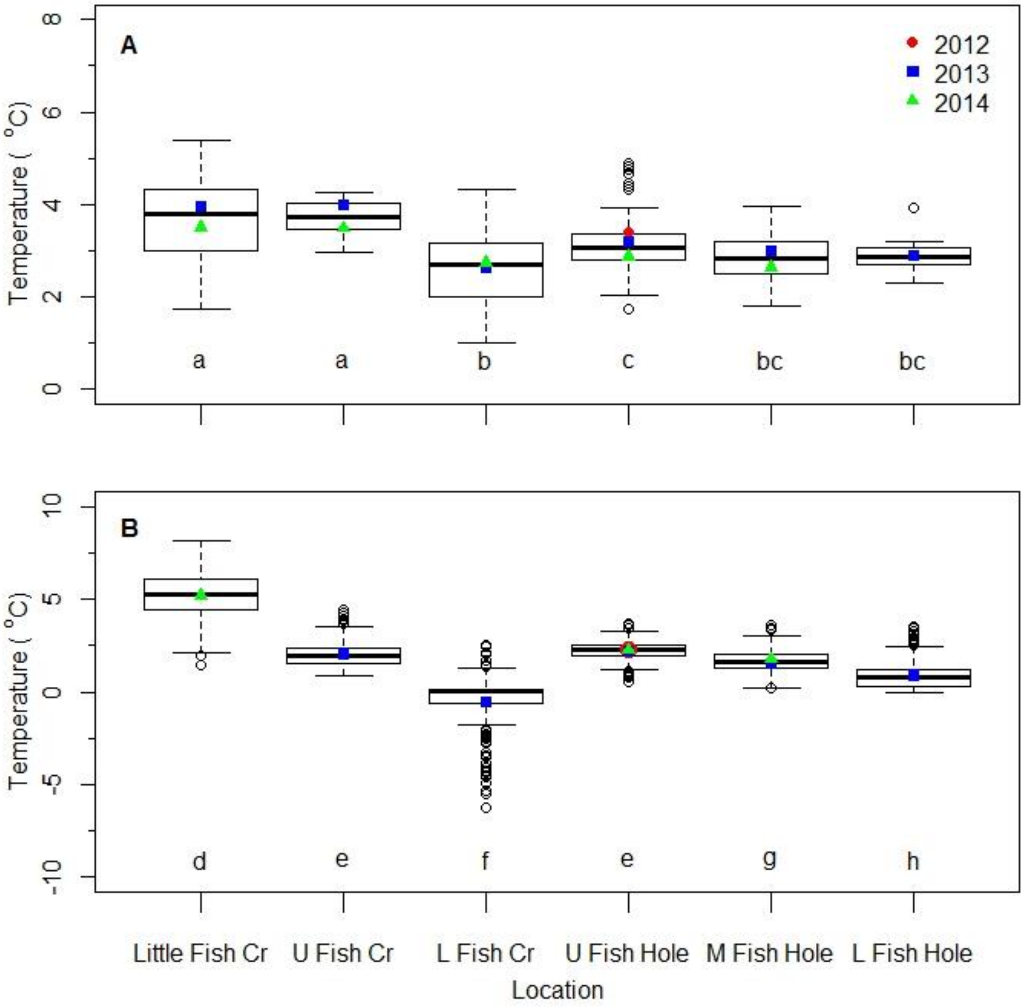
A
B
● 2012
■ 2013
▲ 2014
Temperature (°C)
0
2
4
6
8
-10
-5
0
5
10
a
a
b
c
bc
bc
d
e
f
e
g
h
Little Fish Cr
U Fish Cr
L Fish Cr
U Fish Hole
M Fish Hole
L Fish Hole
Location

Figure 5.2: Boxplots (with the mid-line at the median value, box ends at upper and lower quartiles, highest and lowest values at the extreme lines, and outliers shown with open circles) of average daily water temperature combined for all years for the (A) spawning and (B) incubation timeframes for each location of continuous temperature monitoring: Little Fish Creek (Big Fish River, NT, 68°17'45.6N, 136°21'39.6W), Upper Fish Hole Creek (Babbage River, YT, 68°35'51.04N, 138°44'06.0W), Mid Fish Hole Creek (Babbage River, YT, 68°36'25.2N, 138°44'09.6W), Lower Fish Hole Creek (Babbage River, YT, 68°36'17.4N, 138°43'56.3W), Upper Fish Creek (Rat River, NT, 67°54'18.5N, 136°31'04.4W), and Lower Fish Creek (Rat River, NT, 67°49'30.0N, 136°17'06.0W). The mean water temperature per year, site and spawning or incubation timeframe is also included as points to show the variability in temperatures among years. Significant differences ($P<0.05$) are denoted by different letters.

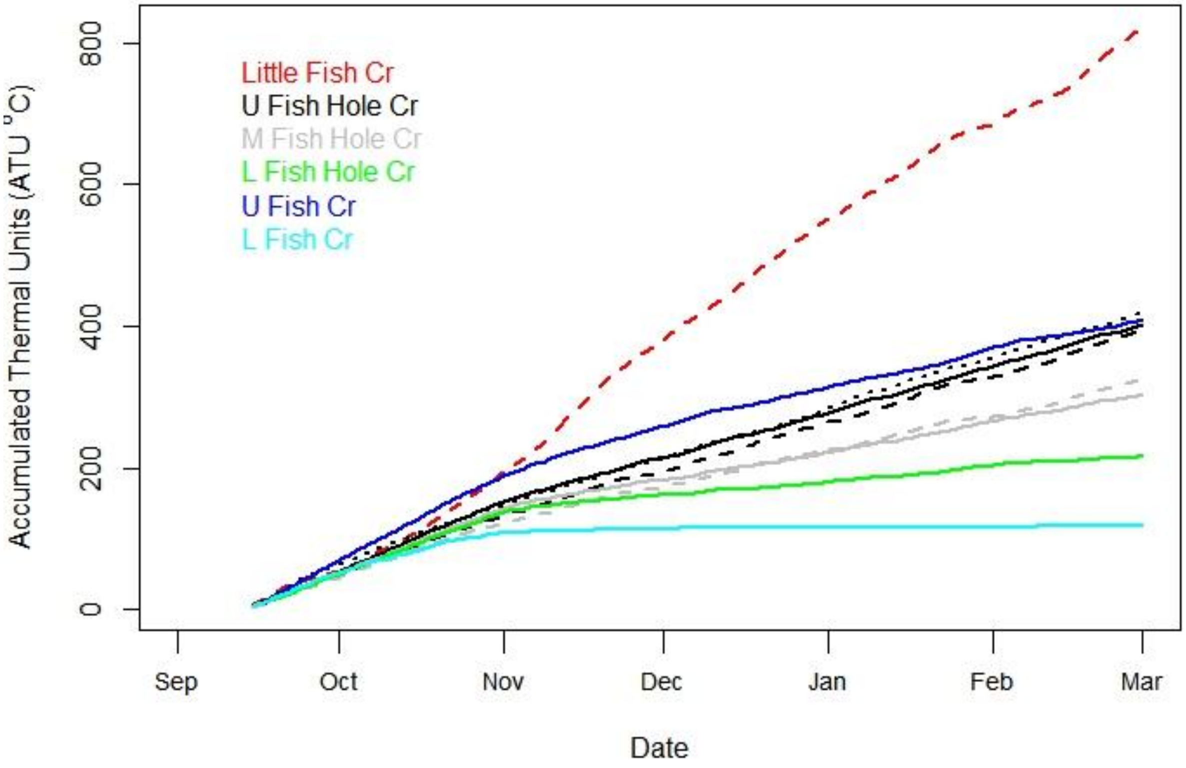

Figure 5.3: The accumulated thermal units (ATU °C) starting on a hypothetical spawn date of September 15 and continuing until March 1 for each of the six study sites selected for thermal monitoring: Little Fish Creek (Big Fish River, NT, 68°17’45.6N, 136°21’39.6W), Upper Fish Hole Creek (Babbage River, YT, 68°35’51.04N, 138°44’06.0W), Mid Fish Hole Creek (Babbage River, YT, 68°36’25.2N, 138°44’09.6W), Lower Fish Hole Creek (Babbage River, YT, 68°36’17.4N, 138°43’56.3W), Upper Fish Creek (Rat River, NT, 67°54’18.5N, 136°31’04.4W) and Lower Fish Creek (Rat River, NT, 67°49’30.0N, 136°17’06.0W). The thermal profile for 2012/13 is represented by a dotted line, 2013/14 is a solid line, and 2014/15 is a dashed line.

Chapter 6 - Evidence for historic and modern post-glacial colonizations of chum salmon at northern range edge

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Abstract

Biodiversity change in the Arctic coincides with its warming cycles and species' response can manifest as distributional shifts. During warming periods, species shift northward or expand ranges, and as it cools, species go extinct, shift southward or seek refuge. Accurate predictions of these biodiversity shifts, however, require understanding of both the capacity of aquatic species to respond to environmental change and the viability of the Arctic as habitat to support distributional shifts. Here we use chum salmon *Oncorhynchus keta* in the Canadian Arctic to indicate viability of the Arctic as habitat since deglaciation, and demonstrate the capacity of species to adapt to environmental change. Chum salmon are ideal indicators of Arctic marine habitat viability due to their historic persistence in the Arctic, their increasing abundance and distribution, and predictions of species and habitat shifts with continued warming. Using population genetic analyses and by testing colonization scenarios using Approximate Bayesian Computational analyses, we found that chum salmon colonized the Upper Mackenzie River from the Upper Yukon River during deglaciation, and that current vagrancies are occurring from northern Siberian chum salmon population sources. This confirms that the current distribution of chum salmon extends northward to the Mackenzie River, and identifies a genetically distinct, geographically isolated spawning population of chum salmon that has experienced and perhaps adapted to changing Arctic conditions for thousands of years. This has implications for predicting risks and opportunities associated with biodiversity shifts in a future Arctic, and highlights the need for baseline knowledge of Arctic species and habitats in order to accurately predict future changes.

Introduction

Although temperatures in the Arctic are currently increasing at an unprecedented rate (Arctic Monitoring and Assessment Programme 2017), the Arctic has, in the past, been warmer than it is today (Polyak et al. 2010). Warming cycles in the Arctic and the associated spread and contraction of ice sheets has forced species range contractions during periods of high ice coverage and facilitated subsequent range expansions with warming (Wilson and Hebert 1998; Polyak et al. 2010; Foote et al. 2013; Alter et al. 2015). Given current warming trends, northward distributional shifts are again occurring (Grebmeier et al. 2006; Huag et al. 2017), and species exchange between ocean basins is predicted (Vermeij and Roopnarine 2008) and has already occurred (Heide-Jørgensen et al. 2012). Although the ecosystem-level consequences of a warming Arctic are complex (Fossheim et al. 2015), accurate predictions of future Arctic scenarios are needed to adequately manage current and future resources. Predicting biodiversity shifts in a future Arctic, however, requires an understanding of the adaptive capacity of a species to respond to environmental variability, a capacity that may be rooted in its evolutionary history (Waples et al. 2008). As established harbingers of changing marine conditions, chum salmon *Oncorhynchus keta* are well suited to indicate the capacity for marine fishes to respond to current environmental changes (Irvine and Riddell 2007). They have a history in the Arctic (Nielsen et al. 2013), are currently expanding in distribution and abundance (Dunmall et al. 2013), and are predicted to shift northward following viable habitat (Yoon et al. 2015). By employing a multi-disciplinary approach to understand the persistence of chum salmon in the Canadian Arctic, I highlight the viability of the Arctic as habitat for northward colonizing species and the resilience inherent to an evolutionary history of adapting to shifting environmental conditions.

Chum salmon have the broadest geographical distribution of all the Pacific salmon species due to a history of rapid, natural range expansion from glacial refugia following warming conditions (McPhail and Lindsey 1970; Hewitt 1996; Beacham et al. 2009a). However, despite reports of spawning populations in the upper Mackenzie River, Northwest Territories (McPhail and Lindsey 1970; McLeod and O'Neil 1983; Babaluk et al. 2000; Stephenson 2006), the only direct evidence for an established, reproducing population in the Canadian Arctic has been a long history of low-level harvest in the Mackenzie River (Dunmall et al. 2013). The bottleneck of salmon survival during the winter in Arctic marine and freshwater environments has challenged explanations regarding the persistence of chum salmon in Arctic flowing drainages (Irvine et al. 2009; Dunmall et al. 2016). Indeed, salmon in the Northwest Territories are currently excluded from conservation policies due to their rarity and lack of active management (DFO 2005). However, given current warming trends, salmon and their marine thermal habitats are predicted to shift northward (Welch et al. 1995; Kaeriyama 2008; Abdul-Aziz et al. 2011; Yoon et al. 2015). Chum and pink salmon, especially, appear to be responding to shifting environmental conditions as they are being harvested in higher abundances and broader distributions in the Canadian Arctic (Dunmall et al. 2013). It remains unknown, however, if these increases in adult fish are due to increased vagrancies, greater survival of natal chum salmon in the Mackenzie River, or both (Irvine et al. 2009). Using population genetic analyses, I identify the historic and contemporary colonization pathways for chum salmon to the Mackenzie River and therefore characterize the distribution of chum salmon at their northern range edge and inform predictions of ecosystem-level changes associated with continued warming.

Colonization routes for chum salmon to their northern range edge in the Arctic are intuitively simplistic, being either via coastal or inland post-glacial pathways. However, the requirements of viable freshwater habitat for egg development during winter, stable access between the marine environment and freshwater spawning grounds potentially thousands of kilometers upstream, and viable year-round marine habitat create layers of complexity. Many aquatic species colonized the Mackenzie River from the Yukon River using meltwater pathways connecting the upper Yukon to the upper Liard rivers 10,000–8,000 years ago (Lindsey et al. 1981; Macdonald 1983; Jackson 1989), including lake trout *Salvelinus namaycush* (Wilson and Hebert 1998), Arctic grayling *Thymallus arcticus* (Stamford and Taylor 2004), Dolly Varden *S. malma* (Redenbach and Taylor 2002), and broad whitefish *Coregonus nasus* (Harris and Taylor 2010). Alternatively, some of these and other aquatic species, including lake trout (Wilson and Hebert 1998), Arctic char *S. alpinus* (Wilson et al. 1996), and broad whitefish (Harris and Taylor 2010), also colonized the Mackenzie River from the Arctic coast, perhaps facilitated by the decreased salinity due to freshwater inputs during deglaciation (Wilson and Hebert 1998). Finally, current warming marine temperatures and changing sea-ice conditions may be facilitating northward distributional shifts of chum salmon (Dunmall et al. 2013), leading to the potential for contemporary colonizations of chum salmon in novel locations (Dunmall et al. 2016).

By characterizing the contemporary genetic structure of chum salmon in the Mackenzie River, NWT, I test the hypotheses that chum salmon historically colonized the Mackenzie River system using inland and/or coastal post-glacial dispersal routes and that modern-day post-glacial colonization of this species is currently occurring in the Arctic, perhaps due to warming marine temperatures. This identifies whether Mackenzie River chum salmon represent a reproducing population at their northern distributional edge in North America. More broadly, however, the significance is the indication of timing for availability of viable habitat, which has implications to accurately projecting distributional shifts in the Arctic. Historical colonization indicates viable habitat for chum salmon has been present in the Arctic freshwater and marine environments since deglaciation, whereas contemporary colonization indicates shifting marine conditions to facilitate range expansion of this species into Arctic flowing rivers.

Methods

Tissue sampling

A total of 344 chum salmon were collected from the Northwest Territories, Canada from 2002 to 2013 as part of a community-based monitoring program to monitor salmon presence in the Canadian western Arctic (Table 6.2; Dunmall et al. 2013). DNA was extracted using DNeasy® 96 Tissue Kit by QIAGEN® (Valencia, CA) at the Fisheries and Oceans Canada Freshwater Institute (Winnipeg, Canada). Genotyping was completed at the Alaska Department of Fish and Game Gene Conservation Laboratory (Anchorage, Alaska) using the 96 SNP panel inherent to the Western Alaska Salmon Stock Identification Program (WASSIP, Jasper et al. 2012). SNP genotyping was completed using a 96.96 array (Fluidigm Corporation) and genotypes were visualized using BioMark (Fluidigm Corporation) software program and scored for each marker by two people simultaneously. Scores were entered and archived in the Gene Conservation Laboratory Oracle database, LOKI. Six markers were later excluded because they were either mitochondrial DNA markers (Oke_Cr30, Oke_Cr386, Oke_ND3-69) or were linked to other markers (Oke_U1022-139, Oke_pgap-92, Oke_gdh1-62). Forty-one chum salmon were missing genotypes for more than 20% of the loci, and were therefore excluded. The remaining 303 chum salmon were then added to the existing Western Alaska Salmon Stock Identification Program (WASSIP) chum salmon baseline (Table 6.2). This baseline consists of 82 other populations of chum salmon from around the Pacific Rim, and a target of 100 individual chum salmon was collected per population (Figure 6.1; Jasper et al. 2012). Three additional Mackenzie River chum salmon were excluded from genetic analyses requiring sampling location information as the specific location of harvest on the Mackenzie River was unknown.

Data analyses

I used the hierfstat package (Goudet and Jombart 2015) and the Adegenet package (Jombart 2008) in R (R Core Development Team 2015) to test for deviations from Hardy-Weinberg equilibrium (HWE) for each locus and sample and to calculate observed (Ho) and expected (He) heterozygosities. I used a Bonferonni correction for multiple tests (α=0.05/90) to reduce likelihood of type I errors (false-positive significance).

Chum salmon harvested in the Mackenzie River were analyzed in relation to the WASSIP chum salmon baseline to identify potential post-glacial and contemporary colonization pathways for chum salmon to the Mackenzie River. I divided the Mackenzie River chum salmon into three groups based on hypothesized colonization scenarios. Those harvested upstream from the Sahtú, called the upper Mackenzie group, were considered one group and considered to represent the colonization pathway from the Upper Yukon River. This group included salmon harvested in the Liard River, Great Slave Lake and Slave River. Those harvested in the Sahtú area, called the Ramparts group, were considered one group representing the coastal colonization pathway. These included salmon harvested at or near Ft. Good Hope, Norman Wells, Wrigley, and Great Bear Lake. The third group consisted of chum salmon harvested downstream from the Sahtú, called the Mackenzie River Delta group, and included those harvested in or near Aklavik, Inuvik, Ft. McPherson, and Tsiigehtchic (Figure 6.1). To more clearly delineate patterns on a regional rather than population-level scale, representative populations from the WASSIP baseline were selected from likely source regions representing potential colonization routes to the Mackenzie River from northern Russia (Chukotka; Kanchalan River), western Alaska (Kotzebue Sound; Noatak River) and the upper Yukon River (Teslin; Figure 6.1). These populations were selected because they represented the furthest northern populations in the WASSIP baseline for Russia and for western Alaska, and the furthest upstream population for the Yukon River.

The genetic diversity of chum salmon harvested in the Mackenzie River in relation to the WASSIP baseline was explored using principal component analyses (PCA) from the ADE4 package (Chessel et al. 2004) and the data were prepared in the Adegenet package (Jombart 2008), both in R (R Core Development Team 2015). The representative populations from potential source regions and the groupings of chum salmon based on harvest location in the Mackenzie River were plotted using an analysis of their principal components of variation to identify like patterns. As the individual chum salmon representing the Mackenzie River Delta group were scattered among the potential source regions in the PCA, this group was essentially considered a mixed fishery from multiple sources and was excluded from further analyses to identify colonization pathways.

An Approximate Bayesian Computation (ABC) approach was used to evaluate population divergence models using DIYABC 2.0 (Cornuet et al. 2008, 2014). ABC analyses provide a powerful approach for model selection using summary statistics to estimate the posterior probabilities of parameters (Beaumont et al. 2002; Beaumont 2010). Historic post-glacial (proglacial lake, coastal) and contemporary (coastal) colonization scenarios were derived and tested using the representative populations from the potential source regions and the

Ramparts and Upper Mackenzie River groups. For each scenario, a minimum of 10^4 simulated datasets were generated. For each of the source regions (n=3) and Mackenzie River groups (n=2), two one-sample summary statistics (proportion of zero values and mean of complete distribution) and four two-sample summary statistics (proportion of zero values and mean of complete distribution for each of FST and Nei's genetic distances) were used to generate the posterior probability distribution. The analyses were evaluated using PCA to ensure the simulated datasets were representative of the observed dataset. The most probable colonization scenario to explain the contemporary genetic variation was evaluated using the logistic approach, in which a linear regression is used to estimate the posterior probability of scenarios using the DIYABC software package (as described in Cornuet et al. 2008).

Results

Deviations from HWE were tested locus-by-locus (n=90 markers) and site-by-site (n=82 populations). Out of a total of 7,380 tests, only eight were significant, thus indicating almost nil deviations from HWE. The PCA analyses revealed clusters of similar genetic variation among individuals representing the potential source regions (northern Russia, western Alaska, upper Yukon; Figure 6.2). The Ramparts and Upper Mackenzie River groups generally clustered with the northern Russia and Upper Yukon regions, respectively (Figure 6.2).

The DIYABC analyses allowed a comparison of scenarios of evolutionary history based on contemporary genetic variation present in each of the five groups. Based on serial evaluation of possible evolutionary histories among the five groups, the most parsimonious options were included in a final analysis of seven scenarios (Figure 6.3). The pre-evaluation analysis demonstrated reasonable agreement between the simulated and observed datasets for this analysis (Figure 6.4), and the logistic approach showed that scenario 7 was most likely (Figure 6.5). This scenario included the northern Russian sample (Pop 1) as the historic lineage, followed by the divergence of the Upper Yukon sample (Pop 2). From the Upper Yukon River lineage, the Upper Mackenzie River sample (Pop 5) diverged prior to the divergence of the western Alaska sample (Pop 3) from the northern Russian lineage. The Ramparts sample (Pop 4) diverged from the northern Russian lineage most recently; however, subsequent PCA analyses did not reveal any apparent patterns of genetic divergence among these samples (Figure 6.6) and it is not known if the Ramparts group represents a sampling event from the northern Russian lineage or if it is at least one newly established population in that area of the Mackenzie River, or if it is a combination of both a recently established population or populations and new vagrants to the area from a northern Russian source.

Discussion

These population genetic analyses provide compelling evidence that chum salmon colonized the upper Mackenzie River from the upper Yukon River during deglaciation, 8,000–10,000 years ago. During this time, the Arctic marine environment was warmer than today, the Bering Strait was only just opening, and the Mackenzie River was a dynamic, sometimes catastrophic (Murton et al. 2010), but persistent conduit between lower latitude proglacial lakes and the Arctic Ocean. I confirm that the current distribution of chum salmon extends northward to the Mackenzie River, and identify a genetically distinct, geographically isolated spawning population of chum salmon that has experienced and perhaps adapted to changing Arctic conditions for thousands of years. Indeed, chum salmon in the upper Mackenzie River likely represent a new Conservation Unit, or irreplaceable lineage (Irvine and Riddell 2007), that is currently unrecognized, not managed, and not included in Canada's Wild Salmon Policy (DFO 2005; DFO 2008). Harvest numbers suggest the population is quite small (Dunmall et al. 2013) but local knowledge of consistent, traditional harvests in the upper Mackenzie River and the inclusion of salmon in the local languages of the Dehcho and Sahtú peoples (Stephenson 2006) support the presence of chum salmon in the upper Mackenzie River, including perhaps the Liard and Slave rivers, for generations.

Reconstructing the remarkable history of chum salmon in the Mackenzie River from deglaciation requires a multi-disciplinary approach to understand the timing of events, identify the pathways for colonization, and characterize the marine and freshwater environments used by the different life-history stages of salmon. Colonization from the upper Yukon River requires that chum salmon were not only present in Beringia, but had established populations in the upper reaches of the Yukon River. Pacific salmon are characteristically underrepresented in the paleontological record from the Pleistocene; however, archaeological evidence using bones recovered from a cooking hearth confirmed the presence of anadromous chum salmon in the upper Yukon River 11,500 years ago (Halffman et al. 2015). Approximately 9,000 to 10,000 years ago, the McConnell glacier, which covered parts of the upper Yukon River, began to recede rapidly and meltwater channels connected the upper Yukon River to the Liard River via the Pelly River connection to Finlayson Lake (Lindsey et al. 1981; Jackson 1989). By 8,640 years ago, birch (*Betula* sp.) was present in the Continental Divide area of the Selwyn Mountains (Macdonald 1983) and peat bog formation was well underway by 8,800 years ago (Jackson 1989). This indicates that previous meltwater channel connections between the Yukon and Liard rivers may have already disappeared. Several fish species used these connections to colonize the Mackenzie River, including lake trout (Wilson and Hebert 1998), Arctic grayling (Stamford and

Taylor 2004), Dolly Varden (Redenbach and Taylor 2002), and broad whitefish (Harris and Taylor 2010). However, it was generally believed that dispersal from the Beringian refuge may have been restricted to the upper Mackenzie River due to a barrier waterfall on the lower Mackenzie River (Lindsey and McPhail 1986; Wilson and Hebert 1998).

Geomorphology of The Ramparts, a post-glacially developed rock-walled canyon near present day Ft. Good Hope, provides a critical understanding of the Mackenzie River during chum salmon colonizations (Figure 6.7). Upstream of The Ramparts, the Mackenzie River flowed along the Mackenzie Mountains, into the Mountain River delta, and subsequently formed a lake that drained into a waterfall, present from 11,500 to 6,000 years ago (Mackay et al. 1973). The waterfall was likely impassable to chum salmon migrating upstream as it descended 53 m in 250 m of river length. Once the waterfall spillway was abandoned, however, approximately 6,000 years ago, the Mackenzie River flowed freely to the sea (Mackay et al. 1973). The Indian Hare River, which flows into the Mackenzie River just downstream of the waterfall, may have provided a critical alternate route for migrating salmon as it was unglaciated at the last maximum and connected the lower Mackenzie River to Glacial Lake McConnell, which covered present day Great Bear and Great Slave lakes beginning 10,500 years ago (Johnson 1975). This connection to Great Bear Lake via Indian Hare River persisted until the current Great Bear River outflow was established, which was perhaps as recent as 5,000 years ago (Rutherford et al. 1981). The Indian Hare River also formed part of the unglaciated Hare-Mackenzie trench, which was a pathway for the Mackenzie River to flow east of the Franklin Mountains until the ice lobes blocking the current westerly route melted or the coarse sediments from rivers flowing out of the Mackenzie mountains were removed (Mackay et al. 1973). This trench, which guided significant discharge of freshwater outflow from proglacial lakes, was carved to below sea level by intensive river action (Mackay et al. 1973) and perhaps served as a conduit for Lake Agassiz to flow to the Arctic Ocean during the two major outburst floods between 13,000 and 9,300 years ago (Murton et al. 2010). Therefore, while there was an impassable barrier for salmon on the Mackenzie River for over 5,000 years, the Hare-Mackenzie Trench and Hare Indian River may have provided a critical alternate route for salmon to the upper Mackenzie River from the Arctic Ocean.

As chum salmon are anadromous, colonization of the Mackenzie River during deglaciation requires that viable marine habitat be available in the Arctic Ocean for at least a portion of their life-history. Present-day sub-zero winter temperatures in the Pacific-origin surface water layer, however, require that salmon seek refuge either in the Bering Sea, the warmer and more saline Atlantic water layer >200 m in depth, or in the fresh or brackish water either in rivers adjacent to the Beaufort Sea or in the Mackenzie River plume (Irvine et al. 2009). Flooding of Beringia began 11,000 years ago, coinciding with deglaciation, at a time when maximum summer temperatures were warmer than present day but minimum winter temperatures were similar to or colder than current temperatures at similar latitudes (Elias et al. 1996). The opening of the Bering Strait therefore allowed the opportunity for Arctic-origin salmon to seek winter refuge in the north Pacific and stabilized the Atlantic Meridional Overturning Circulation (AMOC, or the ocean conveyor belt circulation, Hu et al. 2012), which contributed to the availability of the deeper Atlantic layer as a winter refuge in the Arctic. Large shoals of fish, presumed to be Arctic cod *Boreogadus saida*, presently use this deep Atlantic water layer as habitat (Crawford et al. 2012). A thermal maximum occurred from 8,500 to 6,000 years ago, and was characterized by a weaker Beaufort Gyre and stronger Transpolar Drift, a pattern consistent with a positive Arctic Oscillation index (Funder et al. 2011). These warmer

Arctic marine temperatures persisted until approximately 6,000 years ago, when a period of cooling began and the open water season became shorter, multiyear sea-ice increased, the Transpolar Drift weakened and the Beaufort Gyre strengthened, which represented a shift to a more negative Arctic Oscillation index (Funder et al. 2011). Despite the cooling period, however, more open water was present at the northern edge of Greenland and northern edge of Ellesmere Island until approximately 4,500 and 5,500 years ago, respectively, than is currently present (Funder et al. 2011). This adds another potential winter refugium for Arctic-origin salmon in the Arctic surface waters south of the sea ice edge until the cooling period increased the sea-ice extent and eliminated open water availability at suitable temperatures. Fluctuating warming and cooling patterns occurred from 2,500 years ago to present, causing open water areas to be present in these locations in Greenland and Ellesmere Island during the warming trends (Funder et al. 2011). Current warming temperatures indicate a shift back to a positive Arctic Oscillation index due to its strong link to northern temperatures (D'Arrigo et al. 2003). Continued warming, therefore, may increase the availability of viable winter marine habitat for salmon in the Arctic due to the decrease in sea ice extent and increase in surface water temperatures.

The viability of the Arctic Ocean as chum salmon habitat over the past 10,000 years may also be inferred from other Arctic-associated indicator species. After deglaciation, bowhead whale *Balaena mysticetus* expanded distributions northward, presumably following suitable habitat (Foote et al. 2013). In the western Arctic, bowhead whale select moderate ice cover habitat in summer and are found on the continental slope at depths between 200 m and 2000 m (Moore et al. 2000). In the spring and autumn, they migrate between over-wintering habitat in the Bering Sea and the Canadian Arctic, are found at shallower depths in autumn on the shelf, and form feeding aggregations along the Alaskan North Slope (Moore et al. 2000). Bowhead whale have a diet similar to that of Pacific salmon (Dunmall et al. 2013) and feed on zooplankton, especially euphausiids and copepods (Ashjian et al. 2010). Gray whale *Eschrichtius robustus*, a once rarely-sighted opportunistic feeder that has been increasing in the Arctic since the 1990's, were recorded over-wintering on the continental slope near Barrow, Alaska, and presumably found suitable habitat despite extensive ice cover (Stafford et al. 2007). Recurring polynyas, which are associated with consistent upwelling of deeper, warmer waters, are critical feeding and over-wintering habitats for many species of marine mammals, including bowhead and beluga whales *Delphinapterus leucas* (Laidre et al. 2008). Beluga primarily feed on Arctic cod *Boreogadus saida*, but also eat cephalopods, shrimps and other fishes (Frost and Lowry 1984). Beluga whales move between these critical habitat areas to the shallower shelf in the autumn, and the deeper slope and basin for summer (Moore et al. 2000). Sections of the M'Clure Strait to Lancaster Sound support large populations of marine mammals and seabirds, suggesting higher productivity in these areas (McLaughlin et al. 2004). Due to overlap in diet and use of warmer water layers in the Arctic Ocean, aggregations of marine mammals may indicate feeding and over-wintering habitats that may be similarly suitable for Pacific salmon. This suggests that the Arctic Ocean contains areas of suitable habitat for both Arctic-origin and vagrant salmon during spring, summer and autumn, and perhaps during winter as well in specific critical habitats such as recurring polynyas or in the deeper Atlantic-origin water layer.

Chum salmon also appear to be responding to Arctic warming trends by continuing northward post-glacial serial colonization into the Arctic. For species that are obligated to use linear habitat, such as a coastline, gene flow to the periphery usually originates from adjacent populations (Petrou et al. 2014; Olsen et al. 2008). These peripheral populations are often adapted to have advanced dispersal abilities, especially if the peripheral habitats are unstable (Hardie and Hutchings 2010) and presumably near tolerance limits. Range-wide chum salmon genetic diversity reflects this colonization strategy and is organized at local population and regional levels due to the relative stability of habitats over the past 5,000 years (Waples et al. 2008). These isolation-by-distance patterns of genetic diversity (Wright 1943), where geographically closer populations are more genetically similar than are geographically distant populations, is indicative of the tendency of strays to remain near natal streams (Hendry et al. 2004; Waples et al. 2008). While it is currently not known if the vagrant chum salmon harvested in the Mackenzie River are spawning successfully, strays originating from northern fringe populations may be adapted to the harsh conditions inherent to Arctic winters, and therefore more likely to colonize novel streams. Chum salmon populations are present in northward flowing rivers on the Siberian Arctic coast (Nielsen et al. 2013); however, they are not yet included in the chum salmon genetic baseline and were not included in the present analyses. Therefore, while it is apparent that a large portion of salmon harvested in The Ramparts area of the Mackenzie River originated in northern Russian rivers, they may have come from rivers not currently included in the baseline. From an Arctic perspective, northward flowing rivers to the Arctic Ocean may be the adjacent populations to those in the Mackenzie River. Future analyses that include baseline samples from those rivers would further delineate origins of vagrant chum salmon to the Mackenzie River and therefore colonization pathways, including potential transarctic routes, for novel species to northern rivers.

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Table 6.1. Collection date and location of adult chum salmon collected as part of a community-based monitoring effort that had sufficient information to be included in the Alaska Department of Fish and Game Western Alaska Salmon Stock Identification Program baseline (i.e., had genotypes for at least 80% of the 90 SNP loci). n=303

Fish ID #	Collection Date (dd/mm/year)	Collection Location (Northwest Territories)	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)
50058	01/09/2003	Aklavik	68.2167	-135.0000
50060	01/09/2003	Aklavik	68.2167	-135.0000
50062	01/09/2003	Aklavik	68.2167	-135.0000
50063	01/09/2003	Aklavik	68.2167	-135.0000
50064	01/09/2003	Aklavik	68.2167	-135.0000
50065	01/09/2003	Aklavik	68.2167	-135.0000
50066	01/09/2003	Aklavik	68.2167	-135.0000
50183	12/12/2003	Great Slave Lake	61.0666	-116.4848
50184	06/01/2004	Great Slave Lake	60.9693	-115.7668
50185	01/10/2002	Ft. Liard	60.2412	-123.4836
50186	01/12/2003	Great Slave Lake	60.8356	-115.3683
50187	01/09/2003	Great Slave Lake	62.7127	-116.0111
50188	01/09/2003	Great Slave Lake	62.7127	-116.0111
50189	15/10/2002	Aklavik	68.2167	-135.0000
50190	06/09/2003	Aklavik	68.2129	-134.9739
50191	15/09/2003	Aklavik	68.2167	-135.0000
50193	01/09/2003	Norman Wells	65.2722	-126.7973

50698	25/10/2002	Ft. McPherson	67.6345	-134.8744
50703	01/12/2004	Great Slave Lake	61.2873	-117.6041
50704	12/09/2004	Great Bear Lake	65.1777	-123.4649
50709	01/09/2004	Norman Wells	65.2730	-126.7949
51602	01/09/2004	Inuvik	68.3692	-134.1810
51606	31/09/2004	Aklavik	68.2167	-135.0000
51607	01/09/2003	Aklavik	68.2129	-134.9739
51608	03/09/2004	Ft. McPherson	67.7000	-134.5000
51610	20/10/2004	Tsiigehtchic	67.4456	-133.7485
51612	20/10/2004	Tsiigehtchic	67.4456	-133.7485
51617	23/09/2004	Ft. McPherson	67.4378	-134.8959
51618	08/09/2004	Inuvik	68.44136	-134.1889
51643	17/09/2004	Aklavik	68.2129	-134.9739
51650	01/09/2003	Tsiigehtchic	67.4456	-133.7485
51653	20/10/2004	Tsiigehtchic	67.4456	-133.7485
51657	01/09/2004	Ft. McPherson	67.4378	-134.8959
51661	17/09/2004	Aklavik	68.2129	-134.9739
51667	13/09/2004	Ft. McPherson	67.4378	-134.8959
51675	01/10/2005	Aklavik	68.2129	-134.9739
51676	15/11/2004	Aklavik	68.2237	-134.9959
51677	08/10/2005	Aklavik	68.2167	-135.0000
51680	01/10/2005	Aklavik	68.2129	-134.9739
51681	11/10/2004	Ft. McPherson	67.481	-134.8642

51682	30/09/2005	Tsiigehtchic	67.4456	-133.7485
51684	31/10/2004	Ft. McPherson	67.4810	-134.8642
51685	26/09/2005	Inuvik	68.5621	-134.2249
51687	30/09/2005	Tsiigehtchic	67.4456	-133.7485
51689	10/04/2005	Great Slave Lake	60.8356	-115.3683
51691	07/10/2005	Tsiigehtchic	67.4456	-133.7485
52538	06/10/2008	Aklavik	68.2198	-134.9927
52539	-	Aklavik	68.2198	-134.9927
52542	09/10/2008	Aklavik	68.2198	-134.9927
52547	-	Inuvik	68.4402	-134.1874
52548	29/9/2008	Aklavik	68.2167	-135.0000
52555	01/10/2008	Aklavik	68.2147	-134.9966
52558	17/09/2008	Norman Wells	65.2730	-126.7949
52559	-	Inuvik	68.4402	-134.1874
52560	-	Inuvik	68.4402	-134.1874
52562	22/08/2008	Inuvik	68.4402	-134.1874
52568	02/09/2012	Norman Wells	65.2730	-126.7949
52571	01/09/2012	Aklavik	68.2147	-134.9966
52572	-	Inuvik	68.4402	-134.1874
52573	-	Inuvik	68.4402	-134.1874
52574	18/09/2012	Norman Wells	65.2730	-126.7949
52575	05/10/2008	Great Bear Lake	65.1704	-123.2254
52801	01/09/2011	Norman Wells	65.2519	-126.6861

52802	01/09/2011	Norman Wells	65.2519	-126.6861
52803	16/10/2011	Norman Wells	65.2688	-126.7615
52804	01/09/2011	Norman Wells	65.2519	-126.6861
52805	01/09/2011	Norman Wells	65.2519	-126.6861
52806	26/10/2011	Ft. Good Hope	66.2440	-128.6660
52807	21/10/2011	Ft. Good Hope	66.2440	-128.6660
52808	20/10/2011	Norman Wells	65.2688	-126.7615
52809	20/10/2011	Norman Wells	65.2688	-126.7615
52810	26/10/2011	Ft. Good Hope	66.2440	-128.6660
52811	01/09/2011	Norman Wells	65.2519	-126.6861
52812	01/09/2011	Norman Wells	65.2519	-126.6861
52813	01/09/2011	Norman Wells	65.2519	-126.6861
52814	20/10/2011	Norman Wells	65.2688	-126.7615
52815	20/10/2011	Norman Wells	65.2688	-126.7615
52816	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52817	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52818	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52819	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52820	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52821	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52822	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52823	25/09/2011	Norman Wells	65.2688	-126.7615
52824	26/10/2011	Ft. Good Hope	66.2440	-128.6660

52825	26/10/2011	Ft. Good Hope	66.2440	-128.6660
52826	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52828	16/09/2011	Great Bear Lake	65.1724	-123.4558
52829	07/10/2011	Great Bear Lake	65.1839	-123.4230
52830	01/09/2011	Norman Wells	65.2519	-126.6861
52831	14/10/2011	Norman Wells	65.2688	-126.7615
52832	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52833	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52834	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52835	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52836	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52838	13/10/2011	Ft. Simpson (Liard R.)	61.7518	-121.2052
52839	13/10/2011	Ft. Simpson (Liard R.)	61.7518	-121.2052
52840	01/10/2011	Ft. Simpson (Liard R.)	61.6874	-121.3798
52841	01/10/2011	Ft. Good Hope	66.2440	-128.6660
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52843	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52844	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52845	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52846	26/10/2011	Ft. Good Hope	66.2440	-128.6660
52847	24/10/2011	Norman Wells	65.2688	-126.7615
52848	26/10/2011	Ft. Good Hope	66.2440	-128.6660
52849	20/10/2011	Norman Wells	65.2688	-126.7615

52850	24/10/2011	Norman Wells	65.2688	-126.7615
52851	19/10/2011	Norman Wells	65.2688	-126.7615
52852	21/10/2011	Norman Wells	65.2688	-126.7615
52853	24/10/2011	Norman Wells	65.2688	-126.7615
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52855	24/10/2011	Norman Wells	65.2688	-126.7615
52856	19/10/2011	Norman Wells	65.2688	-126.7615
52857	24/10/2011	Norman Wells	65.2688	-126.7615
52858	24/10/2011	Norman Wells	65.2688	-126.7615
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52861	08/10/2011	Norman Wells	65.2519	-126.6861
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52863	27/09/2011	Norman Wells	65.2519	-126.6861
52864	27/09/2011	Norman Wells	65.2519	-126.6861
52866	21/10/2011	Ft. Good Hope	66.2440	-128.6660
52867	21/10/2011	Ft. Good Hope	66.2440	-128.6660
52869	21/10/2011	Ft. Good Hope	66.2440	-128.6660
52871	23/09/2011	Norman Wells	65.2519	-126.6861
52872	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52874	21/10/2011	Ft. Good Hope	66.2440	-128.6660
52875	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52876	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52877	03/10/2011	Ft. Good Hope	66.2440	-128.6660

52878	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52879	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52880	03/10/2011	Ft. Good Hope	66.2440	-128.6660
52881	03/10/2011	Ft. Good Hope	66.2440	-128.6660
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52883	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52884	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52885	03/10/2011	Norman Wells	65.2519	-126.6861
52886	01/10/2011	Norman Wells	65.2519	-126.6861
52887	01/10/2011	Norman Wells	65.2519	-126.6861
52888	01/10/2011	Norman Wells	65.2519	-126.6861
52889	01/10/2011	Norman Wells	65.2519	-126.6861
52890	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52891	01/10/2011	Norman Wells	65.2519	-126.6861
52892	01/09/2011	Norman Wells	65.2519	-126.6861
52893	01/10/2011	Norman Wells	65.2519	-126.6861
52894	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52895	01/10/2011	Ft. Good Hope	66.2440	-128.6660
52896	01/09/2011	Ft. Good Hope	66.2440	-128.6660
52897	01/10/2011	Norman Wells	65.2519	-126.6861
52898	05/10/2011	Norman Wells	65.2519	-126.6861
52899	03/10/2011	Norman Wells	65.2519	-126.6861
52900	08/10/2011	Norman Wells	65.2519	-126.6861

52901	28/09/2011	Norman Wells	65.2519	-126.6861
52902	28/09/2011	Norman Wells	65.2519	-126.6861
52903	03/10/2011	Ft. Good Hope	66.244	-128.666
52904	03/10/2011	Ft. Good Hope	66.244	-128.666
52905	03/10/2011	Ft. Good Hope	66.244	-128.666
52906	08/10/2011	Norman Wells	65.2688	-126.7615
52907	10/10/2011	Norman Wells	65.2688	-126.7615
52908	05/10/2011	Norman Wells	65.2519	-126.6861
52909	03/10/2011	Norman Wells	65.2519	-126.6861
52910	10/10/2011	Norman Wells	65.2688	-126.7615
52911	28/09/2011	Norman Wells	65.2519	-126.6861
52912	14/10/2011	Norman Wells	65.2688	-126.7615
52913	08/10/2011	Norman Wells	65.2519	-126.6861
52914	10/10/2011	Norman Wells	65.2688	-126.7615
52915	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52916	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52917	01/10/2011	Norman Wells	65.2519	-126.6861
52918	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52919	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52920	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52921	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52922	18/09/2011	Norman Wells	65.2519	-126.6861
52923	01/10/2011	Ft. Good Hope	66.2563	-128.6411

52924	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52925	01/10/2011	Ft. Good Hope	66.2563	-128.6411
52926	01/10/2011	Ft. Good Hope	66.2563	-128.6411
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52928	01/09/2011	Inuvik	68.269	-133.8002
52929	01/09/2011	Inuvik	68.269	-133.8002
52930	09/10/2011	Norman Wells	65.2688	-126.7615
52931	24/09/2011	Norman Wells	65.2519	-126.6861
52932	29/09/2011	Ft. Good Hope	66.2440	-128.6660
52933	15/10/2011	Norman Wells	65.2688	-126.7615
52934	01/10/2011	Norman Wells	65.2688	-126.7615
52935	07/10/2011	Ft. McPherson	67.3385	-134.8741
52936	24/09/2011	Norman Wells	65.2519	-126.6861
52937	09/10/2011	Norman Wells	65.2688	-126.7615
52938	14/10/2011	Norman Wells	65.2688	-126.7615
52939	24/09/2011	Norman Wells	65.2519	-126.6861
52940	10/10/2011	Norman Wells	65.2688	-126.7615
52941	14/10/2011	Norman Wells	65.2688	-126.7615
52942	01/10/2009	Inuvik	68.2690	-133.8002
52943	01/09/2011	Inuvik	68.2690	-133.8002
52944	01/10/2011	Inuvik	68.43815	-134.2142
52948	21/09/2011	Aklavik	68.2159	-135.0015
52949	01/12/2010	Inuvik	68.3551	-133.7354

52950	07/10/2011	Ft. McPherson	67.3385	-134.8741
52951	06/10/2011	Norman Wells	65.2519	-126.6861
52952	11/10/2011	Inuvik	68.43815	-134.2142
52953	05/10/2011	Norman Wells	65.2519	-126.6861
52954	05/10/2011	Norman Wells	65.2519	-126.6861
52955	05/10/2011	Norman Wells	65.2519	-126.6861
52956	2011	Ft. Good Hope	66.2563	-128.6411
52957	2011	Ft. Good Hope	66.2563	-128.6411
52958	2011	Ft. Good Hope	66.2563	-128.6411
52959	2011	Ft. Good Hope	66.2563	-128.6411
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52972	2011	Ft. Good Hope	66.2440	-128.6660

52973	2011	Ft. Good Hope	66.244	-128.666
52974	2011	Ft. Good Hope	66.244	-128.666
52975	2011	Ft. Good Hope	66.2563	-128.6411
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52977	2011	Ft. Good Hope	66.2563	-128.6411
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52980	2011	Ft. Good Hope	66.2440	-128.6660
52981	2011	Ft. Good Hope	66.2440	-128.6660
52982	19/09/2011	Tsiigehtchic	67.4546	-133.7568
52983	19/09/2011	Tsiigehtchic	67.4546	-133.7568
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52985	07/10/2011	Tsiigehtchic	67.4467	-133.7480
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52991	07/10/2011	Tsiigehtchic	67.4467	-133.7480
52992	08/10/2011	Aklavik	68.2159	-135.0015
52993	09/10/2011	Aklavik	68.2159	-135.0015
52994	12/10/2011	Tsiigehtchic	67.4546	-133.7568
52995	20/11/2011	Ft. McPherson	67.3385	-134.8741

52996	14/10/2011	Ft. McPherson	67.3386	-134.8742
52997	10/10/2011	Tsiigehtchic	67.4468	-133.7481
52998	10/10/2011	Tsiigehtchic	67.4468	-133.7481
53000	12/10/2011	Tsiigehtchic	67.4547	-133.7569
53001	12/10/2011	Tsiigehtchic	67.4547	-133.7569
53002	12/10/2011	Tsiigehtchic	67.4547	-133.7569
53003	05/10/2011	Tsiigehtchic	67.4468	-133.7481
53004	05/10/2011	Tsiigehtchic	67.4468	-133.7481
53006	05/10/2011	Tsiigehtchic	67.4468	-133.7481
53007	21/10/2011	Great Slave Lake	60.9745	-116.2207
53008	16/12/2011	Great Slave Lake	60.9745	-116.2207
53009	24/10/2011	Fort Providence	61.3023	-117.5954
53010	21/10/2011	Jean Marie River	61.5279	-120.6288
53011	06/09/2011	Inuvik	68.2195	-134.4338
53013	09/10/2011	Inuvik	68.4382	-134.2143
53014	30/09/2011	Tsiigehtchic	67.4547	-133.7569
53015	30/09/2011	Tsiigehtchic	67.4547	-133.7569
53016	26/09/2011	Tsiigehtchic	67.4547	-133.7569
53017	27/09/2011	Tsiigehtchic	67.4547	-133.7569
53019	11/10/2011	Inuvik	68.3551	-133.7354
53020	05/10/2011	Norman Wells	65.2761	-126.8121
53021	18/10/2011	Norman Wells	65.2761	-126.8121
53022	29/09/2010	Norman Wells	65.2519	-126.6861

53024	10/10/2011	Norman Wells	65.2761	-126.8121
53025	10/10/2011	Norman Wells	65.2761	-126.8121
53026	2011	Ft. Good Hope	66.2440	-128.6660
53027	2011	Ft. Good Hope	66.2440	-128.6660
53028	2011	Ft. Good Hope	66.2440	-128.6660
53029	2011	Ft. Good Hope	66.2440	-128.6660
53030	2011	Ft. Good Hope	66.2440	-128.6660
53031	2011	Ft. Good Hope	66.2440	-128.6660
53038	2012	Ft. McPherson	67.4810	-134.8642
53042	09/10/2012	Ft. Liard	60.2422	-123.4758
53043	26/10/2012	Ft. Simpson	61.8820	-121.3595
53047	12/10/2012	Tsiigehtchic	67.4468	-133.7481
53048	21/10/2012	Inuvik	68.2690	-133.8002
53049	2012	Ft. McPherson	67.4810	-134.8642
53050	2012	Ft. McPherson	67.4810	-134.8642
53051	04/10/2012	Norman Wells	65.2519	-126.6861
53052	26/11/2012	Great Bear Lake	65.1839	-123.4231
53053	13/10/2012	Norman Wells	65.2519	-126.6861
53171	07/10/2014	Ft. McPherson	67.3420	-134.8800
53172	15/10/2014	Great Slave Lake	60.8316	-115.7748
53173	29/09/2014	Aklavik	68.2167	-135.0000
53174	2014	Aklavik	68.2167	-135.0000
53175	09/10/2014	Great Slave Lake	60.8819	-115.1080

53229	22/10/2013	Great Bear Lake	65.1904	-123.4464
53230	25/10/2013	Ft. Liard	60.2430	-123.4740
53231	07/10/2013	Inuvik	68.3774	-134.0958
53232		Unknown		
53235	01/10/2009	Inuvik	68.2690	-133.8002
53237	01/10/2009	Inuvik	68.2690	-133.8002
53238	01/10/2009	Inuvik	68.2690	-133.8002
53239		Unknown		
53241	30/09/2013	Ft. Simpson (Liard R.)	61.7071	-121.2904
53246		Unknown		

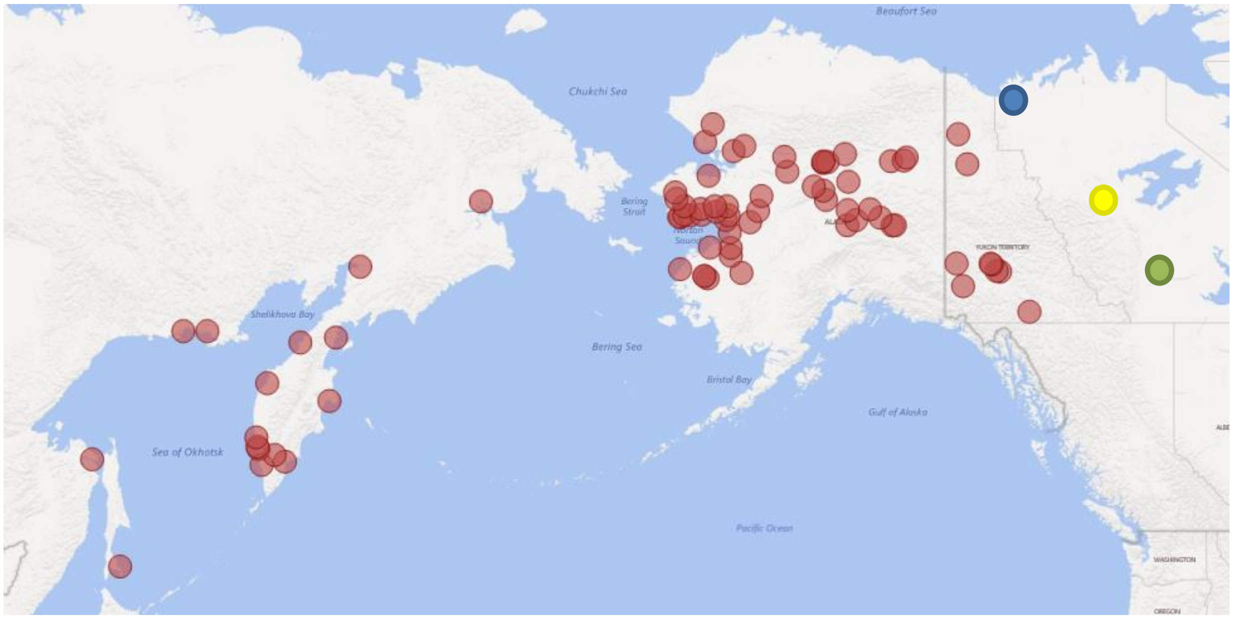


Figure 6.1: WASSIP populations (in red) and three groups of chum salmon harvested in Mackenzie River: Mackenzie River Delta (in blue), Ramparts (in yellow), Upper Mackenzie River (in green).

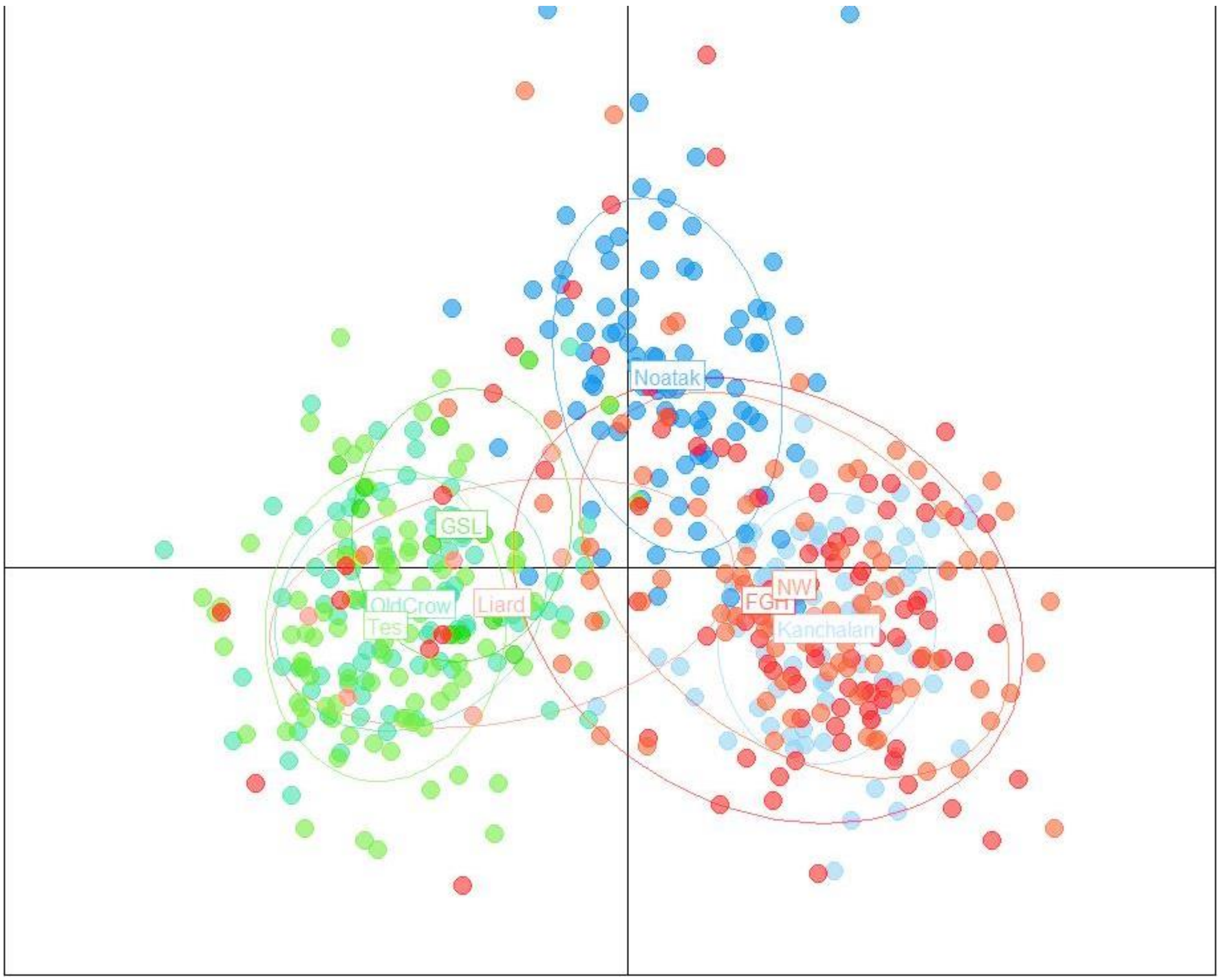
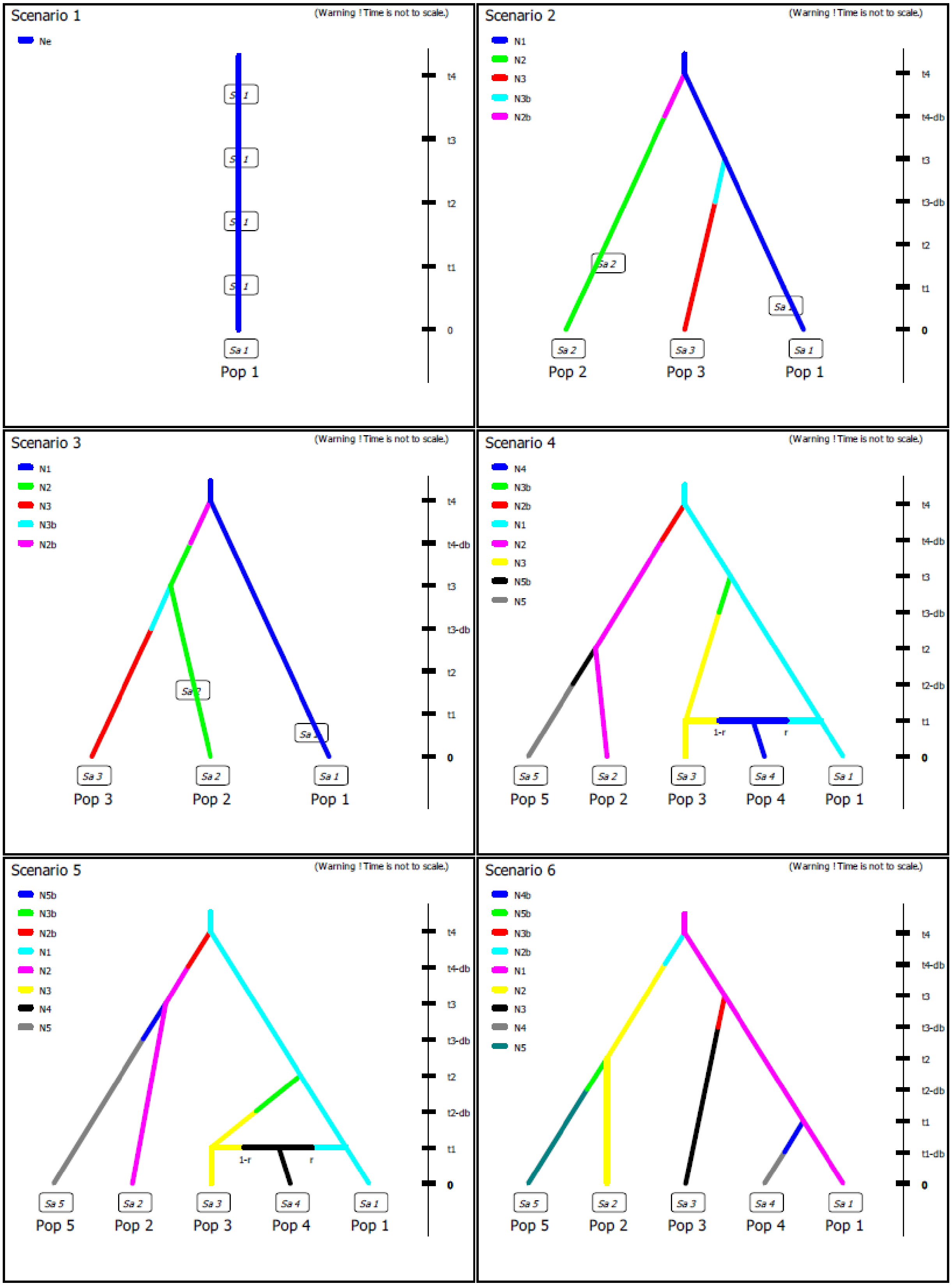


Figure 6.2: Principal Component Analysis (PCA) of Western Alaska Salmon Stock Identification Program (WASSIP) regions and Mackenzie River groups. For WASSIP regions, Kanchalan represents Russia, Noatak represents western Alaska, and Old Crow and Teslin represent the Upper Yukon river origins. For Mackenzie River groups, Liard and GSL (Great Slave Lake) represent Upper Mackenzie River group and NW (Norman Wells) and FGH (Ft. Good Hope) represent The Ramparts group. The colors are based on the first three PCs of the PCA, recoded respectively on the red, green, and blue channel, and therefore represent genetic differentiation.


Scenario 1
(Warning ! Time is not to scale.)
Ne
t4
t3
t2
t1
0
Sa 1
Pop 1
Scenario 2
(Warning ! Time is not to scale.)
N1
N2
N3
N3b
N2b
t4
t4-db
t3
t3-db
t2
t1
0
Sa 2
Sa 1
Sa 2
Sa 3
Sa 1
Pop 2
Pop 3
Pop 1
Scenario 3
(Warning ! Time is not to scale.)
N1
N2
N3
N3b
N2b
t4
t4-db
t3
t3-db
t2
t1
0
Sa 2
Sa 1
Sa 3
Sa 2
Sa 1
Pop 3
Pop 2
Pop 1
Scenario 4
(Warning ! Time is not to scale.)
N4
N3b
N2b
N1
N2
N3
N5b
N5
t4
t4-db
t3
t3-db
t2
t2-db
t1
0
1-r
r
Sa 5
Sa 2
Sa 3
Sa 4
Sa 1
Pop 5
Pop 2
Pop 3
Pop 4
Pop 1
Scenario 5
(Warning ! Time is not to scale.)
N5b
N3b
N2b
N1
N2
N3
N4
N5
t4
t4-db
t3
t3-db
t2
t2-db
t1
0
1-r
r
Sa 5
Sa 2
Sa 3
Sa 4
Sa 1
Pop 5
Pop 2
Pop 3
Pop 4
Pop 1
Scenario 6
(Warning ! Time is not to scale.)
N4b
N5b
N3b
N2b
N1
N2
N3
N4
N5
t4
t4-db
t3
t3-db
t2
t2-db
t1
t1-db
0
Sa 5
Sa 2
Sa 3
Sa 4
Sa 1
Pop 5
Pop 2
Pop 3
Pop 4
Pop 1

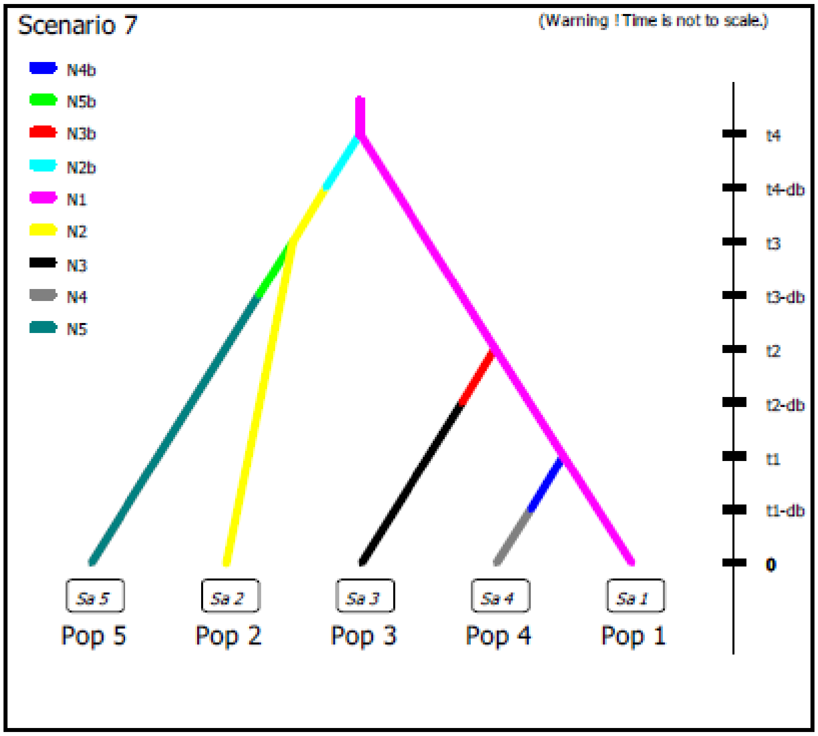


Figure 6.3: Historic post-glacial or contemporary coastal colonization scenarios for chum salmon to the Mackenzie River tested using Approximate Bayesian Computational analysis where Pop 1 is Kanchalan River (representing Russia), Pop 2 is Teslin River (representing Upper Yukon), Pop 3 is Noatak River (representing western Alaska), Pop 4 is The Ramparts Mackenzie River group, and Pop 5 is the Upper Mackenzie River group. Subsequent analyses identified Scenario 7 as the most probable colonization scenario for chum salmon to the Mackenzie River (Figure 6.5). Sa# are the sampling events, t# is the timing from present (0) of the sampling events, Pop# are the populations resulting from those events, N# is the effective population size of those populations, N#b is the effective population size at the bottlenecks, and db represents a bottleneck.

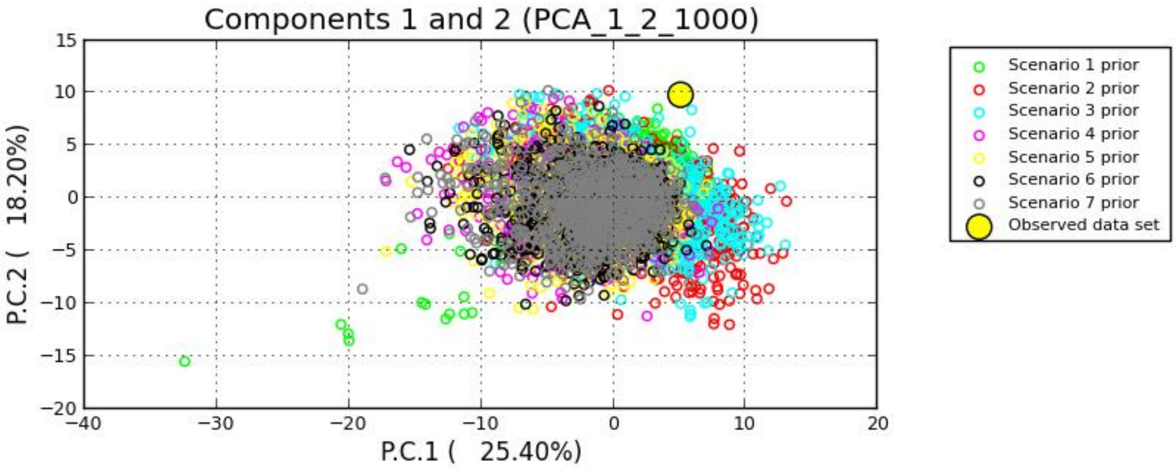


Figure 6.4: Pre-evaluation of simulated data compared to observed data for Approximate Bayesian Computational analysis of historic post-glacial or contemporary coastal colonization scenarios for chum salmon to the Mackenzie River tested in Figure 6.3.

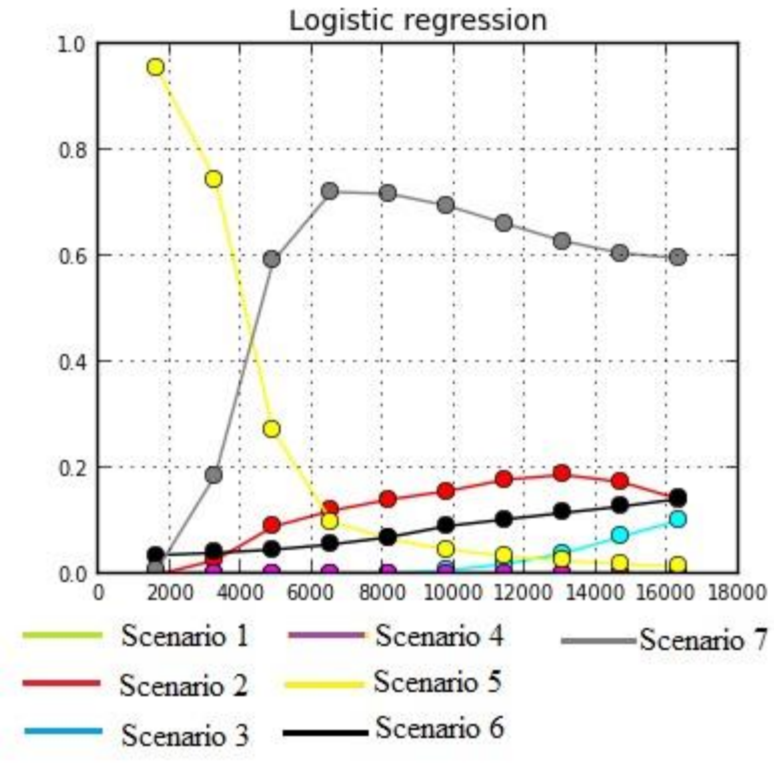


Figure 6.5: Logistic approach identified Scenario 7 as the most probable colonization scenario for chum salmon harvested in the Mackenzie River, compared to other ecologically-derived scenarios using DIYABC analyses. The Y axis represents the posterior probability for each scenario and the X axis is the number of simulated datasets chosen for the logistic regression analyses out of a total 1,634,200 simulated datasets generated to infer the posterior probability of each scenario.

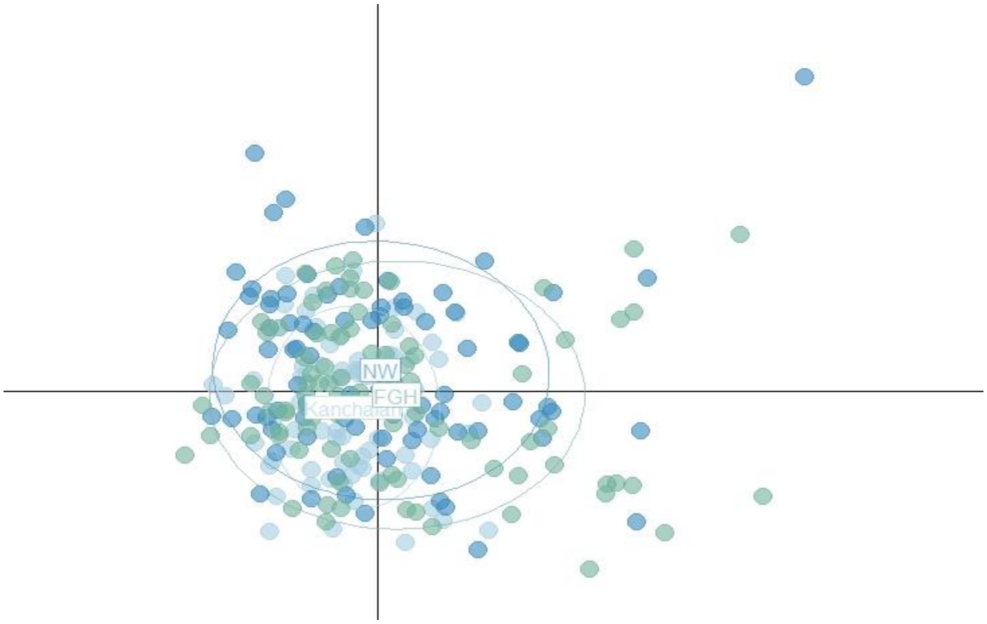


Figure 6.6: Principal component analysis (PCA) of chum salmon harvested in Norman Wells, NW) and Ft. Good Hope (FGH), Northwest Territories, collectively called The Ramparts region, with Kanchalan, representing the northern Russian region.

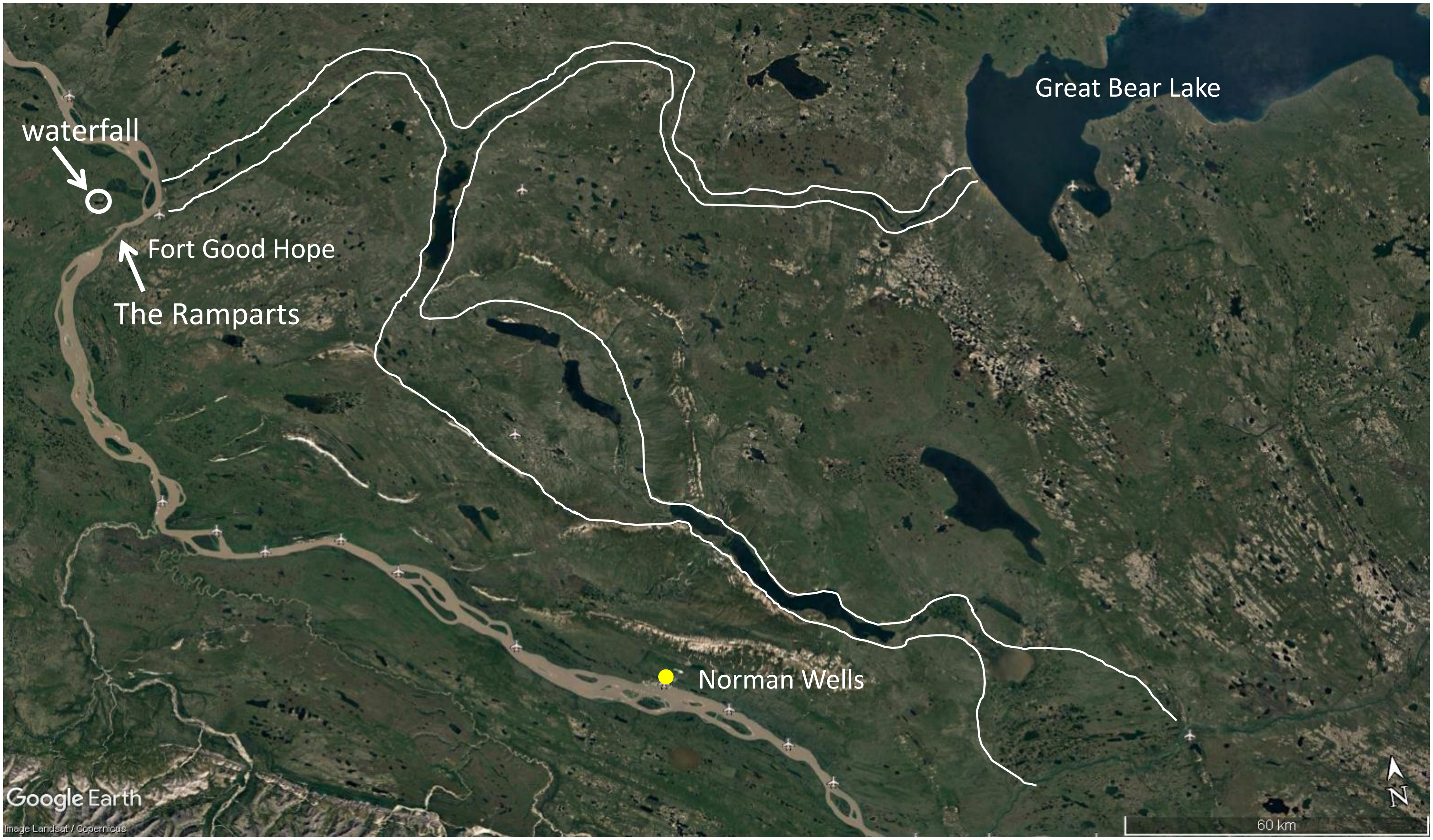


Figure 6.7: Reconstruction of historic flow pathways (white lines) for Mackenzie River, NWT and historic outflow for Great Bear Lake based on analyses in Mackay et al. (1973) and Johnson (1975).

Chapter 7 – Synthesis: Are salmon the new char of an Arctic in the Anthropocene?

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"Humans are now the most significant driver of global change, propelling the planet into a new geological epoch, the Anthropocene." The Stockholm Memorandum; May 18, 2011

Human attention is shifting northward as rapidly as the temperatures are warming in the Arctic. Melting sea ice is creating new opportunities for shipping (CBC 2015), massive cruise ships now pilot the Northwest Passage (CBC 2016), and industry is expanding with new mines and increasing production (CBC 2017), potential fisheries (Walker et al. 2015), and renewed interest in oil and gas development (Gulas et al. 2017). These increasing human pressures are additive to the impacts of climate change, which are more rapid and most pronounced at the poles, and represent the greatest threat to biodiversity in the Arctic (Meltofte 2013). Collectively, these anthropogenic impacts are fueling initiatives to conserve species and their habitats (e.g., Canada Target 1). Arctic biodiversity, however, is already changing (Meltofte 2013). Species are shifting northward following favorable conditions or prey (Chapter 2, Dunmall et al. 2013). Arctic-adapted species are also changing distributions or migration patterns, declining, or facing potential extinction in response to environmental change (Meltofte 2013). Therefore, Arctic biodiversity in a warming climate will be the net result of gains due to successful range expansions and losses due to range contractions or extinctions (Meltofte 2013). Salmon (*Oncorhynchus* spp.) and char (*Salvelinus* spp.), both iconic and culturally-essential fish genera in their current ranges, are increasingly being harvested together in subsistence fisheries in the Arctic (Chapter 2, Dunmall et al. 2013). The mutual interest from scientists and Indigenous peoples to explore these increasing salmon harvests represents an opportunity to integrate scientific and indigenous knowledge systems and establish salmon as an ecosystem-level indicator of change in the Arctic. However, this requires an innovative shift in the scientific ethos regarding distributional changes. Rather than perceiving the Arctic as a conservation haven for invading species, I reserve judgement and instead investigate the potential impacts and opportunities of colonizing species on ecosystem function and subsistence culture. By listening to Indigenous peoples, I learn from their observations of change, develop tools to address their questions, and integrate subsistence and science to help predict a rapidly changing Arctic in the Anthropocene epoch.

The rapid rate of change in the Arctic appears to currently exceed the pace of science needed to inform conservation initiatives, contribute to effective management, and proactively anticipate interactions between species, their environment, and stakeholders. The lack of basic information about species and their habitats (Reist et al. 2006b) contributes to the already significant challenges of assessing biodiversity change in the vast, remote and sparsely-populated Arctic. Compounding this, it is difficult to apply scientific approaches developed for sub-Arctic assessments to the Arctic due to its harsh, cold, dynamic, and often inaccessible environments. However, Arctic biodiversity is irrevocably linked to the culture of Indigenous peoples in the north and their perceptions of change are rooted in their dependence on the environment and social values to protect subsistence opportunities (Meltofte 2013). In this thesis, the development of community-based monitoring applications for data gathering recognizes the validity of local observations (Gofman 2010) and facilitates broad-scale assessments of biodiversity change (Chapter 3) and fine-scale assessments of key areas and species (Chapter 4). Human innovations and associated impacts are characteristic of the Anthropocene (Lewis and Maslin 2015). Innovatively creating the opportunity to assess change by those directly observing immediate effects provides a powerful approach to facilitate human influence on the pace of science as well as our role in the pace of change.

Citizen science is a rapidly-developing method of monitoring that builds on social networking, observations and reporting to engage non-professionals in data gathering (Gofman 2010; Newman et al. 2012). However, participation may be lacking in under-represented groups due to a lack of alignment of research questions with community priorities (Pandya 2012). The development of a citizen science framework that bridges scientific and indigenous knowledge, allows for mutual reporting and continuous communication between scientists and community observers, and connects those observations to broader assessments of change, citizen science can be successful in Arctic applications (Chapter 3). Using this novel citizen science framework, community members from across the Canadian Arctic voluntarily report harvests of Pacific salmon and Atlantic salmon in a project called Arctic Salmon. This project, which is the largest citizen science program in the Canadian Arctic, successfully documents trends in salmon abundances and the broadening distribution of salmon harvests (Chapter 2, Dunmall et al. 2013). At inception, in 2000, the focus originally was on increased harvests of chum salmon *Oncorhynchus keta*; however, it is now apparent that all Pacific salmon species are being harvested in increasing abundances and in broadening distributions in the Canadian Arctic. While increased reporting does not necessarily translate to increased abundances of salmon, the general increasing trends are corroborated by local knowledge of higher numbers and broadening distributions of salmon in the Canadian Arctic. Arctic Salmon is also beginning to track harvests of other fishes outside known distributions, as Dolly Varden *Salvelinus malma* has been reported outside its known distribution using the Arctic Salmon citizen science program. This new information and possible distributional changes are leading to simultaneous questions from community members about the potential impacts of potentially colonizing fishes on native species and about how to prepare salmon as food using traditional methods. These questions highlight the desire to protect biodiversity, and also the ability to adapt to rapid changes and interest in taking advantage of new resources.

Although the first pink salmon *O. gorbuscha* in the Canadian Arctic was reported near Tuktoyaktuk, Northwest Territories in 1936 (Dymond 1940 as reported in Stephenson 2006), they were very rarely harvested in the Canadian Arctic until 2004 (Chapter 2, Dunmall et al. 2013). Now, pink salmon are reported almost every year, although harvests are more consistent and are higher in even-numbered years than in odd-numbered years (Chapter 2, Dunmall et al. 2013). The distribution of pink salmon harvests is also increasing in the Canadian Arctic, and has expanded to include all communities in the Mackenzie River Delta and Beaufort Sea by 2014. In 2016, the distribution of pink salmon harvests extended into Nunavut for the first time when two pink salmon were harvested in Kugluktuk. Pink salmon distribution is also expanding Arctic-wide as pink salmon are occurring in almost all of the salmon rivers in Finnmark, Norway, can be found in nearby tributaries in Finland, have spread into 40 rivers in northern Norway, and are caught in Spitsbergen, Iceland, England and Scotland (Niemelä et al. 2016). In addition, the first pink salmon was harvested in east Greenland in 2012 (Chapter 2, Dunmall et al. 2013), in Nain, Labrador in 2014 (Dempson 2016), and now also in Ireland in 2017 (BBC 2017b). In Russia, pink salmon are found in most rivers flowing to the Arctic Ocean, including on the Kola Peninsula, in the Arkhangelsk region, the Pechora River, on the Yamal Peninsula, further east to Dixon Island (Niemelä et al. 2016), and from the Lena River east and south to the Anadyr Gulf (Groot and Margolis 1991). Range expansions of pink salmon are likely related to their tendency to stray (Hendry et al. 2004). However, successful spawning of pink salmon at northern latitudes is also dependent on timing of spawning; those populations that spawn early benefit from the development of juveniles while water temperatures are warmer (Niemelä et al. 2016). Warming temperatures, including earlier sea ice melts, higher summer temperatures, and warmer temperatures extending later in the season, will likely contribute to the continued expansion of salmon at high latitudes (Dempson 2016; Chapter 5, Dunmall et al. 2016; Niemelä et al. 2016). Their high straying rate (Quinn 1993), combined with the short two year life-cycle and the higher tolerance of colder temperatures by juvenile pink salmon, make pink salmon more likely to colonize Arctic rivers than other species of Pacific salmon (Dempson 2016).

Although sockeye salmon *O. nerka* are rarely harvested in the Canadian Arctic, they are increasingly being reported in subsistence harvests in Beaufort Sea communities, as well as in communities upstream in the Mackenzie River as far as Norman Wells, Northwest Territories. They were first reported in the Canadian Arctic in 1966 in Ulukhaktok, Northwest Territories and in Bathurst Inlet, Nunavut in 1967 (Hunter 1974 as cited in Stephenson 2006). Since 1993, 47 sockeye salmon have been reported in the Canadian Arctic (Chapter 2, Dunmall et al. 2013), including 10 between 2003 and 2012 (Chapter 2, Dunmall et al. 2013), three in 2015 and 28 in 2016. It seems unexpected for sockeye to be present in the Arctic because they have strong philopatry to natal spawning sites (Quinn 1993), usually spawn in lake-fed systems, and juvenile sockeye spend 3-5 years in lakes before migrating to the ocean (Quinn 2005). However, sockeye salmon also have the coldest upper thermal limit (8.9^{o}C) (Welch et al. 1995, 1998), shallowest vertical distribution at less than 40 m (Walker et al. 2007), and feed primarily on crustaceans, including euphausiids, hyperiids and copepods (Karpenko et al. 2007). The diet of sockeye salmon is actually similar to that of bowhead whale *Balaena mysticetus*, which feed on zooplankton, especially euphausiids and copepods (Ashjian et al. 2010). As reductions in sea ice may benefit bowhead whale through increased feeding opportunities (Moore and Laidre 2006), it is possible that diminishing sea ice will similarly increase feeding opportunities for Pacific salmon, including sockeye salmon (Chapter 2, Dunmall et al. 2013). Therefore, the interaction of warming sea-surface temperatures, increased feeding opportunities, and a higher tolerance for colder temperatures compared to other species of Pacific salmon (Welch et al. 1995, 1998), may contribute to a continued increasing trend in sockeye salmon harvests in the Arctic.

Harvests of Chinook and coho salmon (*O. tshawytscha* and *O. kisutch*) are exceedingly rare in the Canadian Arctic (Chapter 2, Dunmall et al. 2013). The first Chinook salmon reported in the Northwest Territories was in Ft. Liard in 1979 (McLeod and O'Neil 1983), and the first reported in Nunavut was in 1950 in Kugluktuk (Hunter 1974 as cited in Stephenson 2006). Verified harvests of single Chinook salmon occurred in the Slave River in 1995 and near Aklavik in 2002 (Stephenson 2006). There is an increasing trend in Chinook salmon harvests, however, as six were reported in the Northwest Territories in 2004, one was harvested in 2005, three were harvested in 2007 and one was harvested in 2008 (Chapter 2, Dunmall et al. 2013). Since 2008, seven additional Chinook salmon have been reported in the Northwest Territories, including one in 2013, one in 2015 and five in 2016, including the first Chinook salmon reported in Paulatuk, NT, and the first reported in Ft. Resolution, NT. Coho salmon are the rarest of all Pacific salmon species reported in the Canadian Arctic. A total of four have been reported in the Northwest Territories and none have been reported in Nunavut. The first coho salmon in the Northwest Territories was harvested in 1987 in Great Bear Lake (Babaluk et al. 2000), an additional coho salmon was harvested in 1998 (Stephenson 2006), one was harvested in 2011 in Tsiigehtchic, NT (Chapter 2, Dunmall et al. 2013), and one coho salmon was harvested in Norman Wells, NT in 2016.

Although chum salmon have a long history of harvest in the Northwest Territories and the Mackenzie River is included in chum salmon distributions (Chapter 2, Dunmall et al. 2013), they are not currently included in Canada's Wild Salmon Policy (DFO 2005) and their strategies for survival in the Arctic are debated (Irvine et al. 2009). Recently, harvests of chum salmon in the Northwest Territories are trending upwards and years of high harvest levels, called exceptional years, are becoming more frequent (Chapter 2, Dunmall et al. 2013). Using tissue samples from chum salmon traded into the Arctic Salmon citizen science program for population genetic analyses, I was able to establish that chum salmon colonized the upper Mackenzie River from the upper Yukon River at deglaciation and represent an established, reproducing population of chum salmon in the upper Mackenzie River (Chapter 6). I also found that chum salmon most closely resembling those from a Chukotka population are being harvested in the central and perhaps lower Mackenzie River, although it is not known if they are successfully spawning or are vagrants (Chapter 6). These findings solidify that the northern range edge for chum salmon in North America is the Mackenzie River, NT and that the Arctic marine and freshwater environments have supported chum salmon for thousands of years. These findings also suggest that the warming marine conditions are facilitating continued serial colonization of the Mackenzie River via coastal pathways by chum salmon originating from northern Russian sources, which are presumably adapted to range edge conditions. The lack of availability of chum salmon samples from populations in major northward flowing rivers in Siberia prevent assessments of colonization via trans-Arctic or Bering Strait pathways. This represents an area for future research as it may be the most parsimonious explanation, especially given the probability of pink salmon completing trans-Arctic straying (Chapter 2, Dunmall et al. 2013).

While chum salmon is currently the only salmon species that is known to successfully spawn in rivers flowing to the Arctic Ocean in Canada (Chapter 6), vagrants of all other species of salmon are also harvested in subsistence fisheries in the Canadian Arctic. Therefore, salmon appear to be dispersing to the Canadian Arctic in higher abundances and wider distributions; however, colonizations will depend on successful establishment of those vagrants in novel locations (Chapter 5, Dunmall et al. 2016). As early-life stages in fish (i.e., egg, larva, fry) have narrow thermal tolerance windows and are vulnerable to changes in temperature (Reist et al. 2006a; Pörtner and Farrell 2008), this may represent a colonization bottleneck for stream fishes in extreme environments (McHugh and Budy 2005; Chapter 5, Dunmall et al. 2016). To predict watersheds vulnerable to colonizations by chum and pink salmon, I linked the thermal tolerances of vagrants with thermal refugia, and focused temperature monitoring and assessments at critical perennial groundwater springs areas (Chapter 5, Dunmall et al. 2016). These areas are virtual oases of viable freshwater habitat in the harsh Arctic environment, providing critical cold-water refugia during the summer and warm-water refugia during the winter (Meisner et al. 1988; Power et al.1999). By developing a novel method to monitor instream and hyporheic water temperatures year-round in extreme environments and apply this method using a community-based monitoring approach (Chapter 4), I was able to assess which groundwater springs on the North American North Slope were within the known thermal tolerances of chum and pink salmon during over-wintering egg incubation and juvenile development life stages (Chapter 5, Dunmall et al. 2016). This facilitated assessments regarding the potential for competition between colonizing salmon and native Dolly Varden by identifying which known Dolly Varden spawning sites were most likely to be successfully colonized by chum and pink salmon based on thermal tolerances (Chapter 5, Dunmall et al. 2016). This strategy uses a community-based monitoring approach to focus the broad predictions of range shifts to specific habitats, allowing for deliberate choice of key locations for more detailed assessments. The use of this strategy has now expanded to assess potential interaction at spawning sites among Pacific salmon, Arctic char

S. alpinus and Dolly Varden, which were identified through the Arctic Salmon citizen science program as potentially co-occurring in the Hornaday River, near Paulatuk, NT.

The potential displacement of char by salmon is a tangible example of the fundamental biodiversity challenge of a rapidly changing Arctic. Assessing the effects of a changing environment on native species, identifying the potential for new species to colonize novel areas, and assessing the impacts and opportunities of potential interactions among these species are each significant conservation and management issues associated with biodiversity change. Establishing protected areas to conserve species and their habitats may be a way to prevent or reduce biodiversity loss globally (Secretariat on the Convention of Biological Diversity 2014), but it may not be a viable strategy to protect Arctic-adapted species against the challenges of warming temperatures. The options for species to respond to thermal stress are either to track thermally-suitable habitats northward, adapt to warming temperatures, or undergo local extinctions (Reist et al. 2006b). While northward movement is possible for some Arctic fishes, others may be restricted by geography (e.g., coastline). In addition, the adaptations to the cold, harsh environment of the Arctic may have narrowed the thermal tolerance window for these fish (Pörtner and Farrell 2008), a trade-off that may be detrimental with the projected increase in temperatures (Reist et al. 2006a). Ultimately, predicting the response of Arctic freshwater and diadromous fishes to climate change requires knowledge regarding the current distribution and ecology of the species, and characteristics of its habitat. However, that information is sparse for Arctic species (Reist et al. 2006b). Generally, if warming temperatures remain within the thresholds of Arctic-adapted species, they may initially benefit due to increased feeding opportunities in freshwater systems, as well as increased hydrology and decreased ice cover and thickness in rivers during winter (Reist et al. 2006b). Anadromy, however, may decrease as the benefits gained from migrating from the freshwater to the nearshore marine habitat for increased feeding opportunity may no longer outweigh the costs (Reist et al. 2006b). This will affect subsistence culture as many traditional fishing locations harvest anadromous fish while they are in the marine environment or intersect anadromous or freshwater fish migrations within systems.

Overlaid on top of these factors, however, is the potential for interaction between Arctic fish and those that are shifting distributions northward following warming temperatures. These vagrant species may compete for resources with Arctic fishes, or they may also introduce diseases or parasites from outside sources. While it is premature to predict impacts of unknown colonizations, insights into the potential effects of opportunistic species colonizing novel locations can be gained by assessing locations where the species currently co-occur (Chapter 5, Dunmall et al. 2016), and also by assessing interaction among native and introduced fish species in other locations. Dolly Varden and Pacific salmon currently both occupy streams in Western Alaska, and are spatially separated within rivers based on differences in thermal tolerances (Chapter 5, Dunmall et al. 2016). Indeed, thermal tolerances appear to be an important determinant in the early colonization process in cold-water environments (Milner et al. 2008) and may spatially stratify colonizing and native fish species within watersheds (McHugh and Budy 2005). In the northeastern United States, thermal gradients also contribute to spatial segregation between native brook trout *Salvelinus fontinalis* and introduced brown trout *Salmo trutta* (Fausch and White 1981). While low water temperatures generally have been implicated in limiting the upstream distribution of brown trout (Vincent and Miller 1969; Fausch and White 1981), specifically cold incubation temperatures inherent to high elevations are now believed to influence their upstream distributional limit (McHugh and Budy 2005). Similarly, where white-spotted char *Salvelinus leucomaenis* and Dolly Varden co-exist (Fausch et al. 1994), Dolly

Varden are found in the colder headwater areas, white-spotted char are distributed downstream in warmer habitat and there is an area of syntopy in the middle with moderate temperatures (Taniguchi and Nakano 2000). This distributional pattern may be attributed to the cold tolerance of Dolly Varden, which may be better adapted than white-spotted char to the cold-water temperatures inherent to the headwater areas (Dunham et al. 2008). Therefore, when thermal tolerances differ among colonizing and native species and a thermal gradient exists, spatial segregation may occur.

Pacific salmon have an evolutionary history of adapting to dynamic environments and are therefore well-suited for persistence during continued environmental change (Waples et al. 2008). They also have an established ability to colonize newly accessible habitats as they have recolonized following glacial retreat to their current distributions (Waples et al. 2008), and can also colonize rivers or sections of rivers once barriers are removed (Anderson and Quinn 2007; Pess et al. 2012). However, the occurrence of salmon in the Arctic does not immediately imply successful reproduction. Pacific salmon have a history in the Arctic, but only chum and pink salmon appear to be successfully spawning, and only in certain areas (reviewed in Nielsen et al. 2013). Pink salmon have colonized rivers along the Kola Peninsula in Russia after introductions, and their distribution appears to be continuing to expand (Niemelä et al. 2016). Critically, however, reproductive success of introduced pink salmon is linked to timing of spawning as odd-year pink salmon that formed successful spawning populations in the White Sea after stocking efforts spawned earlier than even-year pink salmon, which were not successful despite multiple introductions (Gordeeva et al. 2015). In addition, the introduced odd-year pink salmon appear to have adapted to conditions at northern latitudes by shifting timing of spawning earlier than their originating population, and by producing larger numbers of smaller larvae (Gordeeva et al.

2015). Also, although chum salmon have been present in the Mackenzie River since deglaciation, and therefore have had access to Canadian Arctic watersheds for thousands of years, they are currently only known to successfully spawn in the upper Mackenzie River (Chapter 6). This remains an area for future investigation, especially as chum salmon distribution and abundance in the Canadian Arctic is expanding (Chapter 2, Dunmall et al. 2013), chum salmon were found in a Dolly Varden spawning site in 1986 (Babaluk et al. 2000a) and again in 2016, and as vagrant chum salmon from outside sources are now also confirmed in the Mackenzie River (Chapter 6). The combination of warming temperatures facilitating earlier access to the Arctic (Chapter 2, Dunmall et al. 2013), the appearance of vagrant salmon from northern origins in Russia (Chapter 6) and therefore presumably adapted to colder conditions, and the extension of warmer temperatures in rivers later in the fall (Chapter 5, Dunmall et al. 2016) may all facilitate successful colonizations by salmon in novel areas in the Arctic.

The disparity between the rapid rate of change in the Arctic, the high level of attention to the Arctic, and the lack of basic data for species and their habitats represents a key call to action. This is especially relevant given the current International mandate to conserve biodiversity through the protected areas process. It is difficult to assess the impacts and opportunities associated with biodiversity shifts when current biodiversity is unassessed, and it is difficult to predict impacts of these rapid environmental changes on key habitats when the presence and characteristics of those key habitats are hardly known. Salmon in the Canadian Arctic highlight this challenge. Despite the intensive study of Pacific salmon throughout their sub-Arctic distributions, we are only now scientifically identifying a population of chum salmon in the Mackenzie River that has been present for thousands of years and is inherent to the culture of Indigenous peoples as evidenced through the inclusion of salmon as a word in their languages.

The impetus for research on salmon in the Canadian Arctic came from community members who observed changing salmon harvests beginning almost 20 years ago, and was only possible because of samples provided from subsistence nets. Scientific interest in assessing and protecting Arctic biodiversity is increasing as global attention follows the shift of species northward and the rapid environmental changes in the Arctic. Incentive, therefore, is rooted in a mutual desire from Indigenous peoples and scientists to understand the implications of biodiversity shifts from cultural and biological perspectives. The unique and irrevocable linkage between the Indigenous peoples and their environment represents an opportunity for scientists to view the Arctic through an Indigenous peoples' lens and the Arctic Salmon project provides a tangible example of the successful integration of local and scientific knowledge to address an international challenge. By learning together and communicating effectively, we can better predict a future Arctic.

The overall goal of this thesis was to establish Pacific salmon in the Arctic as indicators of climate-driven shifts in freshwater and marine habitat availability, and assess the potential associated risk of competitive interactions with native substrate-spawning salmonids. To reach that goal, I have developed an integrated body of work that advances science regarding: 1) the application of citizen science and community-based monitoring in the Arctic; 2) predictions of distributional shifts to extreme environments; and 3) assessing the viability of the Arctic freshwater and marine environments as habitat for fishes over the past several thousand years. More broadly, however, I have developed tools and strategies to help assess the impending biodiversity crisis in the Arctic. While climate change is the biggest threat to biodiversity in the Arctic (Meltofte 2013), balancing the associated opportunities for development with its conservation impacts will be our biggest challenge. So the question, really, is not whether salmon will replace char in a future Arctic. The broader question is how do we, as humans and the drivers of these rapid changes, predict and adapt to a future Arctic? The answer is to apply our collective ingenuity to conservation as intensely as we have been doing to development.

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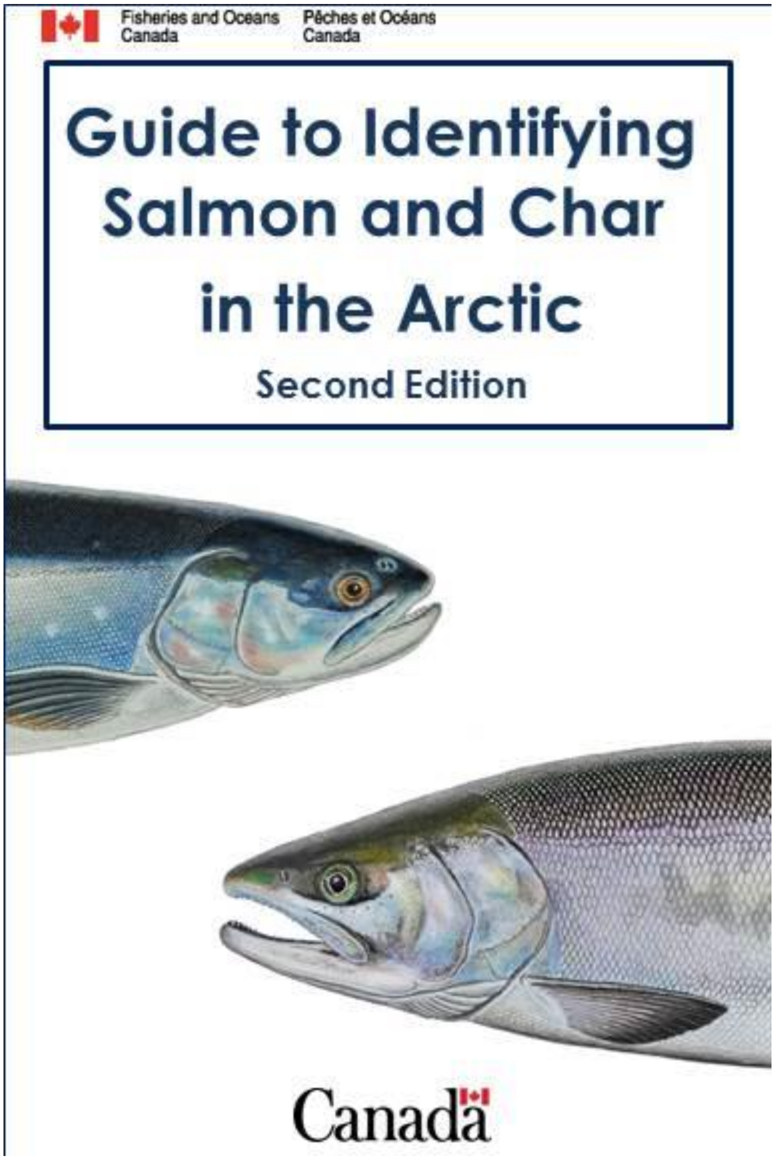
Supplementary Appendix A.

Fisheries and Oceans Canada 2015. Guide to identifying salmon and char in the Arctic, Second Edition. By: P. Vecsei, K. Dunmall, and J. Reist.



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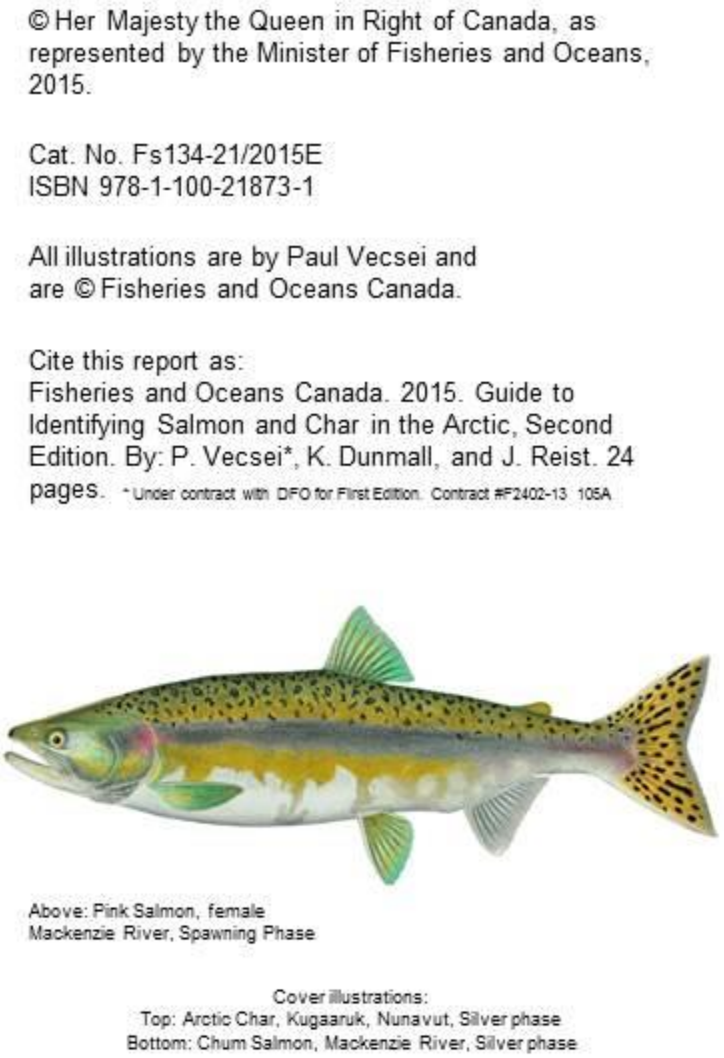
Guide to Identifying Salmon and Char in the Arctic

Second Edition

Canada



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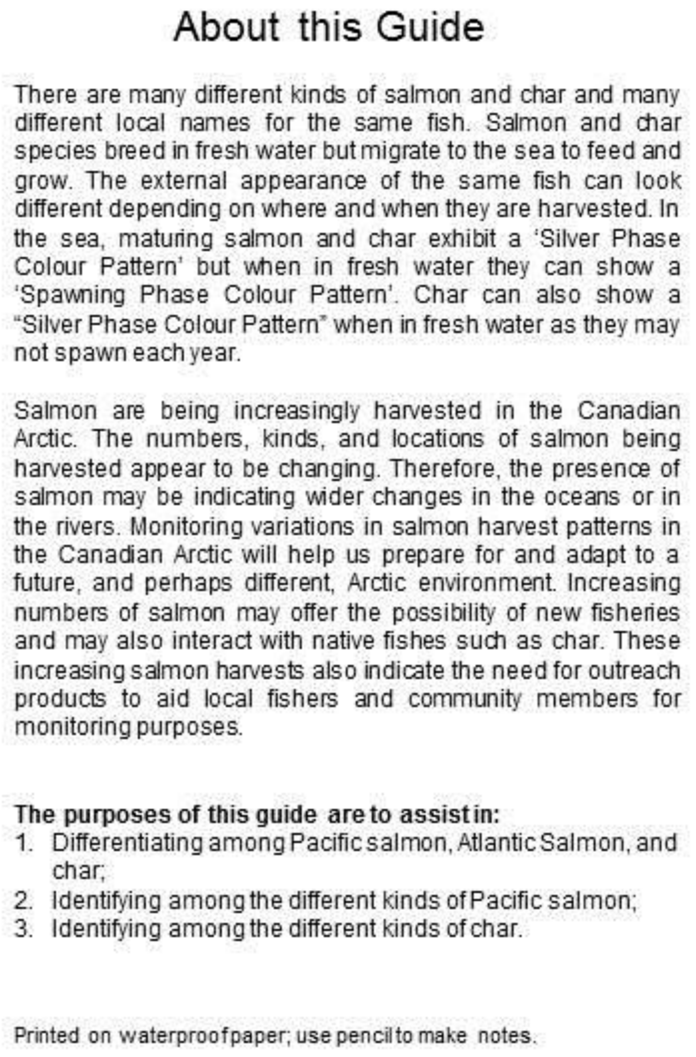
Above: Pink Salmon, female
Mackenzie River, Spawning Phase

Cover illustrations:
Top: Arctic Char, Kugaaruk, Nunavut, Silver phase
Bottom: Chum Salmon, Mackenzie River, Silver phase



About this Guide

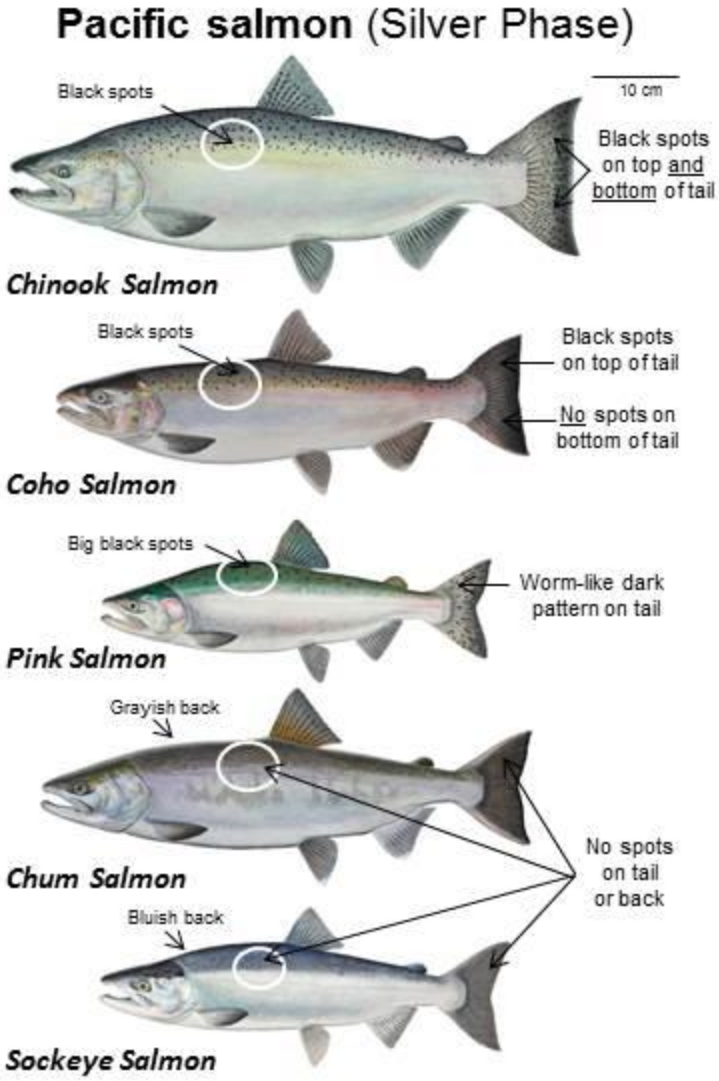
There are many different kinds of salmon and char and many different local names for the same fish. Salmon and char species breed in fresh water but migrate to the sea to feed and grow. The external appearance of the same fish can look different depending on where and when they are harvested. In the sea, maturing salmon and char exhibit a 'Silver Phase Colour Pattern' but when in fresh water they can show a 'Spawning Phase Colour Pattern'. Char can also show a "Silver Phase Colour Pattern" when in fresh water as they may not spawn each year.

Salmon are being increasingly harvested in the Canadian Arctic. The numbers, kinds, and locations of salmon being harvested appear to be changing. Therefore, the presence of salmon may be indicating wider changes in the oceans or in the rivers. Monitoring variations in salmon harvest patterns in the Canadian Arctic will help us prepare for and adapt to a future, and perhaps different, Arctic environment. Increasing numbers of salmon may offer the possibility of new fisheries and may also interact with native fishes such as char. These increasing salmon harvests also indicate the need for outreach products to aid local fishers and community members for monitoring purposes.

The purposes of this guide are to assist in:

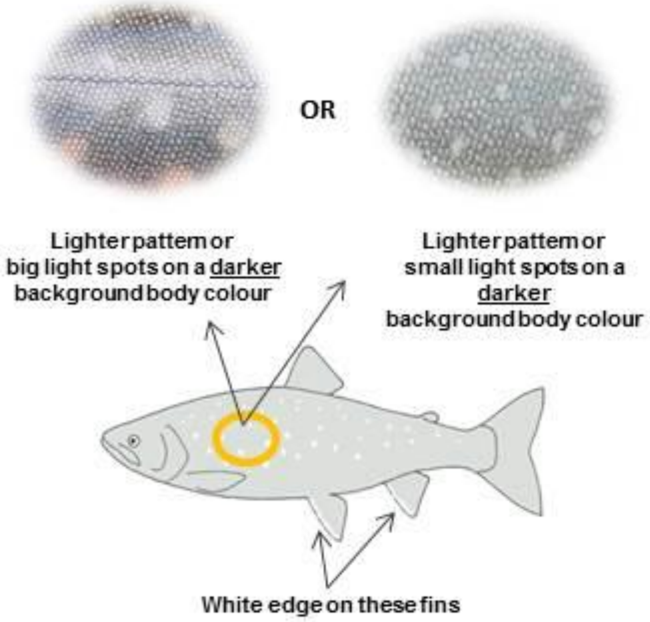
1. Differentiating among Pacific salmon, Atlantic Salmon, and char;
2. Identifying among the different kinds of Pacific salmon;
3. Identifying among the different kinds of char.

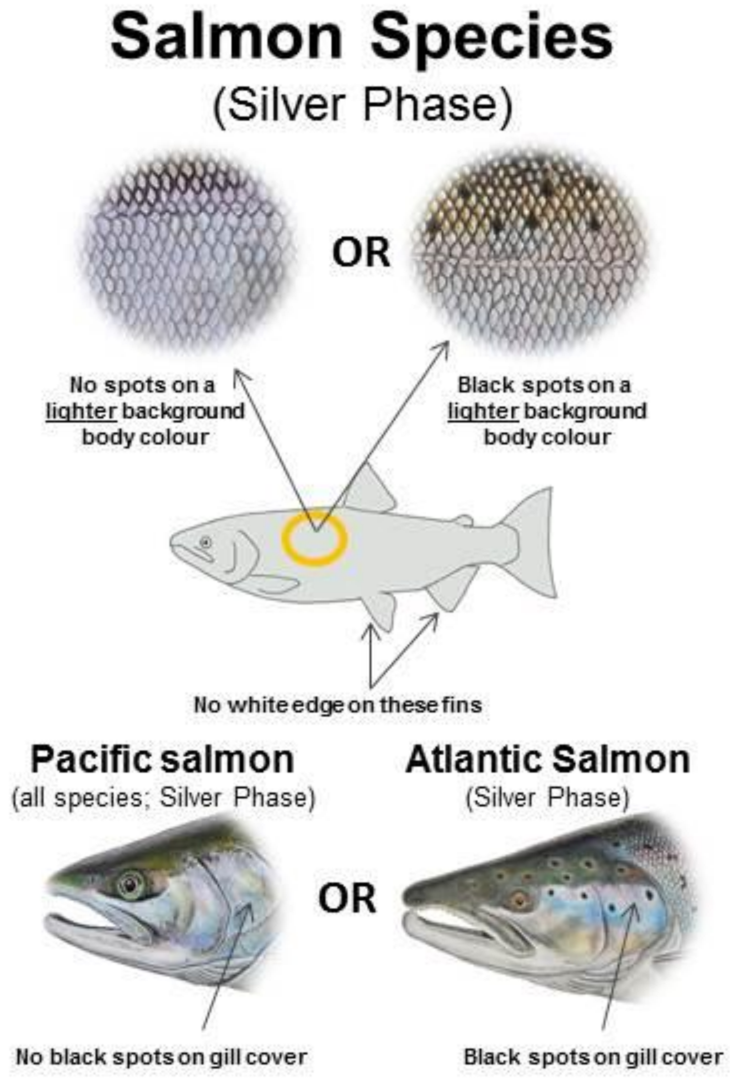
Printed on waterproof paper; use pencil to make notes.

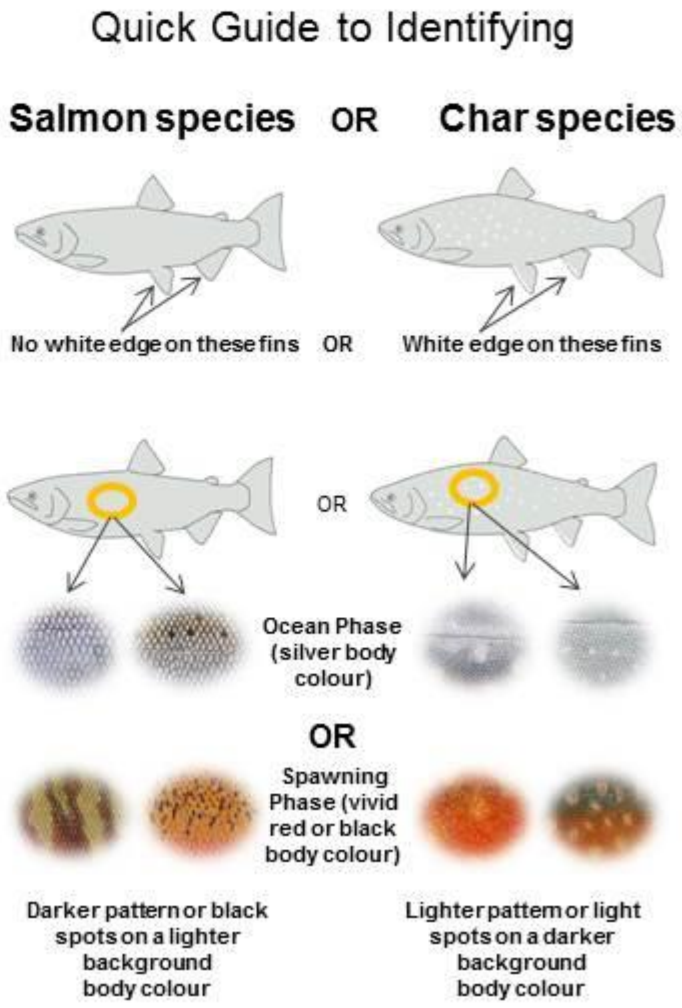

Pacific salmon (Silver Phase)
10 cm
Black spots
Black spots on top and bottom of tail
Chinook Salmon
Black spots
Black spots on top of tail
No spots on bottom of tail
Coho Salmon
Big black spots
Worm-like dark pattern on tail
Pink Salmon
Grayish back
No spots on tail or back
Chum Salmon
Bluish back
Sockeye Salmon

Char Species

(Silver Phase)




Salmon Species
(Silver Phase)
OR
No spots on a lighter background body colour
Black spots on a lighter background body colour
No white edge on these fins
Pacific salmon
(all species; Silver Phase)
Atlantic Salmon
(Silver Phase)
OR
No black spots on gill cover
Black spots on gill cover


Quick Guide to Identifying
Salmon species
OR
Char species
No white edge on these fins
OR
White edge on these fins
OR
Ocean Phase (silver body colour)
OR
Spawning Phase (vivid red or black body colour)
Darker pattern or black spots on a lighter background body colour
Lighter pattern or light spots on a darker background body colour

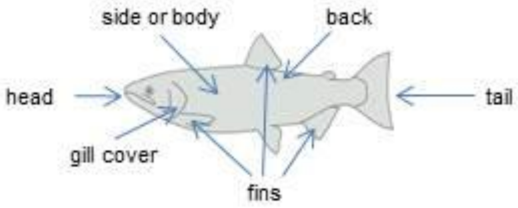
How to Use this Guide

Identifying among different kinds of fish can be difficult. There is a great deal of variation in colour patterns, sizes, and shapes within the different species of salmon and char. Therefore, if something does not exactly fit these descriptions or illustrations, it may not be new or different. However, if the fish is unlike anything that is commonly known in that area, please bring it to a Fisheries and Oceans Office for identification.

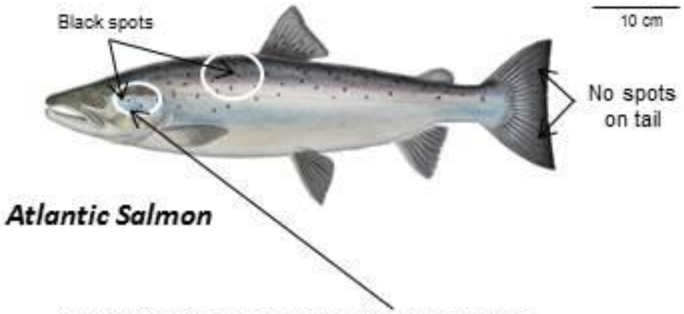
Providing the actual fish to Fisheries and Oceans Canada will: 1) greatly assist in species identification, especially if the fish is difficult to identify; and 2) provide tissue samples for genetic testing to identify species, if necessary.

If you have harvested a salmon, please report it to your local Fisheries and Oceans Canada Office with the date and location of capture. This will help research on climate change in the Arctic by documenting changes where salmon are harvested, how many are captured each year, and what kinds of salmon are appearing.

Names of Fish Parts Used in this Guide



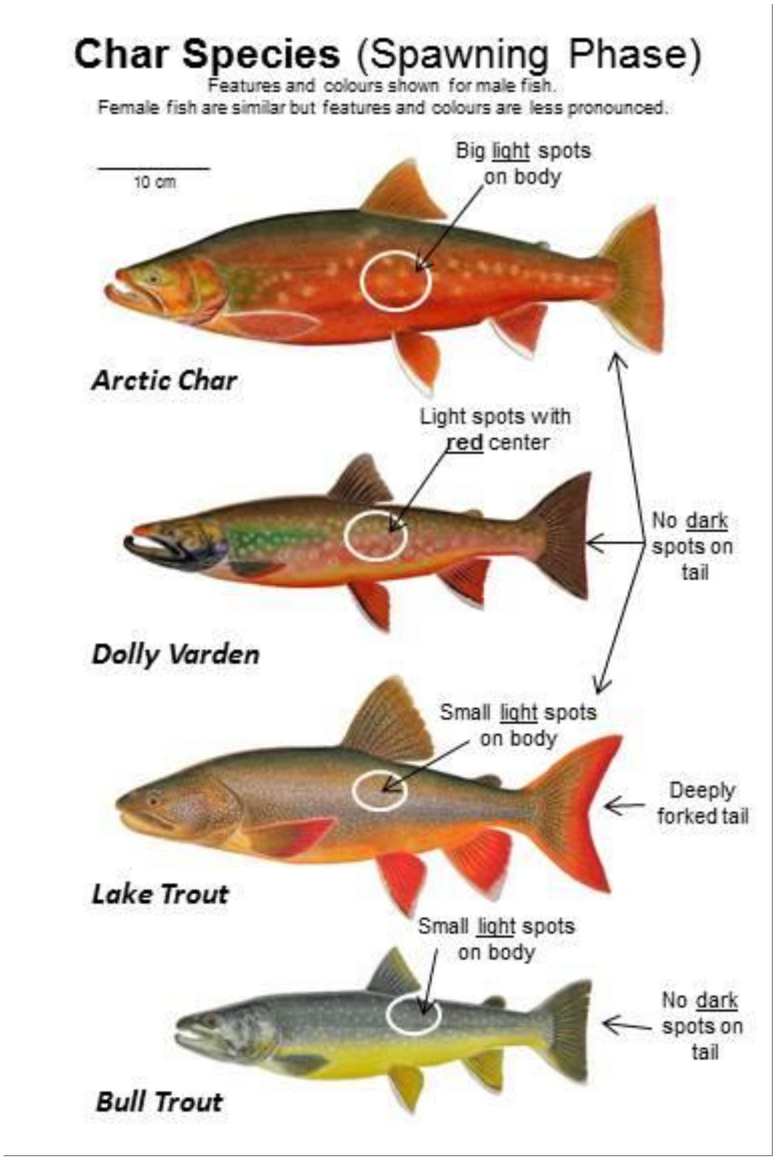
Atlantic Salmon (Silver Phase)

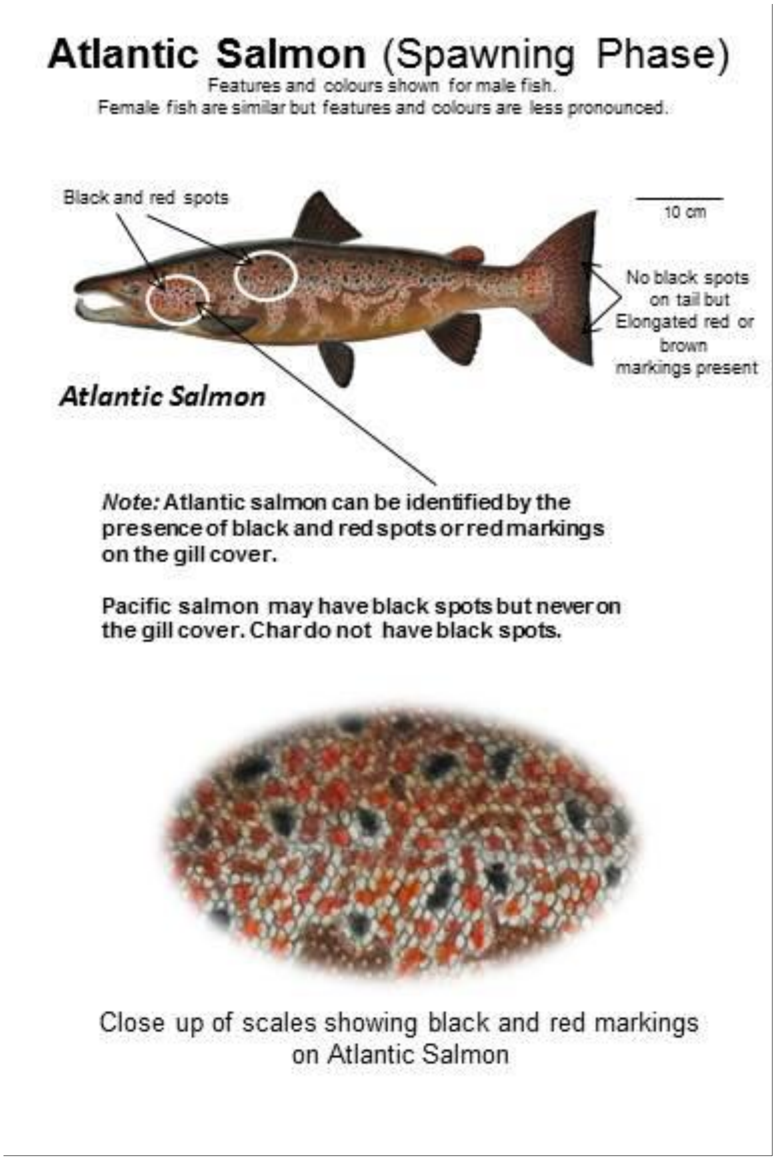


Note: Atlantic salmon can be identified by the presence of black spots on the gill cover.

Pacific salmon may have black spots but never on the gill cover. Char do not have black spots.

Black spots on gill cover of Atlantic Salmon


Char Species (Spawning Phase)
Features and colours shown for male fish.
Female fish are similar but features and colours are less pronounced.
10 cm
Big light spots on body
Arctic Char
Light spots with red center
No dark spots on tail
Dolly Varden
Small light spots on body
Deeply forked tail
Lake Trout
Small light spots on body
No dark spots on tail
Bull Trout



Atlantic Salmon (Spawning Phase)

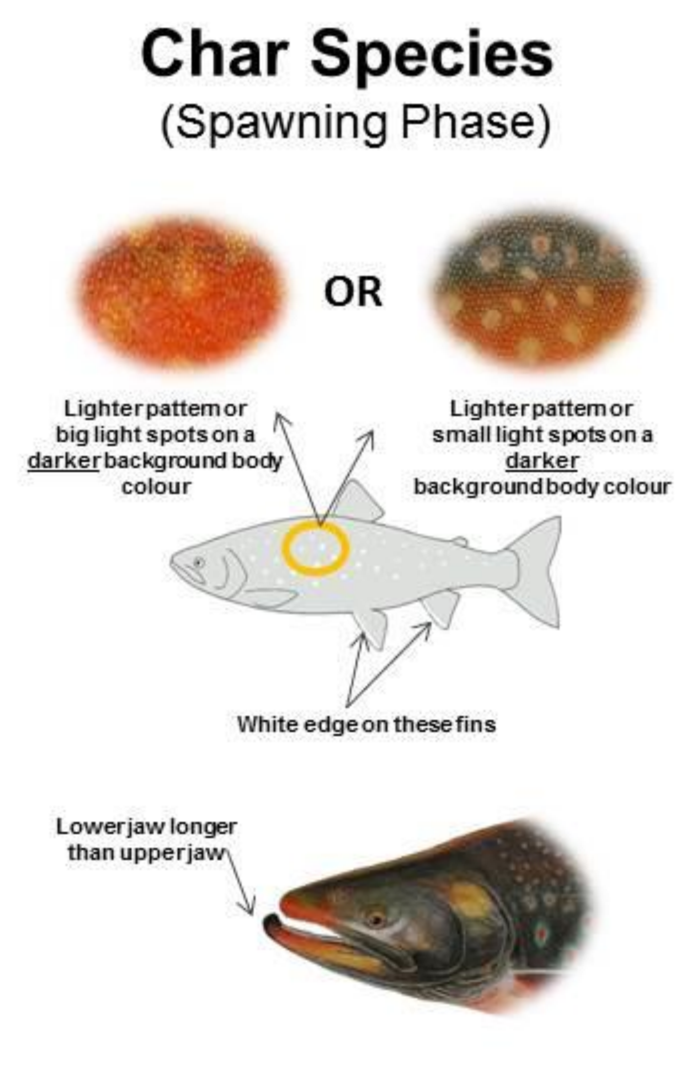
Features and colours shown for male fish.
Female fish are similar but features and colours are less pronounced.

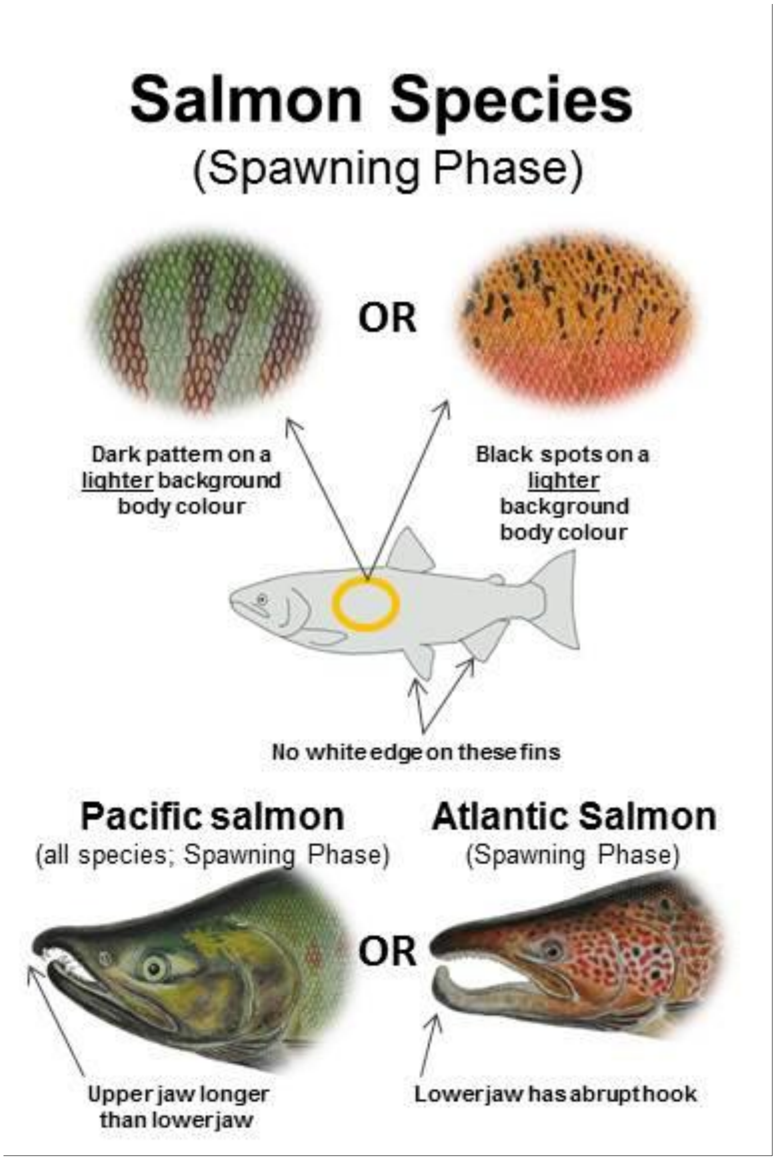
Note: **Atlantic salmon can be identified by the presence of black and red spots or red markings on the gill cover.**

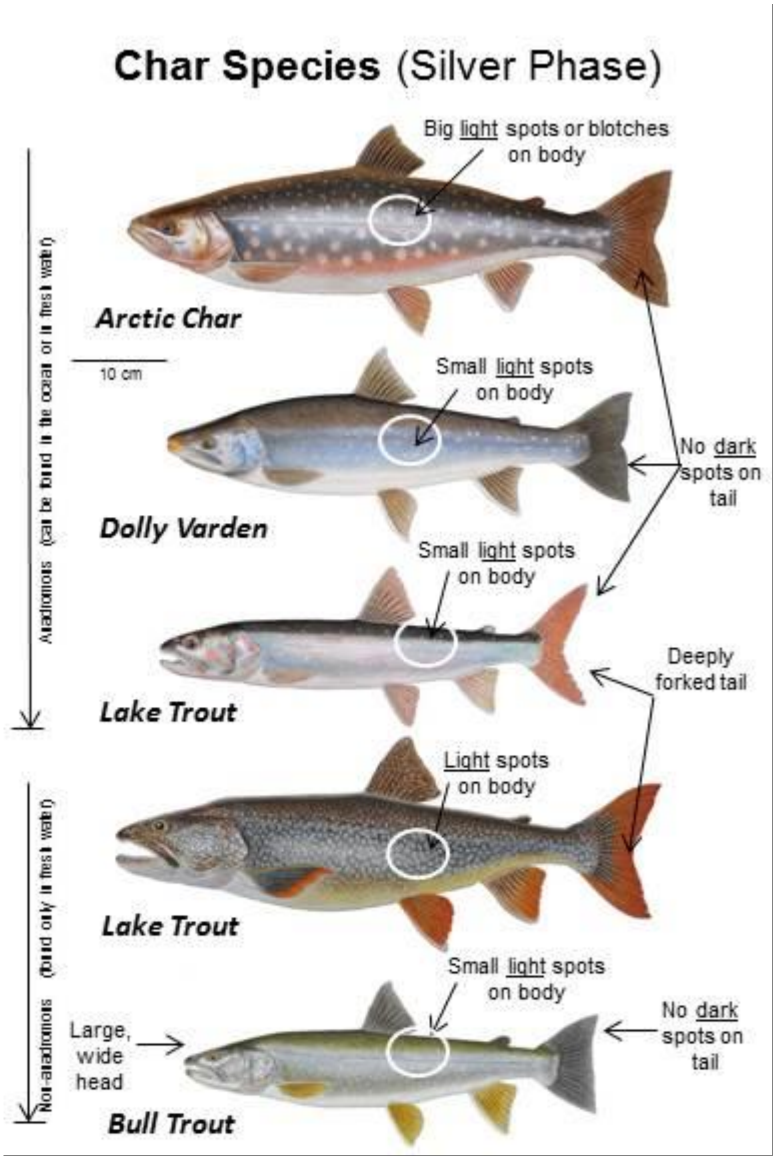
Pacific salmon may have black spots but never on the gill cover. Char do not have black spots.

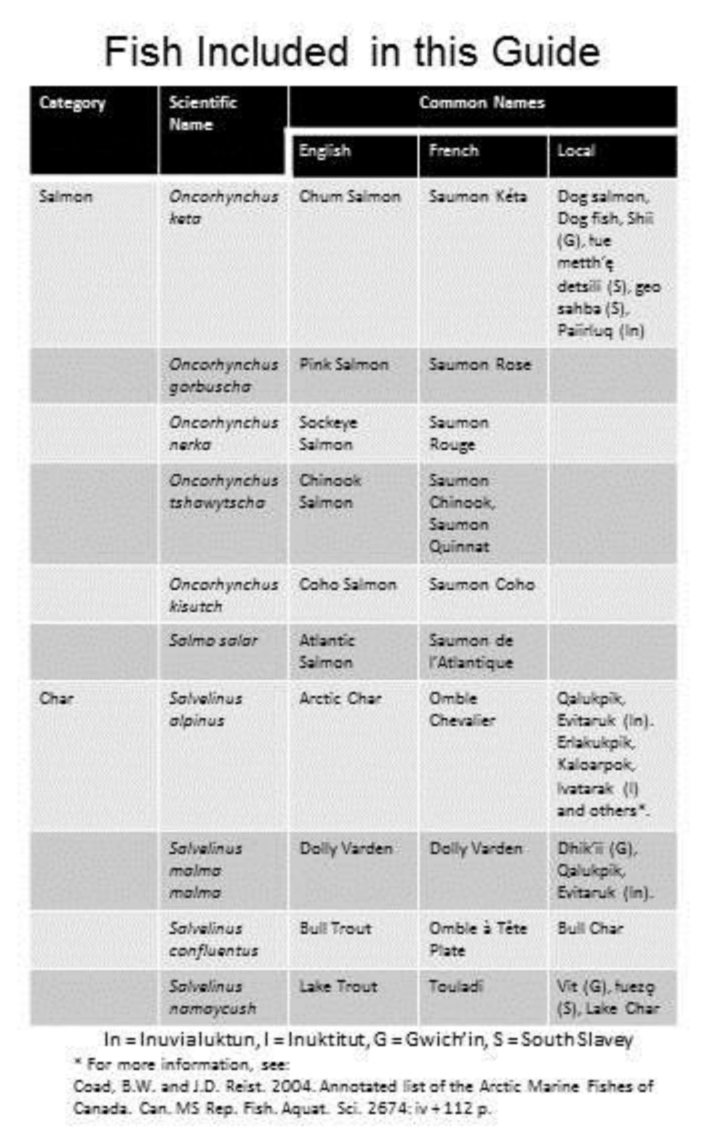
Close up of scales showing black and red markings on Atlantic Salmon


Pacific salmon (Spawning Phase)
Features and colours shown for male fish.
Female fish are similar but features and colours are less pronounced.
10 cm
Black spots
Black spots on top and bottom of tail
Chinook Salmon
Black spots
Black spots on top of tail
No spots on bottom of tail
Coho Salmon
Big black spots and Males have hump
Worm-like dark pattern on tail
Pink Salmon
No spots, red pattern on sides
No spots on tail
Chum Salmon
No spots, red colour on back
Green head
No spots on tail
Sockeye Salmon


Char Species
(Spawning Phase)
OR
Lighter pattern or big light spots on a darker background body colour
Lighter pattern or small light spots on a darker background body colour
White edge on these fins
Lower jaw longer than upper jaw


Salmon Species
(Spawning Phase)
OR
Dark pattern on a lighter background body colour
Black spots on a lighter background body colour
No white edge on these fins
Pacific salmon
(all species; Spawning Phase)
OR
Atlantic Salmon
(Spawning Phase)
Upper jaw longer than lower jaw
Lower jaw has abrupt hook


Char Species (Silver Phase)
Big light spots or blotches on body
Arctic Char
10 cm
Small light spots on body
No dark spots on tail
Dolly Varden
Small light spots on body
Lake Trout
Deeply forked tail
Light spots on body
Lake Trout
Small light spots on body
Large, wide head
No dark spots on tail
Bull Trout
Anadromous (can be found in the ocean or in fresh water)
Non-anadromous (found only in fresh water)



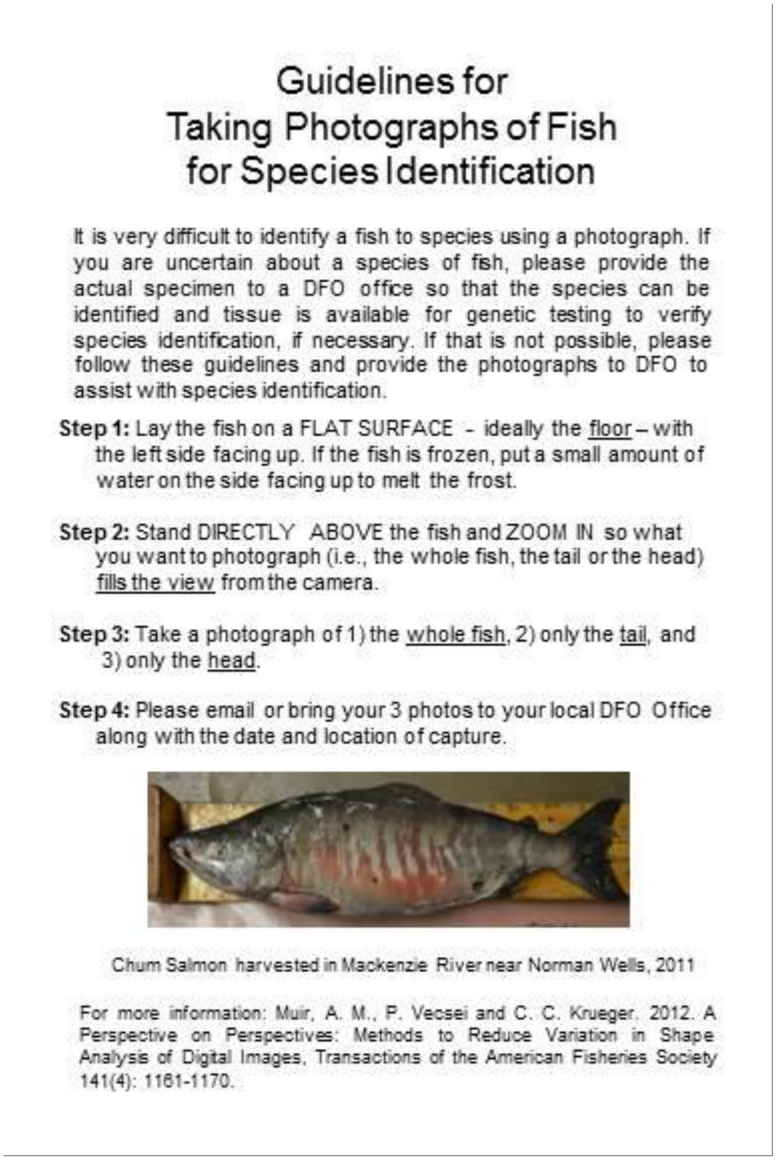
Fish Included in this Guide

Category	Scientific Name	Common Names		
		English	French	Local
Salmon	*Oncorhynchus keta*	Chum Salmon	Saumon Kéta	Dog salmon, Dog fish, Shii (G), łue metth'ę detsilı (S), geo sahba (S), Paiirluq (In)
	Oncorhynchus gorbuscha	Pink Salmon	Saumon Rose	
	Oncorhynchus nerka	Sockeye Salmon	Saumon Rouge	
	Oncorhynchus tshawytscha	Chinook Salmon	Saumon Chinook, Saumon Quinnat	
	Oncorhynchus kisutch	Coho Salmon	Saumon Coho	
	Salmo salar	Atlantic Salmon	Saumon de l'Atlantique	
Char	*Salvelinus alpinus*	Arctic Char	Omble Chevalier	Qalukpik, Evitaruk (In). Erlakukpik, Kaloarpok, Ivatarak (I) and others*.
	Salvelinus malma malma	Dolly Varden	Dolly Varden	Dhik'ii (G), Qalukpik, Evitaruk (In).
	Salvelinus confluentus	Bull Trout	Omble à Tête Plate	Bull Char
	Salvelinus namaycush	Lake Trout	Touladi	Vit (G), łuezǫ (S), Lake Char

In = Inuvialuktun, I = Inuktitut, G = Gwich'in, S = South Slavey

* For more information, see:

Coad, B.W. and J.D. Reist. 2004. Annotated list of the Arctic Marine Fishes of Canada. Can. MS Rep. Fish. Aquat. Sci. 2674: iv + 112 p.



Guidelines for Taking Photographs of Fish for Species Identification

It is very difficult to identify a fish to species using a photograph. If you are uncertain about a species of fish, please provide the actual specimen to a DFO office so that the species can be identified and tissue is available for genetic testing to verify species identification, if necessary. If that is not possible, please follow these guidelines and provide the photographs to DFO to assist with species identification.

Step 1: Lay the fish on a FLAT SURFACE - ideally the floor – with the left side facing up. If the fish is frozen, put a small amount of water on the side facing up to melt the frost.

Step 2: Stand DIRECTLY ABOVE the fish and ZOOM IN so what you want to photograph (i.e., the whole fish, the tail or the head) fills the view from the camera.

Step 3: Take a photograph of 1) the whole fish, 2) only the tail, and 3) only the head.

Step 4: Please email or bring your 3 photos to your local DFO Office along with the date and location of capture.

Chum Salmon harvested in Mackenzie River near Norman Wells, 2011

For more information: Muir, A. M., P. Vecsei and C. C. Krueger. 2012. A Perspective on Perspectives: Methods to Reduce Variation in Shape Analysis of Digital Images, Transactions of the American Fisheries Society 141(4): 1161-1170.

For more information, to report a salmon, or to get additional copies of this guide, please contact your local DFO office.

For more information about Pacific salmon in the Canadian Arctic, visit:

www.facebook.com/arcticsalmon
www.arcticsalmon.ca

Arctic Char
Kugaaruk, Nunavut
Silver Phase

More information on identifying salmons and chars can also be found on the internet.

For example:
www.pac.dfo-mpo.gc.ca/fm-gp/rec/index-eng.html
(and under "What are you fishing for", select the tab: Salmon)

www.env.gov.bc.ca/fw/fish/sport_fish/

www.adfg.alaska.gov
(and select the tabs: Species, Animals, Fish)

DFO is not responsible for the content of non-government websites.

Salmon Collection Program
Data Card

Please use pencil

What kind of salmon did you catch? (circle one)

Chum / Pink / Coho /

Chinook / Sockeye / Atlantic

Date Caught (dd/mm/yyyy):_______________

____

Location Caught (be specific):_____________

____

Nearest Community:_____________________

Gillnet mesh size:_______________________

How many hours was the net set?__________

If you squeeze the belly gently, does eggs/milt come out? Y or N

(please turn over)

Page 1 of 2

Salmon Collection Program
Data Card

Please use pencil

Have you caught salmon before? Y or N

How many salmon do you catch / season?
____

Has that increased, decreased or remained the same over time?________________________

Name & address:________________________

____

Email or phone:_________________________

____

Would you like more information about this project?
Y or N

Gift card received? Y or N

(please turn over)

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