

Life history and migration patterns of Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma malma*) in the Coppermine River and Coronation Gulf

by

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

While the research in this thesis is my own, numerous collaborators provided guidance and valuable contributions. The research was conducted in close collaboration with the Kugluktuk Hunters and Trappers Organization (HTO), and followed from meetings of the HTO, Dr. Heidi Swanson, and Dr. Tracey Loewen (Fisheries and Oceans Canada) in 2017. The specific objectives and ideas in this thesis were developed collaboratively by myself and community members from Kugluktuk through continuous, informal discussions, and with guidance from Heidi Swanson.

The research presented in this thesis would not have been possible without the participation of numerous field researchers from Kugluktuk: Eric Hitkolok, Jonathan Nivingalok, Roger Hitkolok, Andrew Klengenberg, Austin Maniyogena, Pocco Ilgok, McCotter Riffi, Richard Akana, Jonathan Niptanatiak, Adrian Kudlak, Perry Klengenberg, Kirk Kapakatoak, Andrew Nivingalok, Priscilla Hitkolok, Floyd Kaitak, Wendy Bolt, Kanok Bolt, OJ Bernhardt, Darwin Ipakohak, Adam Panioyak, Shaun Klengenberg, and Regan Adjun. Additional field assistance was provided by Heather Dixon, Jessica Kidd, Kent Kristensen, and Lance Goodwin. Invaluable support and insight were provided by Amanda Dumond (HTO Manager), Larry Adjun (HTO Chair, past), Allen Niptanatiak (HTO Chair, present), Darlene Hokanak (HTO Assistant), and Russell Akeeagok (Conservation Officer, Government of Nunavut Department of Environment). The Ikaarvik youth group in Kugluktuk provided images from time-lapse cameras to identify river freeze-up and break-up. Kirsten Nikel assisted with genotyping.

Specific contributions to each chapter are outlined below.

Chapter 1: General Introduction

Amanda Dumond and Eric Hitkolok reviewed the chapter to ensure that content relevant to the community of Kugluktuk was framed appropriately.

Chapter 2: Smith, R., Bottoms, J., del Villar-Guerra, D., Loewen, T., & Swanson, H. 2025. *mort*: An R package to conservatively identify mortalities and shed tags in passive telemetry arrays. *Journal of Animal Ecology* **94**(6): 1120–1132. doi:10.1111/1365-2656.70045.

RS conceived the ideas, designed the framework, and wrote the R package, with guidance from HS. JB contributed the Arctic Grayling dataset. Eduardo Martins, Bryce O'Connor, Ian Clevenger, Devon Smith, Marie Auger-Méthé, Michael Power, David Patterson, Mark Shrimpton, and Steven Cooke contributed to the Arctic Grayling project, which was primarily funded by the Fish and Wildlife Compensation

Programme. DdVG contributed the Atlantic Salmon dataset. Atlantic Salmon data were obtained through the SeaMonitor project funded by the European Union's INTERREG VA Programme. TL contributed the Greenland Cod dataset. RS wrote the manuscript. All authors contributed to manuscript drafts and reviewed the manuscript.

Chapter 3: Smith, R., Hitkolok, E., Loewen, T., Dumond, A., & Swanson, H. 2024. Migration timing and marine space use of anadromous Arctic fish (Arctic Char, *Salvelinus alpinus*) revealed by local spatial statistics and network analysis. *Movement Ecology* **12**(1):12. doi:10.1186/s40462-024-00455-z.

RS, TL, AD, and HS conceptualized the study. HS and TL provided funding. AD provided in-kind support. RS, EH, and HS designed the study. RS, EH, and HS collected the data. RS analyzed the data. RS wrote the manuscript with edits from HS. All authors reviewed the manuscript.

Chapter 4: Smith, R., Hitkolok, E., Dumond, A., DePasquale, S., Thibault, H., Weinstein, S., Craig, P., Loewen, T., & Swanson, H. 2025. Environment influences migration timing of cold-adapted salmonids (*Salvelinus alpinus* and *S. malma malma*) in the Canadian Arctic. Accepted by Canadian Journal of Fisheries and Aquatic Sciences.

RS, TL, AD, and HS conceptualized the study. HS and TL provided funding. AD provided in-kind support. RS, EH, and HS designed the study and collected the data and genetic samples. SD, HT, SW, and PC performed the genetic analyses. RS analyzed the data. RS wrote the manuscript with edits from HS. All authors reviewed the manuscript. Jared Ellenor suggested using logistic regression to model return to fresh water.

Chapter 5: Smith, R., Hitkolok, E., Dumond, A., DePasquale, S., Thibault, H., Weinstein, S., Craig, P., Loewen, T., & Swanson, H. 2025. Return migration to fresh water and overwintering locations used by sympatric anadromous populations of Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma malma*). Submitted to Journal of Fish Biology.

RS, AD, TL, and HS conceptualized the study. HS and TL provided funding. AD provided in-kind support. RS, EH, and HS designed the study and collected the data. RS, SD, HT, SW, and PC performed the genetic analyses. RS analyzed the data. RS wrote the manuscript with edits from HS. All authors reviewed the manuscript. Community members donated samples through community collection programs. Distance calculations were made possible by the facilities of the Shared Hierarchical Academic Research Computing Network (SHARCNET; www.sharcnet.ca) and Digital Research Alliance of Canada (<https://alliancecan.ca/en>).

Chapter 6: General Discussion

Amanda Dumond and Eric Hitkolok reviewed the chapter to ensure that content relevant to the community of Kugluktuk was framed appropriately.

Abstract

Arctic Char (*Salvelinus alpinus*) and Dolly Varden Char (*Salvelinus malma malma*) are of vital importance to Indigenous communities in Arctic Canada. Both species are facultatively anadromous and anadromous individuals exhibit remarkable diversity in migration tactics. Both species are also iteroparous and relatively long-lived, which allows migration patterns of individuals to be studied over multiple years. The Coppermine River, near Kugluktuk, Nunavut, is the only freshwater location where anadromous individuals of both Arctic Char and Dolly Varden have been confirmed to occur in sympatry, thereby providing a unique opportunity to compare habitat use and migration patterns between species. The overarching goal of this thesis was thus to investigate the diverse life history and migration tactics of Arctic Char and Dolly Varden that use the Coppermine River. To achieve this goal, I used an acoustic telemetry dataset from tagged Arctic Char and Dolly Varden that was collected over six years (2018–2023) in the Coppermine River and nearby marine environment of Coronation Gulf.

Acoustic telemetry is widely used in aquatic environments to study animal movement, behaviour, and ecology, but many studies that employ acoustic telemetry neglect to consider the possibility that some detections may be from mortalities or expelled tags, and this can result in biased results. To assist acoustic telemetry practitioners in identifying detections from potential mortalities or expelled tags in a simple and reproducible manner, I developed the R package `mort`. In Chapter 2, the methods and package are described, and application is demonstrated using three diverse acoustic telemetry datasets that represent: 1) a mobile freshwater fish ((Arctic Grayling (*Thymallus arcticus*)) in a river network; 2) a relatively sedentary marine fish (Greenland Cod (*Gadus ogac*)); and, 3) a highly mobile marine fish (Atlantic Salmon (*Salmo salar*)). Detections flagged by `mort` were reviewed and removed from the acoustic telemetry datasets that were analyzed in subsequent thesis chapters (Chapter 3, Chapter 4, and Chapter 5).

Marine feeding is of critical importance for anadromous Arctic Char and Dolly Varden; individuals of both species must acquire sufficient resources for growth and reproduction during the brief ice-free seasons. In Chapter 3, I used network analysis and local spatial statistics to identify and describe high-use locations and movement patterns in the marine environment for char (Arctic Char or Dolly Varden; species was unknown at the time of writing) that overwintered either above or below Kugluk or Bloody Falls (“the falls”; a large cascade). Char exhibited preference for coastal habitats (relative to offshore or island habitats) and habitat use did not appear to be associated with overwintering location. Timing of return to fresh water was associated with overwintering location, however; char that

overwintered above the falls returned to fresh water earlier than char that overwintered below the falls, which suggests that length and difficulty of the migratory pathway was associated with migration timing. Timing of return migration to fresh water was earlier in years when the river froze earlier; this indicates that the timing of char returning to fresh water is responsive to environmental conditions in the system.

Environmental influences on timing of return migration to fresh water are largely unknown for both Arctic Char and Dolly Varden. In Chapter 4, I investigated how environmental variables were related to: 1) timing of return to fresh water by both Arctic Char and Dolly Varden; and, 2) ascension of the falls by Dolly Varden (no Arctic Char were observed ascending the falls in any year). The primary environmental cue for return to fresh water was sea surface temperature (SST); all char returned to fresh water as SST increased. Dolly Varden that overwintered above the falls returned to fresh water at colder SST (earlier) than Arctic Char and Dolly Varden that overwintered below the falls. For Dolly Varden that overwintered above the falls, river temperatures were warm and potentially stressful at the time of return. It is possible that these individuals experienced decoupling between the cue to return to fresh water (SST) and suitable conditions for migration (river temperature). Tide may have facilitated ascension of the falls but was not associated with timing of return to fresh water for Dolly Varden that overwintered above the falls. In contrast, tide was associated with timing of return to fresh water for Arctic Char and Dolly Varden that overwintered below the falls. Together, these results suggest that Dolly Varden that overwintered above the falls made directed return and upstream movements, whereas fish that overwintered below the falls returned to fresh water more passively. Differences in threshold (SST) for return migration and influence of tide between Dolly Varden that overwintered above and below the falls suggests that there may be an underlying physiological cue for migration timing and/or overwintering location.

Fluvial overwintering habitats used by both Arctic Char and Dolly Varden below the falls in the Coppermine River are unusual in that there are no known groundwater inputs. In Chapter 5, I assessed evidence for several potential mechanisms that could explain overwintering below the falls: spawning status, foraging opportunities in the marine environment, and failure to ascend the falls. I found no evidence of foraging from stomach contents, although spatial and temporal coverage of samples was limited. Consistent with intent to overwinter below the falls, Arctic Char staged longer at the river mouth and moved upstream more slowly than Dolly Varden that overwintered above the falls. Dolly Varden that overwintered below the falls exhibited inconsistent movement patterns and I suggested

that some Dolly Varden may thus intend to overwinter below the falls, whereas others may fail to ascend the falls. I found no confirmed evidence of spawning activity below the falls for either Dolly Varden or Arctic Char. Telemetry data indicated that Arctic Char overwintered in alternate rivers in some years, which suggests that spawning could occur in alternate rivers and that the lower reaches of the Coppermine River represent easily accessible overwintering habitat in non-spawning years. Dolly Varden that overwintered below the falls were smaller and younger than Dolly Varden that overwintered above the falls, and I suggested that it is likely that Dolly Varden migrate above the falls in spawning years. Spawning locations and frequency remain unknown for both species that use the Coppermine River.

The research presented in this thesis describes the life history and migration tactics of anadromous Arctic Char and Dolly Varden that use the Coppermine River, the only freshwater system that is known to support anadromous life history types of both species. Similarities in marine habitat use and movement patterns between Arctic Char and Dolly Varden and between overwintering groups (above or below falls) of Dolly Varden may present challenges for fisheries management if conservation concerns are identified in future. I observed inter-individual and inter-annual (within individual) diversity in migration tactics in Arctic Char and Dolly Varden that use the Coppermine River and Coronation Gulf, as well as influences of environmental conditions on migration timing. The observed plasticity in responses among individuals and years may promote resilience of the two species, but future research on spawning locations and spawning frequency is necessary to provide a comprehensive assessment of potential stressors that could affect the species' persistence and inform fisheries management.

Nainaakhimayok Unipkangat

(Inuinnaqtun translation of Abstract)

Ikalukpiit (*Salvelinus alpinus*) tahapkualu Dolly Varden-mik attiktaohimayot Ikaluit ihuukit (*Salvelinus malma malma*) pimagioyot ikaluit nunakakaktot nikkigingmatjuk tahamani Ukkiuktaktumi Kanatami. Tahapkua tamakmik ikaluit ilangit hittuvaktut tagiokmut ilangitaok aullayuitot tattini. Ikaluit hittuvaktut tagiokmut ajikingitot iliitkuhiit hittugangamik, ilangit kakkugungugangat nammutlu hittuvaktot. Tamakmik hapkua ikaluit iglingmingni igniokpaktot kakkugungugangat tatvalu innughaakataktot, taimatot naunaiyaikatagunngaktavut kanok iliitkuhiitnik hittunahuagangata kaffiktaklugit ukkiuni. Tatvani kugluktumi Kuukmi, kanninganiitok Kugluktuk, Nunavut, tatvatuanguyok kaoyimayavut immagiktok hittuviat tahapkua ikalukpiit tatvalu tahapkua ikaluit ihuukit attiktaohimayot Dolly Varden, una Kuuk nayogagiyat attaotikut. Tukkiaktok tahamna Kuuk atjikutakangitok nayogagiyat hittuvigivakhutjuk tahapkua ikaluit. Taimatot ihomagiloaktavut tahamna naunaiyaiyot havagiyomavlutjuk kanok allangayaghaita hittuvigikatakhutjuk tahapkua ikalukpiit tatvalu hapkua Dolly Varden ikaluit ihuukit nayogagiyat tahamna Kugluktumi Kuuk. Tatva taimatot havagiyomavlutjuk, tahapkua ikalukpiit Dolly Varden ikaluit ihuukit attaataliktaktaovaktot nallauhiktokhugitlo tauktaktaovaktot namungaokatakangata 6-sinik ukkiunik havagivlutjuk (2018-min 2023-mut) tahamani Kugluktup Kuukmi tatvalu kaningani tahamani tagiokmi Coronation Gulf-mi.

Ataataktuinik tatvalu tammalaitkutininik nallauhiktoidinik atogaokataktot imakmi nauyiaaotigivlutjuk ikaluit namungauningitnik, iliitkuhiitnik tatvalu nayogagiyaitnik, kihiani ammihiyut tahapkua tammalaitkutininik nallauhiktoidinik ihomagingitait immakak illangit hapkua naunaiyaotait pihimayungnakhiyat ataatakhimayunit ikalunit tukkuhimayunit uvalunin ataatait kattaktitaonikata, taimatot nallukhaotaungmiyot. Ikkayotaongmat inuknun naunaiyaiyunot ummayunik immakak tahapkua ataatait tukkuhimayuningakhimayot ikalunit uvalunin kattakhimayonik ataatanit, ihuaghahimaliktunga naunaitkutikhamik kagitaoyakukutimik attikaktok ~~mort~~-mik. Tatvani unipkat Naunaipkutani 2-mi, naunaiyakhimayaga unipkagivlugo kanok atoktaoyagiaktok una kagitaoyakut naunaiyaotaoyok, ayogiktoitjutigiyaga kano kuna kagitaoyakut naunaiyaotaoyok atoktaoyungnaktok pingahut allatkit naunaipkutini: 1) tattiniotak una ikaluk (Hulukpaugak (*Thymallus arcticus*)) kukanikataktok; 2) tagiokmiotak ikaluk una hangukatangitok (Uugak (*Gadus ogac*)); tatvalu, 3) unghiktoliakataktok una tagiokmiotak ikaluk (Atlantic Salmon (*Salmo salar*)). Tahapkua naunaipkutaoyot naunaiyaktaohimayot kagitaoyakut ahivaktaokataktot tahapkunanga naunaiyaotaoyonit takkuktaohimayot ahianit unipkangita naunaipkutaitni (Naunaipkutani 3, Naunaipkutani 4, tatvanilo Naunaipkutani 5).

Tagiokmi niginiakviat tahapkua ikaluit pimagioyok; tahapkua ikaluit allatkiit nikkikatiagiakaktot akliyaminingnik tatvalu igniugiaminingnik hikkukangititlugo. Tatvani unipkami Naunaipkutani 3, naunaiyakhimayatka titigakhugit tahapkua nayogagiloaktaitnik namungaokatakningitiklo tahamani tagiokmi hapkua ikalukpiit ikaluitlo ihuukit hapkua Dolly Varden; kanogitungmangata tahapkua ikaluit nallukhaotaoyut titigakpalialiktitlugo tahamna unipkalioktaoyok, tahapkua ukkikataktot nalliakni kullani uvalunin natkani tahaffuma Kugluk-mik attikaktuk Kuuk. Ikalukpiit nayogagiyakaktot hinnanikhiokhutik takkunakpalangitot ittinikmi uvalunin kikiktani. Tahapkua nayogagikataktait ikaluit ihomagiyaovalangitat nannikatakhangata ukkiuni. Uttigangata tagiokmit tahamunga tattinut immagiktunut ihomanaktok nanikatakhangata ukkiuni, kihianitaok; hapkua ikalukpiit ukkikataktot kulani tahaffuma kukluakviani Kuukmi uttikataktut immagiktunut tattinut pinnagikataktot ikalukpiitnit ukkihimayunit natkanit haffuma kukluakviani Kuukmi, ihomannaktok tatva hivituninga tatvalu ayoknautigikataktat tahamna ingilgayatik mayogahualigangamik kinguvautivagungnakhiyok. Kakugu mayokvikikataktat tattinut immagiktunut pinnagikatakhimayot ukkiuni kinguani tahamna Kuuk hikkunagikatagaluakmat; taima naunaikhimaliktok tatva kakugu mayokvighaat tahapkua ikalukpiit tattinut immagiktunut hillap kannugininganik nayogiyagiakaliktok.

Hillap kanogininga pitjutaokatakmat kakugu mayokvighaatnik tahapkua ikalukpiit tatvalu ikaluit ihuukit Dolly Varden nallukhaotaoyut. Tatvani unipkami Naunaipkutani 4, naunaiyahimayunga kanok tahamna hillap kanogininganik pitjutaokataka tahapkuninga: 1) Kakugu mayokatakmat tattinut immagiktunut tahapkua ikalukpiit tatvalu ikaluit ihuukit Dolly Varden; tatvalu, 2) mayokpakhutik kullanut kukluaktup Kuukmi tahapkua ikaluit ihuukit Dolly Varden (naunaiyakhimangitot mayoktunik kullannut Kuukmi huli). Ihomagiluaktavut hilla allangugangat mayokvikhaat tattinut immagiktunut tagiok niklakpalialigangat; tahapkua ikalukpiit mayokataktot tattinut immagiktunut tagiok unnakpaliatitlugo. Tahapkua ikaluit ihuukit ukkikataktot kullani kukluaktumi kuukmi mayokatakmiyot tagiok niklakpalialigangat tahapkuataok ikaluit ihuukit Dolly Varden ukkikataktot natkani tahaffuma kukluaktumi kuukmi. Tahapkua ikaluit ihuukit Dolly Varden ukkikataktot kullani kuukmi, kuukap unnakninga unnatkiyaokatakmat ummilgungnaktokhaoyok mayokpalianiaktitlugit. Immakak tahapkua ikaluit ayughaotigikataktat mayokvikhatik tattinut uttakivagungnakhiyat unnakninganik kukkap. Immaokaomagangat ikkayotaovagungnakhiymiyok kihiani pitjutaovalangituyaaktok mayokvikhaatnik tahapkua ikaluit ihuukit Dolly Varden ukkikataktot kullani kuukmi. Kihianitaok, immaokagangat pitjutaungmiyok mayokvikhaitnik tahapkua ikalukpiit tatvalu ikaluit ihuukit Dolly Varden ukkikataktot natkani kuukmi. taimaitkaluaktitlugit, naunaiyakhimayavut ihomangnaktok tahapkua ikaluit ihuukit Dolly Varden ukkikataktot kullani kukluakviani kuukmi ayoghakhimaitomik mayokatakmat tattinut, tatvataok

tahapkua ikaluit ukkikataktot natkani kuukmi mayokatakmiyot tattinut immagiktunut kayumiitunuamik. Ikaluit ihuukit Dolly Varden ukkikataktot kullani kukluakviani Kuukmi ahianik tagiop unnakpalianinganik pitjutikakmiyot mayokvighait tattinut immagiktunut immaokaknialo allangangmiyok tahapkunanganin ikaluit ihuukit Dolly Varden tatvanganin ukkikataktunit kullani kukliaviani kuukmi. Ihomanaktok immakak ahianik pitjutikakpagungnakhiyot mayokvikhaat tatvalu/uvalunin ukkiumi namungaovikhaitnik inmingnik ikpigiyakagangamik tahapku tamaita ikaluit taima ihomanaktok.

Tahamna Kuuk ikalukaknik atogagiyat tahakmik hapkua ikalukpiit tatvalu ikaluit ihuukit Dolly Varden ukkiukmi natkani tahaffuma Kukluktumi Kuukmi allangayok pitakangituyaakmat tahamna mannigak immak nakingaakmangata illitugingitnamku. Tatvani unipkami naunaipkutani 5-mi, takkukhimayaga kaffiit ihomagivlugit huok ilangit tahapku ikalukpit ukkikatakat natkani tahaffumja kukkiktuk kuukani: igligiyaitlu igniokvigikataktaitniklo naunaiyagahuaklugit, nigginiakvigiyataktaitlo naninmangata tagiokmi, huoklo maayokatangitpat kuukiktumi kuukmit. Tahapkuataok ikaluit ukkiukataktot natkani tahaffuma kuukiktumi kuukmi, takkuhimangitunga hunnanik igginiakatakamangata akkiagoit illuhikangitmata, kihianitaok naunaiyaihimangitnamta ammihunik ikaluknik nannilunin takkukhimangitnaptigo huli. Taima illitkuhiktuyaaktot tahamaninaakniaktok ukkiugalok naatkani tahaffuma kukluakviani Kuukmi; tahamaniikhatkiyaongmiyot kukkap pannani tatvalu maayoknahaatkiyaovakhutik tatvanganin ikaluit ihuukit Dolly Varden mayoknagikataktot ukkikatakhutik kulani tahaffuma kukluakviani Kuukmi. Tahapkua ikaluit ihuukit Dolly Varden ukkikataktot naatkani kukluakviani Kuukmi ajikingituit ingilgayangit, ilangit tahapkua ikaluit ihuukit ukkikataktot naatkani kukuakviani Kuukmi, ilangitaok ammukatangitot naatkanit haffuma kukluakvianin Kuukmi. Illitkugingitatka pikagiaghaita igliitnik naatkani tahaffuma kukluakviani Kuukmi tahapkua ikaluit ihuukit uvaluni ikalukpiit. Tahapkua ikaluit naalautait naunaipkutigivlugit illitugihimayavut ukkikataktutaok ahinni kukkani ilangitni ukkiuni, taima ihomanaktok iglikakpagungnaghiyok tahapkua ikaluit ahinni kukkani tatvalu ukkiyaktokpakhutik tahamunga Kugluntumi Kuukmit ukkiuni igliliungitagangamik igniukvikhamingnik, ayungnaitkiyaoyungnakhingmat. Tahapkua ikaluit ihuukit Dolly Varden ukkiktaktaktot tahamani naatkani Kuukmi mikitkiyaovakhutik ikalukpiakjuut tatvanganin tahapkuninga ikaluit ihuukitnit Dolly Varden ukkikatakмата kullani tahaffuma kukluakviata Kuukmi, ihomanaktok immakak tahapkua ikaluit ihuukit Dolly ammukpagungnakhiyot kullanut kukluakviani Kuukmi igliligiaktokhutik igniokvikhamingnik. Igliliokviit tatvalu kanovalaak iglilokatakamangata tammakmik tahapkua allatkik ikaluit nalluyaoyut huli tahamani Kugluktumi Kuukmi.

Tahamna naunaiyaktaohimayok unipkalioktaovluni tahapkuninga ikaluit hiitokataktot iliitkuhiitnik ikalukpiit tatvalu hapkua Dolly Varden ikaluit ihuukit nayogagiyat tahamna Kugluktuk Kuukmi, ahiani taima pittakangitok immagiktumik Kuukmik hittuviovaktumik tahapkuninga allatkinguyunik ikalungnik. Ajikiiktoktut tagiokmut hiitovakhutik namungaokatakangatalo tahapkua ikalukpiit tahapkulo ikaluit ihuukit Dolly Varden tatvalu ammugangata ukkiukhivikhamingnut (kullanut uvalunin natkannut tahaffuma Kuukmi kuukikningani) tahapkua ikaluit ihuukit Dolly Varden ayungnavakniaktot tatva hapkua ikaluknik naunaiyaiyiit havagiyaitnik hivunighami ihomalutaovaliaktuk ikkilivalianingit. Hapkua ikalukpiit tatvalu hapkua ikaluit ihuukit Dolly Varden hiitukataktot Kugluktuni Kuukmit tatvalu tagiokmut Coronation Gulf-mut, uvanga takkukhimayatka tahapkua allatkit ikaluit ajitkingitot hiitugangat ingilgayangit ajikikatangitot ukkiuni. Takkukhimangmiyaga tahamna nuna manigaak hulitjutaongmiyok hittuniahaktitlugit ikaluit tagiokmut. Taima atjikikatangitmata ikaluit hittuviat namungaukataknitlo ikkayutaoniakuktat tahapkua ikaluit annamatjutaitnik hila kannugininganik. Kihiani hivunikhami naunaiyainik pivaligiakaktok naninmangata tahapkua ikaluit igliliovit tatvalu kannuvaklaak igliliovakatak kaoyivaliotiginahuaklugit kanok hunaniklo ullugiangaktomitjutait tatvalu kanok annamatjuktikaohighaitnik tahapkua allatkit ikaluit tatvalu tuhaktinahuakutikhaitnik tahapkua ikaluhikinikut ataniktoiyot.

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Dedication

To my many families: old, new, biological, chosen, unofficially adopted, and Salmonidae.

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Chapter 1

General Introduction

Life history is the age-specific survival and reproductive potential displayed by an organism (Partridge and Sibly 1991). Life history traits are physiological, morphological, and behavioural characteristics that affect the fitness of an organism and are therefore subject to natural selection (Cole 1954).

Inter-population or inter-individual diversity in life history traits can be explained through the theoretical framework of a conditional life history strategy (Gross and Repka 1998), where the traits expressed by an individual are determined by the state (e.g., body size) of the individual at a decision or switch point (Gross 1996). The set of decision rules is considered the life history strategy, and the results of the decision(s) are considered tactics within a single conditional strategy. Although average fitness may differ among resulting phenotypes, fitness of the individual is maximized under a conditional strategy (Gross 1996). Because tactics are determined by individual state, which is influenced by environment, understanding diversity in life history tactics and shifts in tactics in association with environmental change is essential in promoting species' resilience.

Migration is a prominent life history tactic that occurs in response to spatiotemporal variation in environmental conditions and resources (Alerstam et al. 2003; Dingle and Drake 2007) and has important implications for ecosystem structure and function (see Holdo et al. 2011). Anadromy (migration from spawning/hatching locations in fresh water to feeding locations in salt water) is a type of migration that globally (i.e., among species) is associated with, and likely an adaptation to, low productivity in fresh water relative to salt water (Gross 1987; Gross et al. 1988), but involves numerous tradeoffs that directly impact individual fitness. For instance, individuals in partially anadromous populations of fishes (i.e., populations with both resident and anadromous individuals, with migration tactic determined through a conditional strategy; Chapman et al. 2011) must often decide to mature (forego migration and allocate resources to reproduction) or migrate (delay maturation and migrate to gain additional resources for future reproduction; Jonsson and Jonsson 1993). Body size, particularly for females, is associated with reproductive output (Hendry et al. 2004; Barneche et al. 2018), but there is typically a tradeoff between growth and survival for anadromous individuals (Jonsson and Jonsson 1993; Hendry et al. 2004; Jensen et al. 2019). There is evidence that food availability (e.g., Nevoux et al. 2019) and temperature (e.g., Morita et al. 2014) in freshwater environments can influence the occurrence of migration in facultatively anadromous populations and anadromous species of fish are particularly

susceptible to impacts of climate change (Reist et al. 2006). Environmental changes that alter mortality rates and growth benefits for anadromous individuals (relative to residents) will likely result in a shift in migration tactics and have important implications for species conservation.

Remarkable variability in migration tactics can be readily observed both within and among anadromous species of fish. Iteroparous species typically make multiple spawning migrations (e.g., Striped Bass (*Morone saxatilis*), Hocutt et al. 1990; Atlantic Salmon (*Salmo salar*), Persson et al. 2023), whereas semelparous species make a single spawning migration (e.g., Sea Lamprey (*Petromyzon marinus*), Beamish 1980; most Pacific salmon (*Oncorhynchus* spp.), Groot and Margolis 1991). Duration of marine feeding can range from a few months (e.g., Brown Trout (*Salmo trutta*), Jensen et al. 2020) to multiple years (e.g., Green Sturgeon (*Acipenser medirostris*), Colborne et al. 2022). Variability in timing of return migration to fresh water within a given year can affect individual fitness, through rates of spawning success (e.g., Pink Salmon (*Oncorhynchus gorbuscha*), Dickerson et al. 2005; Chinook Salmon (*Oncorhynchus tshawytscha*), Anderson et al. 2013) or risk of mortality (e.g., Sockeye Salmon (*Oncorhynchus nerka*), Hinch et al. 2012; Northern Pike (*Esox lucius*), Tibblin et al. 2016). Through the “portfolio effect” (Figge 2004), maintaining diversity in migration tactics, such as migration timing, is essential to promote resilience of populations and ecosystems (Schindler et al. 2010; Waldman et al. 2016). Because migration and other life history tactics within a conditional life history strategy are influenced by environment, climate change may shift the relative benefits of different tactics and/or decrease diversity in displayed tactics. Arctic regions are disproportionately affected by climate change (Rantanen et al. 2022). It is thus crucial to study life history tactics and migration patterns of anadromous species of fish in the Arctic to understand and potentially mitigate the impacts of climate and other anthropogenic changes on these species and ecosystems.

1.1 Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma malma*)

Research on migration in members of the family Salmonidae has contributed to our understanding of migration ecology and evolutionary biology (Stearns and Hendry 2004). Arctic Char (*Salvelinus alpinus*) and Dolly Varden Char (hereafter, “Dolly Varden”; *Salvelinus malma*) are two closely related species in the family (Taylor et al. 2025). Arctic Char has a Holarctic distribution and is the most northern freshwater species of fish in the world (Scott and Crossman 1973; Johnson 1980; Power and Reist 2018). Dolly Varden is primarily found in Pacific systems; in Canada, northern form Dolly Varden (*S. malma malma*) occurs in the western Arctic (Weinstein et al. 2024) and was recently identified in the central

Arctic (Weinstein 2023). Arctic Char and Dolly Varden are facultatively anadromous and highly plastic species (e.g., Klemetsen 2010; Markevich et al. 2018). Both species display remarkable variability in phenotype and life history, which has likely facilitated their persistence in diverse and challenging Arctic environments and is of interest in the study of adaptation and migration tactics. Because both species are relatively long-lived and iteroparous (Armstrong and Morrow 1980; Johnson 1980), assessment of migration tactics over multiple years and spawning cycles is possible (e.g., Gallagher et al. 2018b; Jensen et al. 2019).

The study of migration and other life history tactics in Arctic Char and Dolly Varden is additionally valuable due to the high cultural and economic importance of both species. In Canada, Arctic Char is essential for both commercial and subsistence fisheries in the Arctic (Priest and Usher 2004; Roux et al. 2011; Harris et al. 2016; Cott et al. 2023) and Dolly Varden is essential for subsistence fisheries in the western Arctic (Lea et al. 2021). Country foods (foods harvested from the land), including char species, are invaluable to the social, economic, cultural, and nutritional well-being of Indigenous communities (Van Oostdam et al. 2005). Harvesting country foods is vital to food security in remote, Arctic communities (Inuit Circumpolar Council 2012) and helps maintain and promote Indigenous languages and traditional skills (e.g., Carter et al. 2025). Indigenous knowledge holders possess an abundance of knowledge about both Arctic Char and Dolly Varden (e.g., Byers et al. 2019; Prno 2019; Dubos et al. 2023). Anadromous Arctic Char and Dolly Varden migrate to the ocean to feed during the ice-free season and return to fresh water to overwinter (Armstrong and Morrow 1980; Johnson 1980). Anadromous individuals of both species are more prevalent than resident individuals in subsistence diets in Arctic Canada (Priest and Usher 2004; Byers et al. 2019). Understanding the diversity and drivers of life history and migration patterns and how these tactics are affected by environmental changes is critical to ensure the future persistence of these important food sources.

Arctic Char and Dolly Varden exhibit considerable variability in occurrence and frequency of anadromy. Partial migration is observed in populations of both species (e.g., Radtke et al. 1996; Gallagher et al. 2019). Food availability during rearing influences the proportion of anadromous individuals within partially anadromous populations (Nordeng 1983), and freshwater productivity has been reported to influence the occurrence of anadromy among populations (Finstad and Hein 2012) of Arctic Char, consistent with the hypothesized global (among species) driver of evolution of anadromy (Gross 1987). Distance and difficulty of the migratory pathway also influence both the proportion of anadromous individuals within populations (Kristoffersen 1994) and the occurrence of anadromy among populations

(Power and Barton 1987; Finstad and Hein 2012) of Arctic Char, which indicates that migration tactics reflect the relative costs and benefits of anadromy.

Substantial diversity in degree of anadromy and migratory tactics (within anadromy) has been observed both among and within populations of Arctic Char and Dolly Varden. Variability in migration tactics among anadromous individuals reflects life history tradeoffs at the individual level. For instance, Dolly Varden that skip migrations (i.e., migrate to the ocean in alternate years and remain in fresh water in intervening years) reproduce less frequently but have greater longevity than individuals that migrate annually (Gallagher et al. 2018b). Skipped marine migrations have also been observed in populations of Arctic Char (Radtke et al. 1996; Mainguy et al. 2023), but have not yet been associated with other life history tactics or tradeoffs. Migration tactics can reflect local environmental constraints in spawning and/or overwintering habitats, such as two-stage migrations in Arctic Char (e.g., Johnson 1989; Beddow et al. 1998). Plasticity in migration tactics has facilitated the occupation of diverse habitats by Arctic Char and Dolly Varden and is essential for adaptation to environmental change, but presents challenges for the management of local fisheries (e.g., Roux et al. 2011)

Management of fisheries for Arctic Char and Dolly Varden is also complicated by stock mixing (i.e., sympatry of multiple populations). Although some populations of Arctic Char use largely distinct habitats in the marine environment (Hollins et al. 2022), others exhibit substantial mixing while in the marine environment (Dempson and Kristofferson 1987; Moore et al. 2013, 2016; Spares et al. 2015; Harris et al. 2022). Mixed stock fisheries of Dolly Varden have also been identified in the marine environment (Gallagher et al. 2018a, 2020). For both species, stock mixing may occur overwinter; overwintering in non-natal systems, typically in non-spawning years, has been observed in populations of both Arctic Char (Moore et al. 2013, 2017; Jensen et al. 2015) and Dolly Varden (Armstrong 1974; DeCicco 1997; Crane et al. 2005; Harris et al. 2015; Brown et al. 2019; Sawatzky and Reist 2021). Sympatry of populations (within species) is thus likely common, whereas sympatry of the two species is less common. Where Arctic Char and Dolly Varden have been documented occurring in sympatry in fresh water, Arctic Char are freshwater-resident (i.e., all individuals are non-anadromous) and Dolly Varden are anadromous (DeLacy and Morton 1943; Craig 1977; Taylor et al. 2008; May-McNally et al. 2015; Dennert et al. 2016). One exception is the marine environment of Darnley Bay, Northwest Territories, where anadromous Dolly Varden are infrequently observed in sympatry with Arctic Char (McNicholl et al. 2020). Recently, sympatry of anadromous Dolly Varden and Arctic Char was confirmed in Coronation Gulf (Weinstein 2023) near Kugluktuk, Nunavut (Figure 1.1). The unusual occurrence of anadromous life

history types of both species presents challenges in the management of local char fisheries, but also valuable opportunities for the study of life history and migration tactics.

1.2 A note on species composition

Char that used the Coppermine River and Coronation Gulf (see Section 1.3 and Figure 1.1) were historically identified as Arctic Char, because Dolly Varden were not thought to occur east of the Mackenzie River, Northwest Territories (Weinstein et al. 2024). Limited older genetic evidence suggested Dolly Varden may also be present in the area (Reist and Sawatzky 2010), however, and presence of Dolly Varden was more recently confirmed (Weinstein 2023). Historic species composition is unknown because it has not been identified whether Dolly Varden were historically present or recently expanded into the area. Contemporary species composition (e.g., related to a sample or observation) is also often unknown because visual identification of Arctic Char and Dolly Varden, particularly of live specimens, is unreliable (pers. obs.) and genetic material for genotyping is not always available. Thus, the generic term “char” will be used in this thesis in cases when species is unknown or potentially misidentified. To avoid undue confusion, other species in the genus *Salvelinus* (e.g., Lake Trout or Lake Char (*S. namaycush*) and Brook Trout or Brook Char (*S. fontinalis*)) will be referred to by full common name.

1.3 Study area

Char is profoundly important to Inuit in the community of Kugluktuk, Nunavut (Figure 1.1; Prno 2019). Char is consistently the most harvested type of fish by community members, both in number of fish harvested and in number of active harvesters (Priest and Usher 2004). Landlocked (resident) char are captured in some lakes, but the majority of harvested char are anadromous. Anadromous individuals are typically captured by gillnet in Coronation Gulf or as they migrate between the marine environment and the Coppermine River, which flows into Coronation Gulf immediately to the east of Kugluktuk (Figure 1.1). Kugluk or Bloody Falls is a large cascade located approximately 17 km upstream of the mouth of the Coppermine River (Figure 1.1; see photos of the cascade in Figure 1.2). Anadromous char are commonly captured by angling, kakivak (spear), or snagging as they migrate above the cascade to overwinter in the upper reaches of the Coppermine River. Anadromous char are also captured by gillnet under the ice in the river below the cascade. Inter-annual and inter-individual variability has been observed in overwintering location; individuals that overwinter above the cascade in one year may overwinter below the cascade in another year (Smith et al. 2022).

The species composition of individuals overwintering in the fluvial environment below the cascade in the Coppermine River is unknown (see Section 1.2). Whereas fluvial overwintering is extremely rare for Arctic Char in Canada (but see Beddow et al. 1998; Harwood and Babaluk 2014), it is common for Dolly Varden. Fluvial overwintering habitats used by Dolly Varden are usually associated with groundwater inputs (Mochnacz et al. 2010; Stewart et al. 2010; Brown et al. 2014; Byers et al. 2019), however, and there are no known groundwater inputs below the cascade in the Coppermine River, water temperature is consistently 0°C, and the under-ice environment is dynamic and likely challenging for overwintering char (Smith et al. 2022). The unusual overwintering habitat used by char and the rare sympatry of anadromous life history types of both Arctic Char and Dolly Varden make the Coppermine River and surrounding area of Coronation Gulf a unique and fascinating study system.

Concerns voiced by Inuit fishers from the community of Kugluktuk about a decline in the abundance and changes in migration patterns of char have been documented since at least 2007 (Prno et al. 2011). In response to community concerns, a research project was initiated in 2017 as a collaboration among the Kugluktuk Hunters and Trappers Organization (HTO; the elected body responsible for local fisheries management), University of Waterloo, and Fisheries and Oceans Canada. The primary objective of the project was to identify char spawning locations; spawning locations are unknown to local fishers and researchers alike and identifying these critical habitats is essential to assess population health and identify potential stressors. Although research efforts have been ongoing since 2017, spawning locations remain unknown. Through numerous methods attempted by the project team to identify spawning locations, we learned that the study system is more complex than first thought (e.g., the recent confirmation of the occurrence of both Dolly Varden and Arctic Char in the Coppermine River). Research questions have thus evolved over time, and reflect observations from local fishers, preliminary scientific data, discussions about findings with community members, and hundreds of casual conversations about char (often while waiting to catch one) with Inuit team members. The research presented in this thesis is a direct result of new and evolving questions from both Inuit and University researchers, and represents one step toward improving understanding of the char populations that use the Coppermine River and surrounding area, which are of great importance to the community of Kugluktuk.

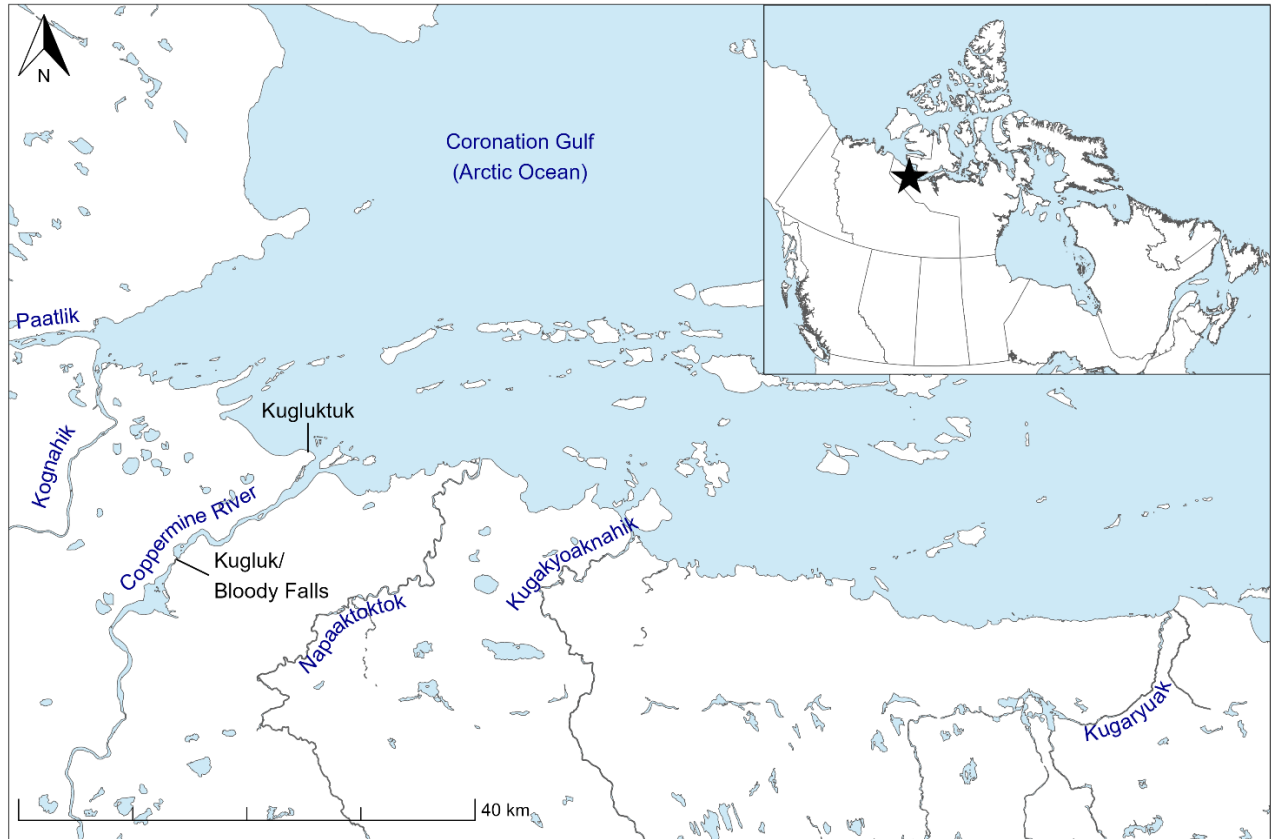


Figure 1.1: Map of the study area. The community of Kugluktuk is located in western Nunavut. The study area focuses on the Coppermine River and the surrounding marine environment of Coronation Gulf. Kugluk or Bloody Falls, a large cascade, is located ~ 17 km upstream of the mouth of the Coppermine River.



Figure 1.2: Photos of Kugluk/Bloody Falls, facing downstream from the right (A) and left (B) river banks.

1.4 Research objectives

Research objectives followed directly from questions and concerns voiced by community members about observed changes in migration patterns and harvest numbers of char. I primarily used acoustic telemetry to address the overarching goal of investigating the diverse life history and migration tactics of Arctic Char and Dolly Varden that use the Coppermine River, Nunavut.

Acoustic telemetry is a valuable tool to track wildlife in aquatic environments and has been successfully used to study life history and migration patterns, as well as inform fisheries management and species conservation, in diverse taxa and systems (Donaldson et al. 2014; Crossin et al. 2017). Acoustic arrays typically generate large numbers (thousands to millions) of detection records, some of which may be from mortalities or expelled tags. Removing detections from potential mortalities or expelled tags in a reproducible manner is important to reduce potential bias, but was reported by previous authors to be considered in only 50% of behaviour and ecology studies that used acoustic telemetry (Klinard and Matley 2020). To contribute to better methods and workflows used in processing acoustic telemetry data, I developed a tool that can be used to screen data for potential mortalities and expelled tags. Chapter 2 describes the R package that was developed to identify potential mortalities and expelled tags in detection records of char in the Coppermine River and Coronation Gulf, and demonstrates use of the package for three additional taxa and study systems. The package was used to identify and filter potential mortalities and expelled tags from the datasets used in Chapter 3, Chapter 4, and Chapter 5. Note that the study species in Chapter 2 is referred to as Arctic Char; the occurrence of Dolly Varden within the study system was unconfirmed at the time of writing and publishing (Smith et al. 2025).

Marine feeding is of critical importance for anadromous Arctic Char and Dolly Varden; anadromous individuals of both species reduce or cease feeding during the ice-covered season in fresh water (Moore and Moore 1974; Boivin and Power 1990; Rikardsen et al. 2003; Stewart et al. 2009) and must therefore acquire enough resources for recovery of body condition, growth, and reproduction during the brief ice-free season. Char that migrate above Kugluk or Bloody Falls in the Coppermine River (Figure 1.1) have a longer and more challenging migratory pathway than char that overwinter below the cascade, which may affect the duration of their marine migration or movement patterns within the marine environment. In Chapter 3, I used network analysis and local spatial statistics to identify high-use locations in the marine environment, and to describe and compare marine movement patterns and habitats used between fish that overwinter in different freshwater locations (above or below the

cascade). Although the occurrence of Dolly Varden within the study system was unconfirmed at the time of writing and publishing (Smith et al. 2024), findings in Chapter 3 are discussed in relation to both species and consider uncertainty in species composition.

The date that char returned to the Coppermine River differed between overwintering locations (above or below the cascade) and was earlier in years with earlier freeze-up of river ice (Chapter 3; Smith et al. 2024). Community members in Kugluktuk are concerned about the effects of warm water temperatures and low water levels on the health and migration patterns of char (Prno et al. 2011; Prno 2019), but effects of environmental conditions on migration timing are largely unknown for both Arctic Char and Dolly Varden (but see Bond and Quinn 2013). In Chapter 4, I used generalized linear mixed models and circular statistics to investigate how environmental variables were related to timing of return to fresh water by both Arctic Char and Dolly Varden, as well as cascade ascension by Dolly Varden. I also compared migration timing and cues between species and overwintering locations.

Arctic Char and Dolly Varden were observed overwintering in sympatry in the fluvial environment below Kugluk or Bloody Falls (Chapter 4). The fluvial environment in this stretch of the Coppermine River is challenging (Smith et al. 2022) and unusual (Stewart et al. 2010; Harwood and Babaluk 2014) overwintering habitat for both species. The response to environmental variables during return migration to fresh water differed between Dolly Varden that overwintered above the cascade and Dolly Varden that overwintered below the cascade, which suggested an underlying physiological cue for migration timing and perhaps overwintering location for Dolly Varden (Chapter 4). In Chapter 5, I used physical samples and acoustic telemetry to describe and assess the evidence for potential drivers of overwintering in the fluvial environment below Kugluk or Bloody Falls for both Arctic Char and Dolly Varden: spawning status, foraging opportunities in the marine environment, and failure to ascend the cascade.

The findings of Chapter 3, Chapter 4, and Chapter 5 are synthesized in Chapter 6; the tool developed and used in Chapter 2 is also briefly discussed. Recent confirmation of the occurrence of Dolly Varden in the study area is discussed and interpreted in relation to Chapter 3. Because the local char fishery is managed by the community through the HTO, the implications of primary findings for fisheries management are reviewed in Chapter 6, and key knowledge gaps that remain and pathways for future research are highlighted.

Chapter 2

mort: An R package to conservatively identify mortalities and shed tags in passive telemetry arrays

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2.1 Abstract

1. Telemetry is commonly employed to track animals and support ecological inferences, yet the possibility that tagged animals have died or shed their tags is often not fully considered. Neglecting to consider mortality and/or tag shedding can lead to biases in the interpretation of results.
2. We introduce the R package `mort`, developed to identify potential mortalities or shed tags in passive telemetry arrays. `mort` was designed for aquatic acoustic receivers with primarily non-overlapping detection radii, but the methods can be applied to any telemetry study that uses passive tracking (i.e., stationary receivers). We describe the primary functions and key options that are supported, provide guidance on the general use of the package, and demonstrate use with three case studies.
3. The thresholds to identify mortalities are either user-defined or derived from the dataset itself (using observed durations of residences of animals that are known to be alive). This flexibility, along with numerous customizable options, allows application to multiple species and systems.
4. `mort` fills an important gap in standardized workflows when processing and analyzing passive telemetry data. The R package is a useful tool and will improve reproducibility in ecological research and management decisions that rely on results from passive telemetry.

2.2 Introduction

Acoustic telemetry is a valuable tracking tool in the study of ecology, animal behaviour, and fisheries management (Donaldson et al. 2014; Crossin et al. 2017). The widespread and rapidly increasing use of acoustic telemetry (Matley et al. 2022) is leading to a concurrent increase in analytical tools for the data that are generated. There continue to be, however, critical gaps in how telemetry data are processed

and analyzed. For example, between 2015 and 2019, 50% of published ecological and behavioural studies that used acoustic telemetry did not consider the possibility that tagged animals had died or shed their tags (Klinard and Matley 2020). Neglecting to consider mortality can result in biased estimates of variables, such as activity rates and home ranges, and affect the interpretation and application of findings.

Widespread and consistent consideration of mortality and tag shedding in studies of passive telemetry (i.e., stationary receivers) is made challenging by the diverse species, locations, array designs, and budgets used. Methods developed to identify potential mortalities in one setting may not be applicable in another. For instance, in aquatic systems, methods comparing observed tag movement to water currents (e.g., Morfin et al. 2019) are not feasible without detailed, site-specific water current information. Similarly, results from studies that tag dead fish to study how carcasses may move within a study system (e.g., Yergey et al. 2012; Capizzano et al. 2016) are typically not applicable outside of the study area. In arrays where receivers are arranged with overlapping detection radii, fine-scale positioning (via triangulation) is possible (e.g., Espinoza et al. 2011). This allows researchers to differentiate between stationary tags and tags that move within the detection radius of a single receiver (e.g., Williams-Grove and Szedlmayer 2016; Bohaboy et al. 2020; Runde et al. 2021), but requires extensive and costly receiver coverage. Tags that transmit additional information, such as depth or acceleration, have been used to identify mortalities (e.g., Currey et al. 2014; Villegas-Ríos et al. 2014; Curtis et al. 2015; Capizzano et al. 2016; Runde et al. 2020), but there is typically a trade-off between sensors and other specifications, such as battery life, transmission interval, and/or cost. Similarly, radio tags may be programmed with a “mortality signal”, where the transmission rate changes after an animal has stopped moving for a specified period of time, but such programming is typically associated with an additional cost. Predation tags, which transmit an altered signal following digestion, have been successfully used to identify predation events (e.g., Halfyard et al. 2017; Weinz et al. 2020; Waters et al. 2024), but do not identify potential mortalities from other causes or expelled tags. There is thus a need for a method to identify potential mortalities and/or tag expulsion that is applicable across a wide range of species and systems, particularly in studies that use non-sensor tags in arrays of non-overlapping receivers.

As telemetry becomes increasingly prevalent as a tool to track animals, there are growing calls and efforts to improve reproducibility and standardization in data processing and analysis (e.g., Udyawer et al. 2018; Joo et al. 2020; Flávio and Baktoft 2021; Dhellemmes et al. 2023). Although multistate

capture-recapture models have been successfully implemented to infer mortalities in acoustic telemetry (e.g., Ellis et al. 2017; Hightower and Harris 2017), these models are relatively complex and the objective is often to estimate mortality or survival, rather than use estimates of mortality as a validation tool or step in data processing. Further, we believe that a method that is simple and intuitive will benefit the growing number of telemetry practitioners with diverse analytical backgrounds. For this reason, we have developed the framework presented in the R package `mort`. The intent is to flag potential mortalities or expelled tags during filtering and quality control steps in data processing (before conducting data analyses), rather than infer fates and/or provide survival estimates. The package was developed for non-sensor tags in arrays of non-overlapping receivers. The framework is designed to be conservative in that it considers the possibility that an animal is dead unless there is evidence to the contrary.

Here, we describe the package `mort`, review the primary features that allow customization and applicability to other species and study areas, and demonstrate application in three case studies: 1) a network of mountain rivers; 2) a relatively sedentary species in the ocean; and, 3) a mobile species in the ocean. Although the development of `mort` and the workflow presented here are for aquatic acoustic telemetry, the principles and methods are applicable to other telemetry methods with stationary receivers, and considerations for application to other methods are provided where appropriate.

2.3 Overview of the `mort` package

The `mort` package was developed using a telemetry dataset resulting from a study of Arctic Char (*Salvelinus alpinus*) movements in Nunavut, Canada. Acoustic receivers were non-overlapping and irregularly spaced. Details regarding the dataset and study area can be found in Smith et al. (2022). All Arctic Char in the dataset are anadromous; fish migrate to the ocean to feed during the ice-free season each year and return to fresh water before freeze-up. The ice-covered season typically comprises more than eight months of the year, and movement in fresh water is reduced during this period (Smith et al. 2022). The species thus exhibits complex movement patterns that require multiple criteria to identify potential mortalities. This complexity led to the multiple, customizable options that are found in `mort`, along with thresholds that are user-defined or data-derived.

A sample dataset is provided with the R package and can be accessed by calling `detections` (e.g., `View(detections)`) when `mort` is loaded into the user's workspace. These detection data were subset from the dataset used to develop the package. The data are valuable to the community of

Kugluktuk, and are also sensitive due to their pertinence to the local fishery for Arctic Char. For this reason, the detections have been given generic station names and fish IDs, and the years of the time stamps have been changed. Otherwise, the detections are real, and therefore have all the challenges and intricacies of biological data. All code presented can be run in R when `mort` is loaded into the user's workspace and will call on the sample dataset.

The package `mort`, including the example Arctic Char dataset, is open-source and available on CRAN (<https://CRAN.R-project.org/package=mort>). The source code is also available at <https://github.com/rosieluain/mort>. The version of the package used in this manuscript is available from the Zenodo repository <https://doi.org/10.5281/zenodo.14956890> (Smith 2025). The code for the case studies, along with subsets of the datasets, are also available from the Zenodo repository <https://doi.org/10.5281/zenodo.14956950> (Smith et al. 2025).

2.3.1 Input data

The functions within the `mort` package require an input data frame of residence events. Residence events are generated by condensing consecutive detection records of a given animal at the same location into event records, which have start and end times (Figure 2.1). Any dataset of detections may be used, provided it can be imported or converted into a single dataframe in R and includes (at minimum) three fields: unique animal IDs, unique station IDs, and datetimes (i.e., POSIXt class). Residence events are generated from detection datasets using the function `residences()` with animal *ID*, *station*, and *datetime* arguments:

```
residences(data=detections, ID="ID", station="StationName",  
           datetime="DateTimeUTC")
```

Animal ID may be the tag transmitter ID or a unique ID assigned by the user, thereby accommodating tag redeployments. A station may be a single receiver or a group of receivers (e.g., receivers with overlapping detection radii). If a station is a group of receivers, then any movement among receivers at the station will not be considered movement in the analyses conducted through `mort`. The start of each residence event is the first datetime an animal is detected at a given station, after being tagged or detected elsewhere. The end of each residence event is determined as the last datetime the animal is detected at the station, before it moves and is detected at a new station. The end of each residence event may also be determined as the last datetime before an animal is not detected for a user-defined

period of time (i.e., the animal is detected at a station, is not detected for a period of time, then is detected again at the same station), specified with the *cutoff* and *units* arguments.

In addition to the output of `residences()`, functions within the `mort` package can accept outputs from other packages, including `actel` (movement events; Flávio and Baktoft 2021), `glatos` (detection events; Holbrook et al. 2022), and `VTrack` (residences; Campbell et al. 2012). There is also the option to specify residence events that are generated manually or by packages not currently supported by `mort`. Data frames of residence events generated manually or by packages may have additional fields, but must include: unique animal ID, station name, start datetime, end datetime, and duration of residence event.

2.3.2 Identifying potential mortalities and expelled tags

There are two functions to identify potential mortalities and shed tags: `morts()` and `infrequent()`. Both functions rely on the assumption that a mortality or a shed tag remains relatively stationary, within the detection range of one station.

2.3.2.1 `morts()`

The function `morts()` derives thresholds from the dataset itself, which prevents potential bias from researcher-created subjective thresholds and identification of stationary tags using visual or manual techniques. This function operates by first identifying the most recent station change for each animal (Figure 2.2). The most recent station change is the last known datetime that an animal moved; it is assumed that all observed movements were from a living animal and, therefore, that the animal was alive before this time (though see Section 2.3.3 – Dead and drifting – below). Thresholds for identifying potential mortalities are then derived from the residence events that occurred when animals were assumed to be alive (i.e., before the most recent station change). Thresholds are derived and applied using one of two methods: duration of single residence events or duration of cumulative residence events.

2.3.2.1.1 Duration of single residence events

Using data from all animals, the maximum duration of a single residence event while assumed living is identified (Box 1 in Figure 2.2). This value becomes the single residence event threshold, and is applied to residence events that occurred after the most recent station change of each animal (i.e., when it is unknown if an animal is alive or dead). The threshold may be applied, using the *method* argument, in

two ways. First, the threshold may be applied to the last residence event available for each animal (D in Figure 2.2), using, for example:

```
morts(data=events, type="mort", ID="ID", station="StationName",  
      method="last")
```

Second, the threshold may be applied to any residence events that occurred after the most recent station change (E in Figure 2.2), using:

```
morts(data=events, type="mort", ID="ID", station="StationName",  
      method="any")
```

Any residence events that exceed the threshold are flagged as potential mortalities or expelled tags.

2.3.2.1.2 Duration of cumulative residence events

Cumulative residence events are quantified as the elapsed time between when an animal is first detected at a station and when it is last detected at the same station, including any gaps in detection (Box 2 in Figure 2.2). The dataset of residence events is first converted to a dataset of cumulative residence events. Similar to the method for single residence events, the cumulative residence event threshold is identified as the maximum cumulative residence event that occurred before the most recent station change (Box 2 in Figure 2.2). By definition, there is only one cumulative residence event that occurs after the most recent station change for each animal, and the threshold is applied to this cumulative residence event (F in Figure 2.2), using:

```
morts(data=events, type="mort", ID="ID", station="StationName",  
      method="cumulative")
```

2.3.2.1.3 Selecting a method

Multiple options and methods are provided in `morts` to maximize relevance for diverse species and/or array configurations. The thresholds for cumulative residence events are typically much longer than those for single residence events. For this reason, running `morts()` using the single residence event threshold may identify potential mortalities that have occurred recently, before the cumulative threshold has been reached. Conversely, running `morts()` using the cumulative residence event threshold may identify potential mortalities that appear as multiple short residence events, which individually would not be long enough to exceed the threshold for single residence events. Using both

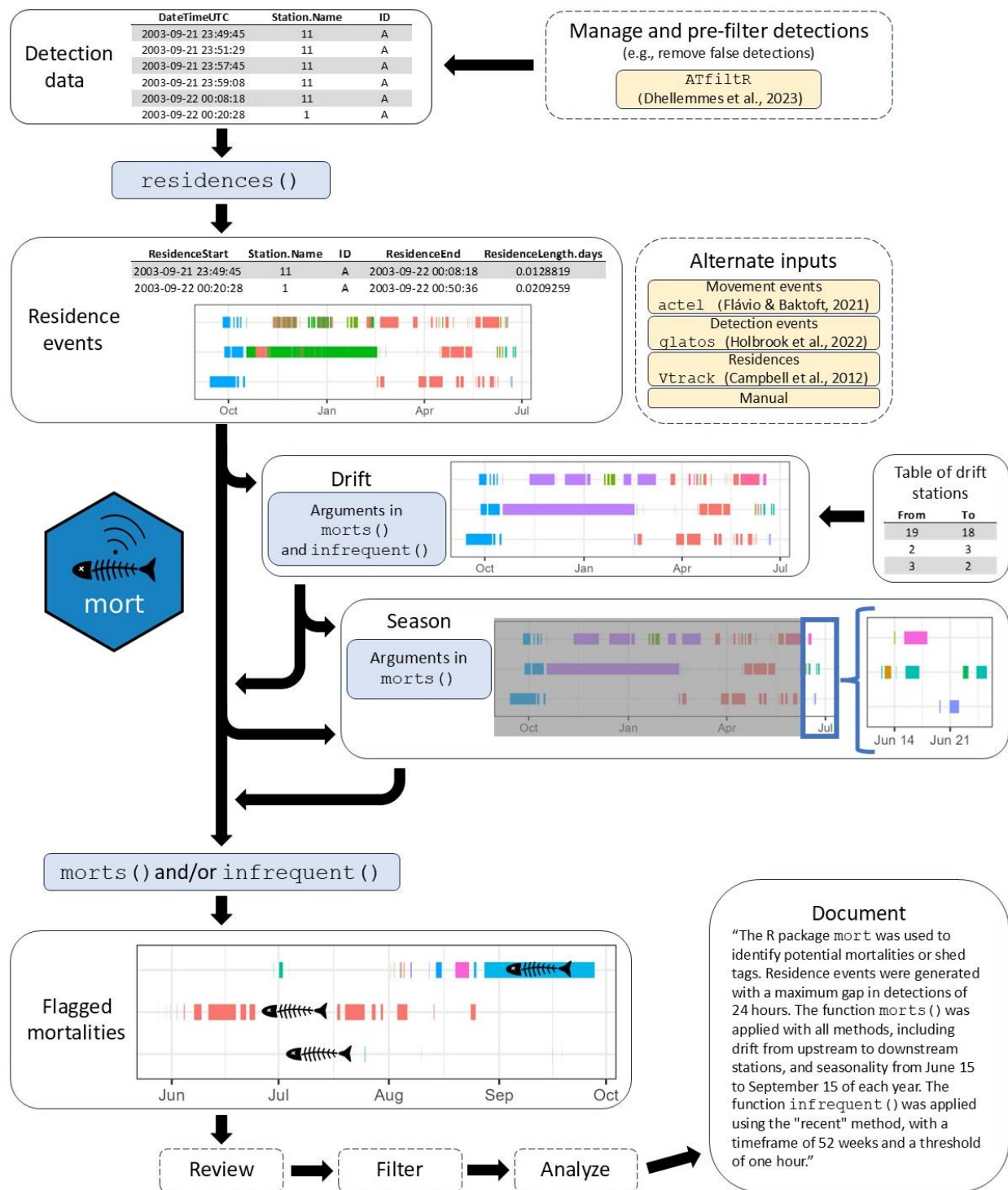


Figure 2.1: Proposed workflow, incorporating *mort* to identify potential mortalities or shed tags as a step in data processing, before conducting further analyses. Solid outlines indicate workflow steps conducted or returned by *mort*; dashed outlines indicate steps conducted or outputs obtained by user

(Figure 2.1 continued): or other R packages. Subplots of residence events were created using the function `mortsplot()` in `mort`, which relies on `ggplot2` (Wickham 2016). Colours of bars in subplots indicate unique stations. To facilitate reproducibility, an example of how to document workflows that use `mort` is provided.

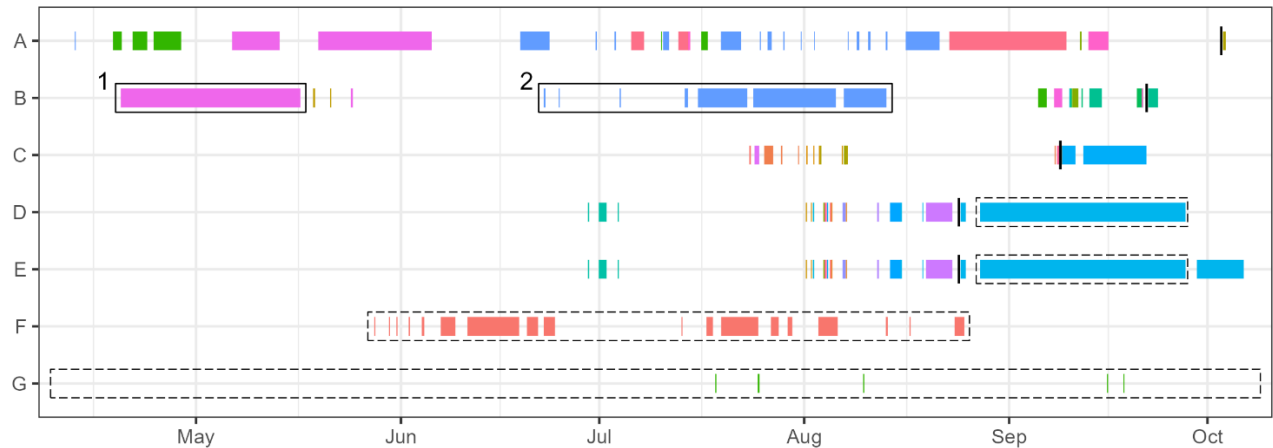


Figure 2.2: Residence events, showing examples of how `mort` identifies thresholds (solid boxes) and potential mortalities or shed tags (dashed boxes). Each line (A to G) represents an individual animal and colours of bars indicate unique stations. The most recent station change for each animal is marked by a black vertical line. Before this mark, it is assumed the animal is alive; after, the animal status is unknown. The thresholds for a single residence event (1) and cumulative residence event (2) are the longest of each event type when the animals are assumed living. The thresholds are then applied to unknown periods (i.e., after the most recent station change). Animals A, B, and C are assumed living. Animal D would be identified as a potential mortality using the “last” method for single residence events in `morts()`; animal E, using the “any” method for single residence events; and, animal F, using the “cumulative” method. Animal G would be identified as a potential mortality with a user-defined threshold of six hours of residence events within six months in `infrequent()`.

single and cumulative events is the most conservative method. We generally recommend running both methods, both separately and together (`method="all"`), and exploring the results.

2.3.2.2 `infrequent()`

In arrays of receivers with non-overlapping detection radii, an animal may die or shed a tag nearby but outside of receiver range. Environmental conditions impact detection range in aquatic acoustic (e.g., Reubens et al. 2019; Winter et al. 2021) and radio (Peters et al. 2008) telemetry. A tag may thus be

recorded by a receiver intermittently, when environmental conditions are favourable. If intermittent detections occur over a sufficiently long period of time, the tag will be flagged as a potential mortality using the cumulative residence event method above. However, the cumulative residence event method will not flag intermittent transmissions that occur over a short period of time and do not exceed the cumulative threshold.

To flag intermittent residence events as potential mortalities, the function `infrequent()` extracts all residence events within a user-defined timeframe. The *method* argument is used to indicate which of two methods is used to identify the timeframe. In the first method, the timeframe is defined with start and end dates, using, for example:

```
infrequent(data=events, type="mort", ID="ID", station="StationName",  
           threshold=1, threshold.units="days", method="defined",  
           start="2023-06-15", end="2023-10-15")
```

In the second method, the timeframe is defined as a period of time (e.g., 52 weeks) that ends with the most recent detection, using:

```
infrequent(data=events, type="mort", ID="ID", station="StationName",  
           threshold=1, threshold.units="days", method="recent",  
           recent.period=52, recent.units="weeks")
```

The durations of residence events within the specified timeframe are summed. If all residence events occur at the same station and the summed duration exceeds a user-defined threshold (*threshold* and *threshold.units* arguments in example function calls above), the earliest intermittent event within the specified timeframe is flagged as a potential mortality or expelled tag (G in Figure 2.2).

2.3.3 Dead and drifting

The configuration of some receiver arrays may cause a mortality or shed tag to move or appear to move among stations. For example, a tag or carcass may move with currents or tides. A stationary tag may also be located within the detection ranges of two overlapping receivers. If the receivers are assigned individual stations, then simultaneous or near-simultaneous detections at the two receivers would be assigned to different residence events, and therefore appear as station changes or movements. To remove potentially invalid movements or apparent station changes when identifying mortalities, drift can be applied within the `morts()` and `infrequent()` functions (Figure 2.1).

To apply drift, the user specifies stations where drift or overlapping receivers may result in a tag moving or appearing to move. To do this, the user must have knowledge of the study system and configuration of the receiver array, and conduct at least preliminary data exploration. Drift may be unidirectional (e.g., from upstream to downstream) or bidirectional (e.g., tides or overlapping receivers), as indicated in the table of drift stations (Figure 2.1). Within the `infrequent()` function, the drift table is specified by the user with the *drift*, *from.station*, and *to.station* arguments:

```
infrequent(data=events, type="mort", ID="ID", station="StationName",
           threshold=1, threshold.units="days", method="recent",
           recent.period=52, recent.units="weeks", drift=ddd,
           from.station="FrStation", to.station="ToStation")
```

Within the `morts()` function, the drift table is specified with the *ddd*, *from.station*, and *to.station* arguments, and drift may be applied when deriving thresholds (which would likely increase thresholds) using the *drift* argument:

```
morts(data=events, type="mort", ID="ID", station="Station.Name",
       method="any", drift="threshold", ddd=ddd, from.station="FrStation",
       to.station="ToStation")
```

Drift may also be applied when identifying potential mortalities only (*drift="morts"*) or for both deriving thresholds and identifying mortalities (*drift="both"*). The most conservative option is to apply drift when identifying potential mortalities only, because the durations of residence events with drift included are the same or longer than the durations of residence events without drift included. This means that thresholds derived without drift included will be the same or shorter than thresholds derived with drift included. Duration of critical residence events – events that occur after the most recent station change and are compared to thresholds to determine if an animal is dead or living – will be the same or longer with drift included than durations of critical events without drift included, and are therefore more likely to exceed the threshold.

2.3.4 Seasonality

Arctic Char exhibit reduced movement during the ice-covered season in the study system (that led to the development of `mort`; Smith et al. 2022). Limited movements can lead to long residence events at a single location, a higher threshold, and potential mortalities to be missed. To account for periods of time when movement may be reduced due to environmental conditions or the biology of the study species,

seasons or periods of interest can be defined using the *season.start* and *season.end* arguments in `morts()` (Figure 2.1). For example, using:

```
morts(data=events, type="mort", ID="ID", station="Station.Name",  
      method="any", season.start="01-06", season.end="01-11")
```

will extract all residence events between 01 June and 01 November of each study year. If seasonality is applied, thresholds are derived and potential mortalities are identified using only residence events from within the period(s) of interest.

2.3.5 Output

The output of `morts()` and `infrequent()` is a data frame, with one record for each residence event that was flagged as a potential mortality or shed tag. There is no function in `morts` to remove detection data or residence events based on flagged mortalities. Instead, it is the responsibility of the user to review the output and assess the validity of the flagged mortalities before filtering detection data and/or residence events and conducting further analyses (see proposed workflow, Figure 2.1).

2.3.6 Review new data

The default and recommended options within `morts` are designed to be conservative. The functions may thus flag animals as potential mortalities that are, in fact, living. When additional data are received, these animals may be observed to change stations. Instead of running the analysis on the original dataset (i.e., dataset that has not been filtered to remove potential mortalities) every time new data are added, the function `review()` compares residence events from flagged mortalities to new data. If the animal is observed to change stations (i.e., be alive), the residence event that marks the station change is provided in the output. The output can be reviewed to assess validity. If the tag has changed stations and the animal is inferred to be alive, the data from that tag can be reintegrated into the previously created filtered dataset. If the animal has not changed stations (including drifting, if drift is applied), then it can be assumed the detections continue to be from a mortality or shed tag.

2.4 Case studies

2.4.1 Arctic Grayling (*Thymallus arcticus*)

Arctic Grayling are highly migratory salmonids with complex annual migrations between overwinter, spring spawning, and summer feeding habitats (Blackman 2002; McPhail 2007). During the summer

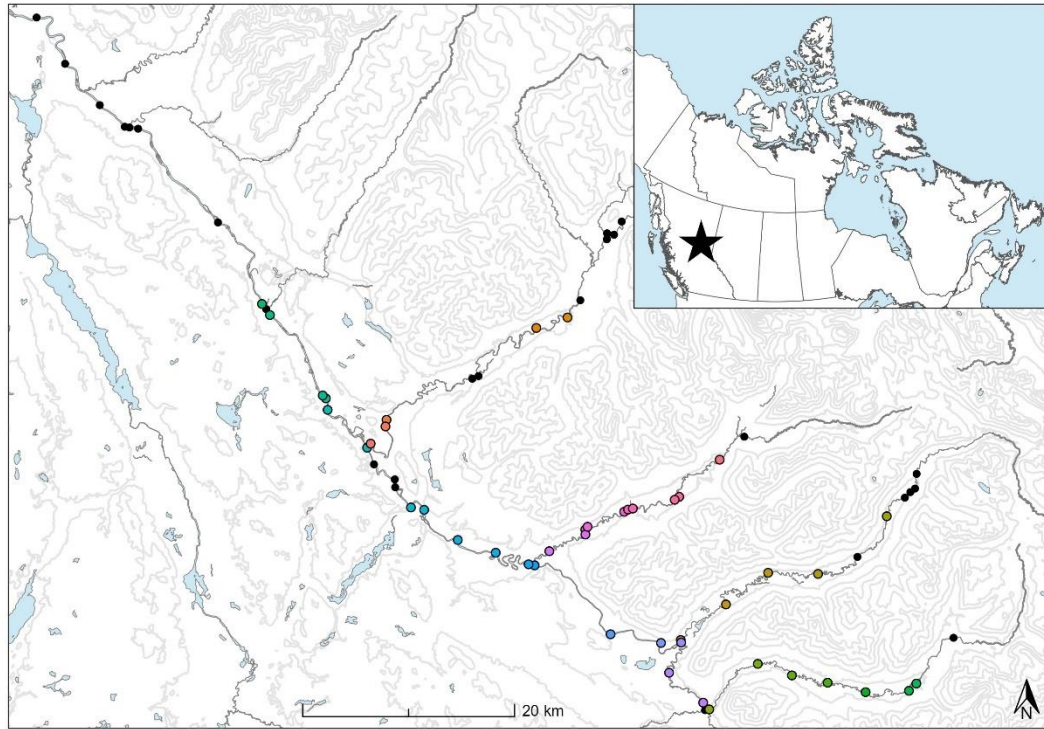
rearing period, Arctic Grayling can position themselves along rivers following upstream dominance hierarchies and may defend a single feeding site for an entire season, sometimes returning to the same site in multiple years to feed (Hughes and Reynolds 1994). We applied `mort` to a dataset of 138 Arctic Grayling tagged with Innovasea (Halifax, NS) V9 tags in 2018–2021 in the Parsnip River watershed of north-central British Columbia, Canada (Martins et al. 2022; Figure 2.3A).

Residence events were generated with a cutoff of 24 hours. Because an expelled tag or a tag in a dead fish may drift downstream in river networks, a drift table was generated with unidirectional drift from each upstream station to the nearest downstream station. The function `morts()` was applied using both single and cumulative residence events (`method="all"`) and drift was applied when identifying potential mortalities (`drift="morts"`). Three Arctic Grayling were identified as potential mortalities (Grayling E, F, and G, Figure 2.3B) because the most recent cumulative residence events exceeded the threshold for cumulative residence events, which was determined automatically by the function `morts()` from the dataset (274 days; Grayling D, Figure 2.3B). No single residence events exceeded the threshold for single residence events, which was relatively high (104 days; Grayling B, Figure 2.3B). The function `infrequent()` was applied using `method="recent"`, a threshold of 24 hours in 52 weeks, and drift. Nine individuals were identified as potential mortalities due to infrequent detections (e.g., Grayling G, Figure 2.3B).

The package `mort` was successful in identifying potential mortalities or expelled tags in a network of mountain rivers. Arctic Grayling in other systems have been observed returning to the same site over multiple years to feed in summer (Hughes and Reynolds 1994). Review of the residence events that were observed for Grayling F (Figure 2.3B) shows consistent residence at a single station in summer (July–September 2019), followed by a gap in detections until return to the initial station in spring (May 2020), which may represent two feeding periods separated by overwintering. The residence events that were flagged as a potential mortality may thus represent a believable detection pattern from a living individual. The package `mort` is designed to be conservative and may overestimate the number of mortalities, underscoring the need for review of the results by the user before filtering the data and proceeding to subsequent analyses.

An additional consideration in river systems is that noise from flowing water can result in low detection efficiency of receivers; tags may not be detected at every station. We recommend using observed

A



B

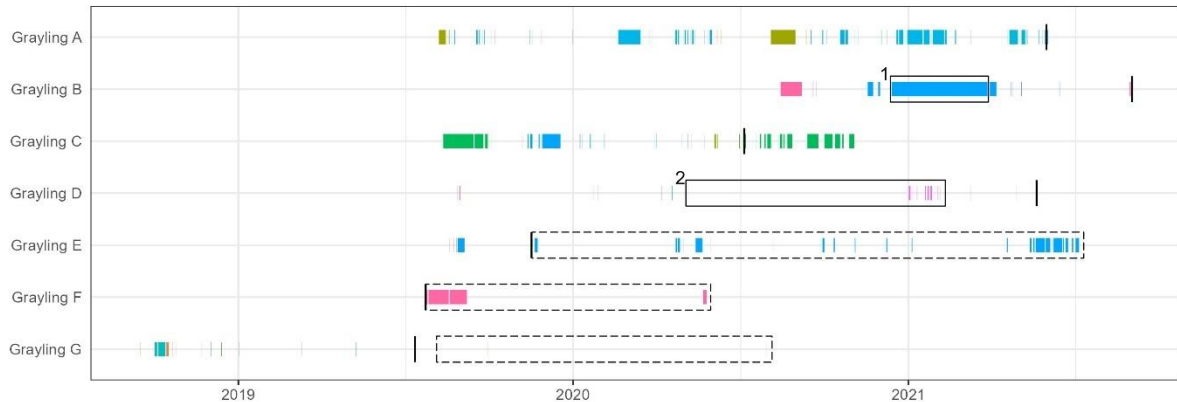


Figure 2.3: Map of the study area (A) and residence events (B) for select individuals from the Arctic Grayling case study. Points in A indicate receiver stations; black points are stations with no detections from selected Arctic Grayling and coloured points are stations with detections. Colours of stations in A correspond to those of residence events in B. Black vertical lines in B indicate the most recent station change for each fish. Solid boxes indicate the thresholds for a single residence event (1) and cumulative residence event (2). Dashed boxes indicate cumulative residence events (Grayling E and F) or infrequent residence events within a specified period (Grayling G) that caused these individuals to be flagged as potential mortalities or expelled tags.

patterns in detection (e.g., using the `advEfficiency` function in the R package `actel` (Flávio and Baktoft 2021)) or information from range testing to identify stations with low detection efficiency and adjusting the drift table accordingly. If efficiency estimates are not available, we recommend generating a drift list that includes non-sequential stations (e.g., include drift from station A to station C without being detected at intermediate station B).

2.4.2 Greenland Cod (*Gadus ogac*)

Greenland Cod are benthic feeders (Morin et al. 1991; Knickle and Rose 2014a) that occupy coastal habitats (Morin et al. 1991; Nielsen and Andersen 2001) in the Arctic Ocean and northwest Atlantic Ocean. The species is considered to be relatively sedentary; Greenland Cod typically exhibit high site fidelity, have small home ranges, and display limited movement (Knickle and Rose 2014b). We applied `mort` to an unpublished dataset from 63 Greenland Cod tagged with V13P acoustic tags (Innovasea, Halifax, NS) in 2019–2022 in the marine environment of Coronation Gulf, in western Nunavut, Canada (Figure 2.4A). The array is the same as that used to track Arctic Char in the study system (that led to the development of `mort`; Smith et al. 2022).

Residence events were generated with a cutoff of 24 hours. No potential mortalities were identified using the function `morts()` with either `method="any"` or `method="cumulative"`, likely due to the extremely high thresholds (determined automatically by the function `morts()` from the dataset) for both single (77 days) and cumulative (629 days) residence events (Cod A and Cod B, Figure 2.4B). Acoustic tags were equipped with depth sensors; depth records indicated that the individuals that generated the high thresholds were alive during the long residence events, as depths were variable. Visual assessment of depth records indicated two individuals with long periods of stable depths (Cod C and Cod D; Figure 2.4C). These depth records occurred after the most recent station change (Figure 2.4B) and were likely indicative of mortalities or expelled tags. Two potential mortalities were identified using the function `infrequent()`, `method="recent"`, and a threshold of 10 hours in 26 weeks. Only a single depth record was available for one individual, and thus we could not infer whether this individual was a mortality or not. Depth records for the second individual indicate it was living (Cod E; Figure 2.4B and C).

Applying `mort` to Greenland Cod provides insights into study design for relatively sedentary species. Movement patterns (indicated by station changes) were indistinguishable between living and dead individuals, which demonstrates the need for utmost caution to be applied when interpreting data from

sedentary species in arrays of non-overlapping receivers. Interpretation of potential mortalities can be aided by simultaneous review of data from sensor tags, and results can be used to refine study design or reveal key considerations for the interpretation of further analyses. We recommend that telemetry practitioners employ complementary tools such as sensor tags (e.g., depth, acceleration) when studying sedentary species and/or design the array to allow for overlapping detection radii and positioning (e.g., Villegas-Ríos et al. 2014).

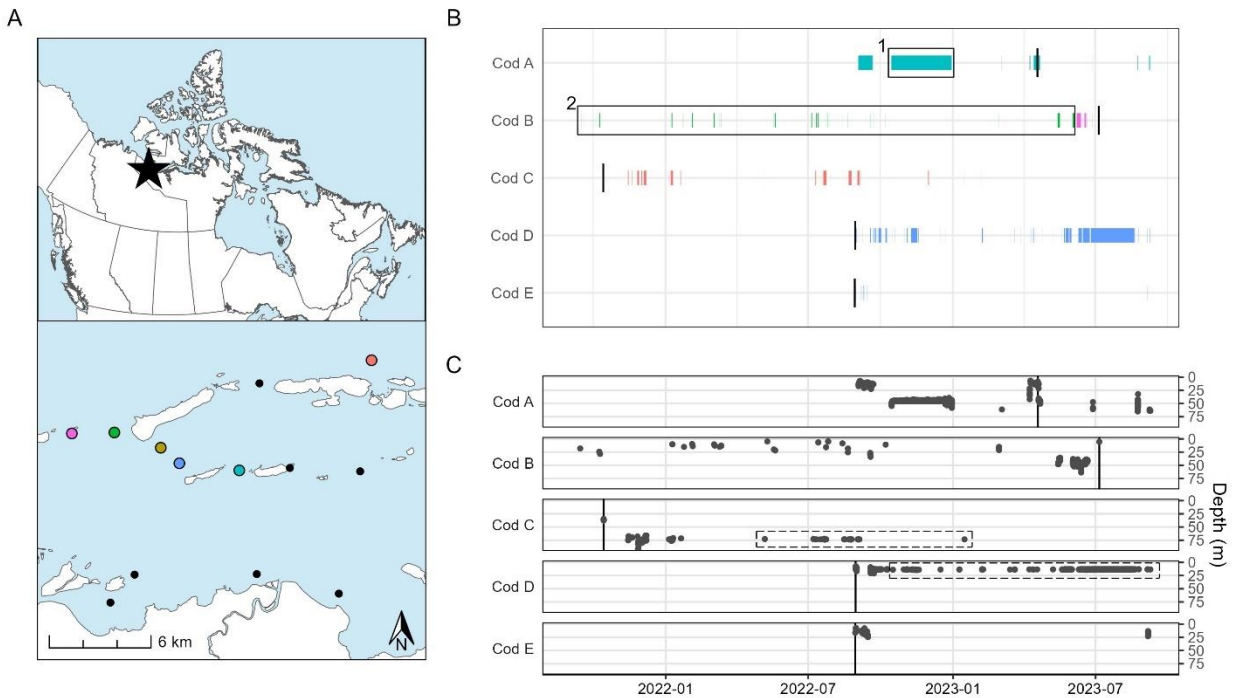


Figure 2.4: Map of the study area (A), residence events (B), and depths from tag sensors (C) for select individuals from the Greenland Cod case study. Points in A indicate receiver stations; black points are stations with no detections from selected Greenland Cod and coloured points are stations with detections. Colours of stations in A correspond to those of residence events in B. Solid boxes in B indicate the thresholds for a single residence event (1) and cumulative residence event (2). Black vertical lines in B and C indicate the most recent station change for each fish. Dashed boxes in C indicate stable depth measurements that were likely indicative of mortalities or expelled tags.

2.4.3 Atlantic Salmon (*Salmo salar*)

Atlantic Salmon is a primarily anadromous species found in temperate waters of the North Atlantic; individuals migrate from natal rivers to the ocean, where they feed for 1–5 years (Klemetsen et al. 2003; Webb et al. 2007). In the Irish Sea, movements are strongly influenced by tidal and current dynamics;

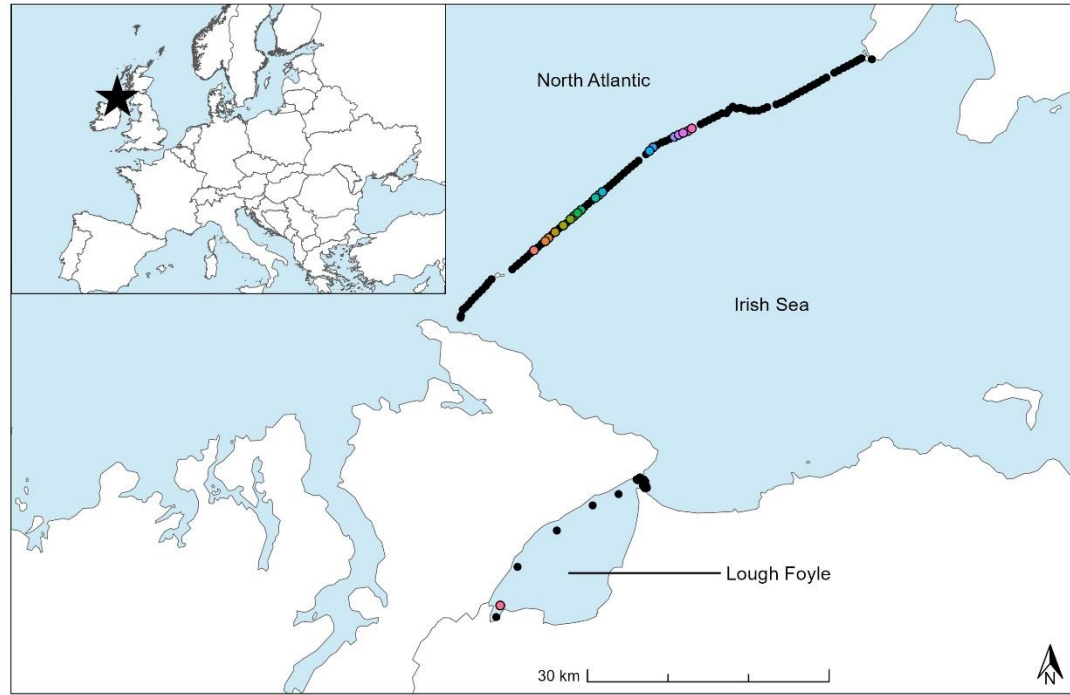
post-smolts typically migrate northward, aided by tidal flows, and exit to the North Atlantic in a west-northwest direction with the outgoing tide (Lilly et al. 2024). Early marine survival is often threatened by high predation rates throughout the range of Atlantic Salmon, including from avian predators and marine mammals that take advantage of predictable migration routes used by smolts (e.g., Dieperink et al. 2002; Flávio et al. 2020; English et al. 2024). We applied `mort` to an unpublished dataset from the European Union's INTERREG VA Programme Sea Monitor project, which tracked Atlantic Salmon smolts from coastal rivers in Northern Ireland. This study specifically examined the migration of smolts through the estuarine environment of Lough Foyle and their subsequent exit into the Irish Sea, marking the beginning of their marine journey – before they encounter the North Atlantic currents (Figure 2.5A).

Residence events were generated with a cutoff of 24 hours. Because simultaneous or near-simultaneous detections were recorded at some pairs of neighbouring stations, a drift table was generated to allow for drift between two stations within 600 m of each other. The function `infrequent()` was not used, because residence events were expected to be short and infrequent for a mobile species such as Atlantic Salmon and the gated array was designed to capture movement between two areas (rather than habitat use). The function `morts()` was applied using both single and cumulative residence events and drift (`method="morts"`). The threshold for single residence events (determined automatically by the function `morts()` from the dataset) was extremely low (1.3 days; Salmon A, Figure 2.5B). Two Atlantic Salmon were identified as potential mortalities or expelled tags due to exceeding the threshold for single residence events (e.g., Salmon C, Figure 2.5B). Both individuals also exceeded the threshold for cumulative residence events (41 days; Salmon B, Figure 2.5). One additional individual exceeded the threshold for cumulative residence events and was identified as a potential mortality (Salmon D, Figure 2.5).

The package `mort` was successful in identifying potential mortalities or expelled tags of a mobile species of fish in the marine environment. It should be noted that tagged fish may be consumed by predators or scavengers, and movement observed within an array may represent movements of the consumers. The package `mort` is intended to be used as a step in data validation and processing before conducting further analyses, and the functions currently available are not designed to identify changes in movement patterns that may indicate a tagged fish has been consumed. Instead, the functions would identify tags that were stationary after being discarded or excreted by consumers within an array, which could be further investigated by the user to examine evidence of predation. For quantifying the effects of

predation in arrays with non-overlapping receivers, we recommend the use of predation tags (e.g., Halfyard et al. 2017; Weinz et al. 2020; Waters et al. 2024).

A



B

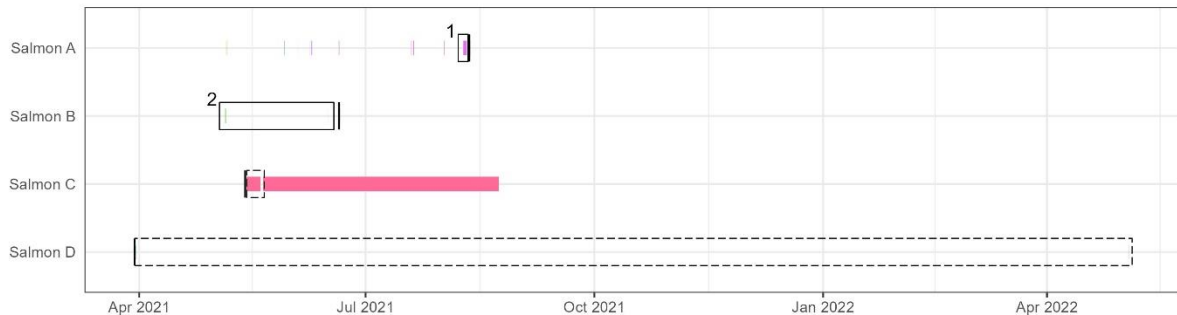


Figure 2.5: Map of study area (A) and residence events (B) for select individuals from the Atlantic Salmon case study. Points in A indicate receiver stations; black points are stations with no detections from selected Atlantic Salmon and coloured points are stations with detections. Colours of stations in A correspond to those of residence events in B. Black vertical lines in B indicate the most recent station change for each fish. Solid boxes indicate the thresholds for a single residence event (1) and cumulative residence event (2). Dashed boxes indicate single (Salmon C) or cumulative (Salmon D) residence events that caused these individuals to be flagged as potential mortalities or expelled tags.

2.5 Conclusions

The method that we have developed and presented here considers the possibility that an animal is dead or a tag is shed, unless there is evidence otherwise. In the case of the primary function `morts()`, evidence is derived from the dataset itself regarding observed patterns of residence in the study species and area and with the assumption that observed movements are from living animals. Thresholds can be refined over time as a dataset grows and greater variability in detection patterns is observed, and drift can be accounted for. For new or small datasets (e.g., less than one year or season), thresholds may not be as reliable. In these cases, it may be helpful to include data from similar tagging programs (i.e., similar array design, species, and study area) to refine threshold estimates until sufficient data are obtained from the study in question.

The method is designed to be conservative, and will therefore likely overestimate the number of mortalities and shed tags. For this reason, the intended purpose of `mort` is not to provide estimates of mortality or survival for stock assessments or studies on tagging effects. Rather, the intent is to create a standardized processing step in user workflows that reduces potential bias that may arise from including data from potential mortalities or shed tags, before conducting further analyses.

This R package contributes to furthering the goal of greater reproducibility in ecology. As not all the methods and options available in `mort` will be relevant for all species and systems, it is important to specify which methods, options, and arguments are used in the Methods section of any publication (see example documentation in Figure 2.1). As mentioned, it is the responsibility of the user to review all flagged potential mortalities or expelled tags and filter the dataset, as applicable. If, after review, any flagged mortalities are considered invalid and data are retained for analysis, the rationale for inclusion should be clearly stated in the Methods. Following these guidelines will help ensure results are reproducible.

The flexibility of `mort` makes it a useful tool for telemetry practitioners. Although developed for aquatic acoustic telemetry, methods are applicable for any passive telemetry system (i.e., stationary receivers) such as automated radio tracking systems (ARTS), like Motus (Taylor et al. 2017). Select methods may even be applicable for some active tracking studies, although further assessment is required. The data-derived or user-defined thresholds, numerous customizable options, and acceptance of manual outputs or outputs from other packages facilitate the application of `mort` to a range of taxa and array

designs. In this way, `mort` can be applied as a quality control step during data processing that is easily incorporated into existing workflows.

Chapter 3

Migration timing and marine space use of an anadromous Arctic fish (Arctic Char, *Salvelinus alpinus*) revealed by local spatial statistics and network analysis

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3.1 Abstract

1. Background: The ice-free season (typically late-June to early-October) is crucial for anadromous species of fish in the Arctic, including Arctic Char (*Salvelinus alpinus*), which must acquire adequate resources for growth, reproduction, and survival during a brief period of feeding in the marine environment. Arctic Char is an important food fish for Inuit communities across the Arctic. Understanding drivers and patterns of migration in the marine environment is thus essential for conservation and management of the species.
2. Methods: We used passive acoustic telemetry to characterize migration patterns of 51 individual anadromous Arctic Char during the ice-free season in the marine environment of Coronation Gulf (Nunavut, Canada; 2019-2022). Based on recent genetic evidence, some tagged individuals were likely Dolly Varden (*Salvelinus malma malma*), a closely related species to Arctic Char. Using local Getis G* (a local indicator of spatial association) and network analysis, we described movement patterns and identified high-use locations in the marine environment. We also related freshwater overwintering location to migration timing and movement pattern.
3. Results: Comparing groups of fish that overwintered in distinct locations, we found: i) limited evidence that marine movements were associated with overwintering location; ii) minor differences in use of marine space; and, iii) timing of freshwater return differed significantly between overwintering groups, and was related to length and difficulty of the migratory pathway in fresh water. Results from both network analysis and local Getis G* revealed that, regardless of overwintering location, coastal locations were highly used by fish.

4. Conclusions: Overwintering locations, and the migratory routes to access overwintering locations, affect the timing of freshwater return. Preference of fish for coastal marine locations is likely due to abundance of forage and patterns in break-up of sea ice. Similarities in marine space use and movement patterns present challenges for managing this and other mixed stock fisheries of anadromous *Salvelinus* spp. Absences or periods of time when fish were not detected prevented comprehensive assessment of movement patterns. Local Getis G* is a helpful tool in identifying locations associated with absences in acoustic telemetry arrays, and is a complementary method to network analysis.

3.2 Background

Migration is an important adaptive behaviour in response to fluctuations in resource availability and/or habitat suitability over space and time. Anadromy (movement from freshwater to the ocean to feed) is a common migration tactic among Arctic species of fish, and is thought to be a response to the low productivity of freshwater systems relative to marine systems (Gross et al. 1988). Arctic Char (*Salvelinus alpinus*) is a facultatively anadromous salmonid with a Holarctic distribution (Scott and Crossman 1973; Johnson 1980; Power and Reist 2018). Anadromous individuals take advantage of rich marine food sources during the brief (often < 3 months) ice-free season and return to fresh water before the ice-covered season due to low salinity tolerance at cold temperatures (Wandsvik and Jobling 1982; Finstad et al. 1989). Anadromous Arctic Char cease or reduce feeding overwinter (Moore and Moore 1974; Boivin and Power 1990; Rikardsen et al. 2003), which results in substantial decreases in body mass and energy stores (Mathisen and Berg 1968; Dutil 1986; Jørgensen et al. 1997). Brief, annual periods of marine foraging during the ice-free season are thus essential for growth and regaining body condition after losses during the ice-covered season, and have major implications for reproduction and survival.

Arctic Char is important for both commercial (e.g., Harris et al. 2016) and subsistence (Priest and Usher 2004) fisheries across the Canadian Arctic; Arctic Char is highly valued by Inuit communities and local harvesting has numerous social, economic, cultural, and nutritional benefits (Van Oostdam et al. 2005). Due to plasticity in life history and migration patterns of Arctic Char, effective stewardship requires location-specific information. Among populations, anadromous individuals exhibit high variability in frequency and timing of marine migrations (e.g., Johnson 1989; Gilbert et al. 2016), as well as distance traveled to reach marine foraging grounds (25–126 km; Morris and Green 2012; Hollins et al. 2022). Extensive stock mixing (multiple populations occurring in sympatry) in the marine environment has been

observed in some regions (Moore et al. 2016; Harris et al. 2022), whereas distinct, stock-specific marine migration routes have been observed in other regions (Hollins et al. 2022).

The Coppermine River supports a critically important subsistence fishery for Arctic Char for the community of Kugluktuk, Nunavut (67° 48' N, 115° 05' W). Whereas anadromous Arctic Char typically overwinter in lakes across their range, they are known by Inuit fishers and more recently by scientists (Smith et al. 2022) to overwinter in the fluvial environment of the Coppermine River. High inter-individual and inter-annual (within individual) variability in overwintering location has been observed within the Coppermine River system, but Arctic Char that overwinter in different locations within the Coppermine River enter the marine environment of Coronation Gulf at a similar time (Smith et al. 2022). The Coppermine River system thus provides a unique opportunity to study and compare the movement patterns of Arctic Char that: i) exhibit plasticity in freshwater migratory pathway and overwintering destination; but, ii) enter the marine environment from the same freshwater system at a similar time.

Acoustic telemetry is a proven tool for tracking of aquatic animals, and a growing number of studies employ acoustic telemetry in both freshwater and marine environments (Donaldson et al. 2014; Hussey et al. 2015; Matley et al. 2022). Historically, research on Arctic Char has focused on the freshwater or estuarine component of migration (e.g., Grainger 1953; Dempson and Green 1985; Guðjónsson 1987; Berg and Berg 1989; Gulseth and Nilssen 2000), because individuals are easier to capture when moving through restricted migration corridors. Studies in marine environments have relied on extensive netting campaigns (e.g., Moore 1975) or tag returns from commercial fisheries (e.g., Dempson and Kristofferson 1987). Acoustic telemetry has allowed researchers to gain insights into the movement and ecology of Arctic Char in the marine environment (e.g., Spares et al. 2012; Moore et al. 2016; Harris et al. 2020; Mulder et al. 2020; Hammer et al. 2022; Hollins et al. 2022), but there remain fundamental gaps in our knowledge of space use and movement patterns in remote and understudied Arctic marine environments. Network analysis is a useful tool for assessing space use and animal movements. When applied to acoustic telemetry data from passive receiver arrays, this approach allows consideration of the interconnectivity of receiver locations (Jacoby et al. 2012; Jacoby and Freeman 2016). Local indicators of spatial association, such as local Getis $G_i^*(d)$ statistics (hereafter, G^* ; Ord and Getis 1995) have been applied to acoustic telemetry data (e.g., Biggs and Nemeth 2016; Smoothey et al. 2019; Rothermel et al. 2020), but their use remains uncommon. Here, we used network analysis and local Getis G^* to address four main objectives that were aimed at informing management of the subsistence

Arctic Char fishery in Kugluktuk, NU, and guiding future research priorities: 1) Describe movement patterns of anadromous Arctic Char in the marine environment; 2) Determine if movement patterns in the marine environment correspond with known variability in overwintering location (Smith et al. 2022); 3) Identify high-use locations for anadromous Arctic Char in the marine environment and qualitatively compare marine space use between overwintering groups; and, 4) Identify locations within the array that were associated with absences or lack of detections.

This study was originally conceived based on the conventional knowledge that all anadromous *Salvelinus* fish east of the Mackenzie River are Arctic Char. Some limited older (Reist and Sawatzky 2010) and very recent (Weinstein 2023) genetic evidence indicates, however, that some of the char that use the Coppermine River are Dolly Varden (*Salvelinus malma malma*). Some individuals tagged in this study may therefore be Dolly Varden rather than Arctic Char. Dolly Varden are closely related to Arctic Char and, together with Bull Trout (*Salvelinus confluentus*), have been considered a “species complex” (see Taylor 2016). Like Arctic Char, Dolly Varden are facultatively anadromous, iteroparous, and intermittent spawners (Armstrong and Morrow 1980; Reist 2018; Gallagher et al. 2018b). Dolly Varden have been documented occurring in sympatry with Arctic Char elsewhere (e.g., Dennert et al. 2016), but visual distinction of the two species is complicated by the fact that phenotypes of both species are highly variable (e.g., Klemetsen 2010; Markevich et al. 2018). We refer to tagged individuals as Arctic Char in the Methods and Results, but consider the findings in relation to presence of both species and uncertainty in species composition in the Discussion.

3.3 Methods

3.3.1 Study location

This study was conducted in the marine environment of Coronation Gulf, located in the western Kitikmeot region of Nunavut, Canada (Figure 3.1). Numerous islands are present in the area, resulting in complex bathymetry. Few bathymetric measurements are available for Coronation Gulf (Canadian Hydrographic Service 2022a); the maximum depth that was opportunistically recorded during this study was 90 m. Coronation Gulf has relatively low salinity, reaching a maximum of ~ 29 PSU (Bouchard et al. 2018). Over a thirty-year period (1991–2020), the typical timing of break-up of sea ice in Coronation Gulf was 16 July and the typical date of freeze-up of sea ice was 29 October (Canadian Ice Service 2021), resulting in a typical ice-free season of fifteen weeks. Local observations indicate that the timing of both

break-up and freeze-up is increasingly variable and, in general, break-up is occurring earlier and freeze-up is occurring later (A. Dumond and E. Hitkolok, pers. obs.).

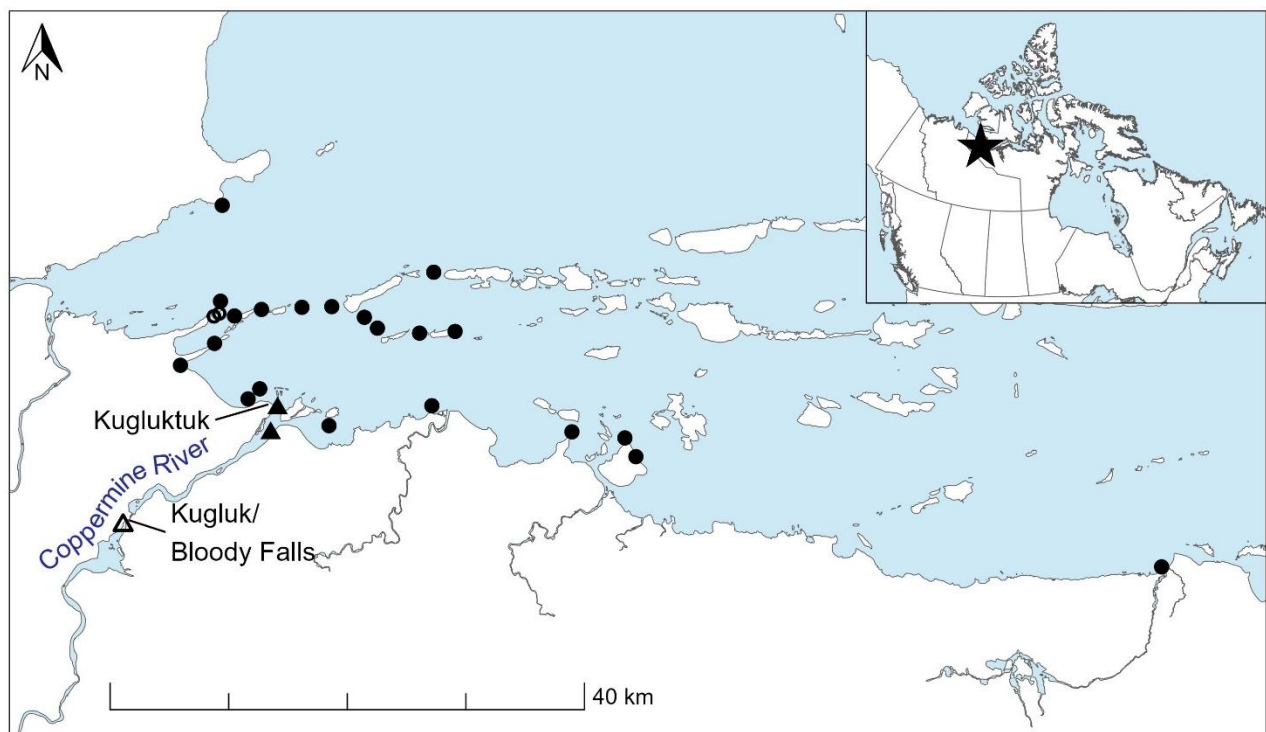


Figure 3.1: Map of the study area and locations of acoustic telemetry receivers that were consistently deployed during the ice-free seasons in all study years (2019–2022). Filled circles indicate marine receivers that were used for both network and local spatial (Getis G*) analyses. Open circles indicate marine receivers that had overlapping detection radii and were used individually to calculate G* and combined to generate networks. Filled triangles indicate receivers located at the mouth of the Coppermine River, which were used to identify timing of return to fresh water. Open triangle indicates a receiver located above Kugluk/Bloody Falls, which was used to identify individuals that overwintered above the falls.

The Coppermine River flows into Coronation Gulf directly to the east of the Hamlet of Kugluktuk, Nunavut (Figure 3.1). The Coppermine River provides a year-round source of fresh water to Coronation Gulf; mean discharge during the ice-free season is 473 m³/s and mean discharge during the ice-covered season is 118 m³/s (Coulombe-Pontbriand et al. 1998). Break-up and freeze-up dates for river ice are earlier than those for sea ice. The dates of river break- and freeze-up during the study period from 2019 to 2022 were determined from time-lapse cameras (Kugluktuk Ikaarvik youth group, unpublished data) and personal observations by the authors. Break-up of river ice ranged from 15–21 June, and freeze-up

ranged from 01–30 October. Kugluk/Bloody Falls (hereafter, “the falls”), which poses a challenging but passable obstacle for migrating Arctic Char, is located approximately 17 km upstream of the mouth of the Coppermine River (Figure 3.1; Figure 1.2).

3.3.2 Acoustic tagging and receivers

Detailed methods for capture and tagging of Arctic Char are available in Smith et al. (2022). Briefly, Vemco V16T acoustic tags (InnovaSea, Halifax, NS) were surgically implanted into 198 adult Arctic Char that were captured in Coronation Gulf or the Coppermine River in 2018 (n = 48), 2019 (n = 117), and 2021 (n = 33). All fish selected for tagging had no evidence of injuries, disease, cysts, or deformities, and had reasonable body condition, based on local knowledge of typical body condition for the time of year that tagging occurred. Tags transmitted fish ID at random intervals, with a mean interval of 90 seconds. All fish captures and tagging were conducted under Animal Utilization Project Protocols 18-07, 30071, and 44099, which were approved by the University of Waterloo Animal Care Committee. All fieldwork was conducted under Nunavut Impact Review Board screening (File no. 18YN023), Kitikmeot Inuit Association Certificate of Exemption to access Inuit Owned Lands (Certificate no. KTX118N005), and Fisheries and Oceans Canada Licenses to Fish for Scientific Purposes (S-18/19-1025-NU, S-19/20-1023-NU, S-21/22-1034-NU, and S-22/23-1008-NU).

An array of acoustic telemetry receivers was deployed year-round in the Coppermine River and Coronation Gulf. Receivers were deployed along migration corridors identified by local Inuit fishers and along coastal features where it was suspected that fish would pass while traveling through the study area. Complete datasets are available from twenty-three receivers in the marine environment, two receivers at the river mouth, and one receiver above the falls during four ice-free seasons from 2019 to 2022 (Figure 3.1). Receivers were deployed ~ 1–1.5 m above the river or ocean bottom and at locations where water depths ranged from 2.8–60 m.

3.3.3 Detection data

Detection data were downloaded from receivers at least once per year and uploaded into VUE 2.8.1 (InnovaSea, Halifax, NS). The VRL File Editor in VUE was used to adjust recorded times to account for drift of receiver clocks. All further data manipulation and analyses were conducted in R version 4.2.2 (R Core Team 2024), including manual correction of clock times that could not be corrected in VUE. False detections (invalid tag IDs resulting from incomplete transmissions or interference among transmitter signals) were removed from the dataset. To account for potential invalid detections with valid tag IDs

that may result from signal collisions, single detections and rapid transitions between receivers were manually reviewed for feasibility. Detection data were condensed into residence events, which were defined as a period of time that an individual fish was detected by a single receiver with no gaps in detection greater than 24 hours. Fish were observed moving only to neighbouring receivers (< 6000 m) in 97% of instances when fish moved away from and then returned to the same receiver within a 24-hour period. We thus considered a threshold of 24 hours acceptable to define residence events. Detections from potential mortalities or expelled tags were removed following Smith et al. (2022) before subsequent analyses.

3.3.4 Overwintering location

Fish were assigned to one of two overwintering locations: 1) above the falls, if they were detected at the receiver located above the falls (Figure 3.1) and were not detected by other receivers until the following spring; or, 2) below the falls, if they were detected during the ice-covered season at one or more receivers deployed in the Coppermine River below the falls. All data analyses were restricted to fish with a complete record of marine migration in a given year (i.e., fish were tagged in a previous year and were not flagged as potential mortalities or expelled tags in the year in question), more than one marine residence event, an identified date of freshwater return (see below), and an identified overwintering location (above or below the falls).

3.3.5 Movement patterns in the marine environment

3.3.5.1 Return to freshwater

The date that each fish entered fresh water following marine migration was identified as the first detection at a receiver at the mouth of the Coppermine River (Figure 3.1), provided all subsequent detections in that year were at river receivers. If multiple consecutive residence events (i.e., detection periods separated by more than 24 hours) were observed at the river mouth, potentially representing fish approaching but not entering the river, the residence event with the latest date was used as the date of freshwater return.

3.3.5.2 Individual network metrics

Network analysis was used to characterize the movement patterns of individual fish through the study area. Individual networks were constructed for each fish and year. Receiver locations were represented by network nodes and movements of individuals among receivers were represented by network edges.

Networks were undirected (did not consider direction of travel). Two marine receivers were located 530 m apart and often had overlapping detection ranges (i.e., an individual tag transmission was recorded by both receivers). To prevent overlapping detections from generating an inordinate number of movements for network analysis, the detections from these two receivers were combined to form a single node. Twenty-three nodes were included in network analyses, including twenty-one nodes representing individual marine receivers deployed in all study years (2019–2022), one node representing the two combined marine receivers, and one node representing two combined receivers at the mouth of the Coppermine River (Figure 3.1). The river node was included to capture movements of fish that briefly entered the river before returning to the marine environment within a single ice-free season.

For each individual fish in a given year, four global or whole-network metrics were calculated to characterize movement patterns and describe network structure: node density, edge density, network diameter, and clustering coefficient. These network metrics were selected for their relevance to Arctic Char movement patterns and each described a different aspect of movement in the marine environment (Table 3.1). Node density was calculated as the proportion of nodes used, and represented the proportion of the network used by an individual (Lea et al. 2016). Edge density, the proportion of edges used, represented the mobility of an individual (Lea et al. 2016), and was calculated using the `edge_density` function in R package `igraph` version 1.2.7 (Csárdi and Nepusz 2006). Although edge density is likely to be lower for fish that occupy areas of the network where receivers are located farther apart, edge density was included because 1) all fish enter and exit the marine environment from the same location at the mouth of the Coppermine River and therefore have equal opportunity to move throughout the network; and, 2) considering edge density in conjunction with other metrics such as Furthest distance (Table 3.1; see below) can reveal differences in movement patterns. Network diameter was determined by calculating the shortest paths (along observed edges) between all pairs of observed nodes, and identifying the longest of these shortest paths (Dale 2017). Network diameter thus provided a distance measure of the spatial extent of the network used by an individual. Network diameter was calculated using the `diameter` function in `igraph`. For the calculation, distances between pairs of nodes were used as edge weights. As the coastline of the study area is highly variable with numerous islands, distances measured along observed edges sometimes crossed land or the detection radii of receivers that had not detected the fish in question. To adjust distance measurements to avoid land and other receivers, shapefiles of waterbodies from the CanVec hydrographic series (Natural Resources Canada 2015) were imported into R and a buffer of 500 m (the approximate

detection radii of receivers) was calculated around each receiver location using the `st_buffer` function in R package `sf` version 1.0-14 (Pebesma 2018). For each pair of receivers, a raster with approximately 10 m x 10 m cells was generated with conductance values of NA (Not Applicable; movement not possible) for raster cells on land or within the buffer of other receivers (i.e., receivers other than the pair in question), and conductance values of 1 for raster cells in water and outside the range of other receivers. Minimum within-water distances were then calculated using the R package `gdistance` version 1.6 (van Etten 2017) with 16-cell neighbourhoods. Finally, the clustering coefficient was calculated as the probability that two neighbours of a given node were themselves connected by an edge (Dale 2017). Fish that have a tendency to circulate within a region or regions, rather than make directed movements through the study area, would have high clustering coefficients. The clustering coefficient of each individual network was calculated using the `transitivity` function in `igraph`. A summary of metrics is provided in Table 3.1.

3.3.5.3 Distance traveled

Minimum total distance traveled (Total distance; Table 3.1) was calculated as the sum of the distance from the mouth of the Coppermine River to the first marine receiver where an individual was detected, the distances between receivers for all observed marine movements, and the distance from the last marine receiver where an individual was detected back to the mouth of the Coppermine River. Distance of furthest observation (Furthest distance; Table 3.1) was identified as the furthest distance from the Coppermine River to a receiver where an individual was detected. All distances were calculated in water (i.e., paths did not cross land features), as outlined above.

3.3.5.4 Days undetected

Estimates for network and distance metrics may be biased due to the configuration and coverage of the network. For example, for individuals that occupy areas outside of the detection radii of network receivers, estimates of node density, edge density, and minimum total distance will likely be lower. To investigate whether observed movement patterns were associated with absences or lack of detections within the array, we calculated the proportion of days that each individual was not detected during the ice-free season (beginning with river break and ending with freshwater return). Day was selected as the unit of time, as 24 hours was used as the gap threshold for differentiating separate residence events (see above).

Table 3.1: Summary of metrics used to describe individual movement patterns and identify high-use locations in the marine environment. Global metrics reflect movement patterns of individual fish in a given year. Local metrics describe space use at a given location (node, for network analysis; receiver, for G*). Italicized metric names indicate metrics that were calculated using network analysis.

	Description	Indicates
Global metrics (individual fish)		
<i>Node density</i>	Proportion of nodes used out of all possible nodes	Proportion of the network used by an individual
<i>Edge density</i>	Proportion of edges used out of all possible edges	Mobility of an individual
<i>Network diameter</i>	Longest of shortest paths along observed edges between all pairs of observed nodes	Spatial extent of the network used by an individual
<i>Clustering coefficient</i>	Probability that two neighbours of a given node are themselves connected by an edge	Circulation within a region (high clustering coefficient) or directed movements (low clustering coefficient)
Total distance	Minimum total distance, from Coppermine River, along observed edges, back to Coppermine River	Minimum observed mobility of an individual
Furthest distance	Furthest distance from the Coppermine River to a receiver where an individual was detected	Minimum furthest distance traveled by an individual
Days undetected	Proportion of days during the ice-free season (until freshwater return) that an individual was not detected	Absence from array or movement outside detection range of receivers
Freshwater return	Decimal day of year when an individual returned to fresh water (the Coppermine River) to overwinter	Time that marine foraging ceased
Local metrics (receiver locations)		
<i>Node strength</i>	Number of movements to and from a given node, including self-edges	Locations with high activity (number of movements)
<i>Restricted betweenness</i>	Number of movements that pass through a given node	Movement corridors
Local Getis G*	Duration of residence events within 6000 m ¹ of a given receiver, relative to time spent at all locations	Regions with high activity (duration of residence events)

¹ A distance of 6000 m was selected to ensure all receivers had at least one neighbour, with the exception of four receivers that had no similar neighbours

3.3.5.5 Cluster analysis

To determine if distinct movement patterns in the marine environment could be identified, cluster analysis was performed on the global metrics calculated for each fish (four network metrics (node density, edge density, diameter, clustering coefficient), total distance, furthest distance, days undetected, and freshwater return; Table 3.1). Clustering was conducted and validated using the `clValid` function in the R package `clValid` version 0.7 (Brock et al. 2008) with four clustering methods (hierarchical complete linkage agglomerative, hierarchical divisive, *K*-means, *K*-centroid), 2–6 clusters, and both internal and stability validation measures. Silhouette analysis, the gap statistic, and the elbow method were implemented using the `fviz_nbclust` function in the R package `factoextra` version 1.0.7 (Kassambara and Mundt 2020) to identify the optimal number of clusters. Clustering was based on Euclidean distances among scaled and centred variables. Clustering methods were ranked using the `RankAggreg` function in the R package `RankAggreg` version 0.6.6 (Pihur et al. 2020). Assigned clusters were compared for individual fish among years to determine if fish consistently

displayed the same pattern. To visualize results of the cluster analysis, principal components analysis (PCA) was conducted using all variables that were used to identify clusters (eight global metrics; Table 3.1).

3.3.5.6 Movement patterns and overwintering location

To investigate whether there were differences in movement patterns between overwintering locations (above or below falls) and among years, two-way fully-crossed ANOVAs were used to compare global network metrics, minimum distances traveled, and freshwater return (Table 3.1) among overwintering locations and years (2019–2021). The year 2022 was excluded from this analysis, as no fish were detected overwintering below the falls in 2022. When a fish met the criteria for inclusion in more than one year, only one year was included in ANOVAs to avoid dependence issues due to repeated measures. Years when the overwintering location was below the falls were preferentially included, as well as records from 2021, to improve balance in sample sizes among groups. The final sample size for ANOVAs was forty-nine individuals. Levene's tests were used to assess homogeneity of variance and Shapiro-Wilk tests were used to assess normality of residuals from the models. Edge density, diameter, furthest distance, and clustering coefficient were log-transformed to better meet the assumption of normality. Significant differences ($p \leq 0.05$) among groups were investigated using post hoc Tukey HSD tests.

While ANOVAs allowed us to directly compare metrics among overwintering locations and years, linear mixed models allowed the full dataset to be modeled, including all years and repeated measures. For this reason, mixed models were used to relate global network metrics, minimum distances traveled, and overwintering location (categorical) to date of freshwater return (Table 3.1). All explanatory variables were scaled and centred. Multi-collinearity among variables was assessed using the function `vif` in the R package `car` version 3.1-2 (Fox and Weisberg 2019). After removing edge density and minimum total distance travelled, all variance inflation factors were < 3 (maximum 2.9; Zuur et al. 2010). Because the study spanned multiple years and marine conditions were expected to vary among years, year was included as a categorical random factor. Fish ID was also included as a random factor in this analysis, because eighteen fish were detected in multiple study years. Following Zuur et al. (2009), the global model (all fixed factors) was fit twice, using restricted maximum likelihood estimation, to identify the appropriate random structure with: i) both random factors; and, ii) fish ID only. Likelihood ratio tests were used to compare models, with the p value adjusted to account for testing on the boundary (Zuur et al. 2009). The model with both fish ID and year as random factors was significantly better than the

model with fish ID as a random factor ($p < 0.001$). Therefore, both random factors were retained. All possible models, including a null model (random factors only), were fit using maximum likelihood estimation and compared using AICc. Generalized linear models were implemented in the R package `lme4` version 1.1-32 (Bates et al. 2015). AICc, conditional R^2 , and marginal R^2 were computed in the R package `MuMIn` version 1.47.5 (Barton 2019).

3.3.6 High-use locations and space use in the marine environment

Local (location-based) metrics were used to identify high-use locations for Arctic Char in the marine environment, and to compare use of space between overwintering groups. Two local network metrics were calculated for individual fish: node strength and restricted betweenness (Table 3.1). Local network metrics for individual fish were first standardized for inter-individual and inter-annual differences in freshwater return by dividing by the number of ice-free days before each individual returned to fresh water. Mean metrics were then calculated for each overwintering location (above or below the falls)

Node strength was calculated as the number of movements both to and from a given node. Node strength included self-edges (consecutive residence events at the same receiver, separated by an interval greater than 24 hours). Self-edges indicate repeated use of an area (Fletcher and Fortin 2018) and were included to reflect the importance of frequently used locations. Network configuration can bias node strength, as fewer movements are likely to be observed to/from nodes that are farther from neighbouring nodes than to/from nodes that are closer to neighbouring nodes. Self-edges are more likely to occur at nodes that are farther from neighbouring nodes and can be considered as movements to/from an unknown node. Thus, self-edges were included to help mediate bias due to network configuration. Node strength was calculated using the `strength` function in `igraph`.

Betweenness in weighted networks is a measure of the flow (in this case, movement) along the shortest path between each pair of nodes that depends on passing through a given node (Freeman et al. 1991). A modified definition of betweenness, used by Lea et al. (2016), is the number of movements that pass through a given node (i.e., two consecutive edges, where the start and end nodes are different). We used the modified definition of betweenness, hereafter called restricted betweenness, because paths are restricted to two adjacent edges connecting three nodes. Restricted betweenness was calculated by identifying time series of residence events for each fish, where three consecutive residence events were at different receivers (i.e., no self-edges or movements back and forth between two receivers). High values of restricted betweenness indicated nodes that were used as movement corridors.

Both local network metrics (node strength, restricted betweenness) were calculated using observed movements, and did not consider length of time spent at each receiver location. Local Getis G^* was used to identify hotspots (clusters of high activity; positive values of G^*) and coldspots (clusters of low activity; negative values of G^*) in terms of time, rather than movement. As a local measure of spatial association, G^* relates the values within a distance, d , of a location relative to all values within the study area (Getis and Ord 1992). The durations of residence events at each receiver were summed and used to calculate G^* values. To verify that our threshold for identifying residence events (24 hours) did not impact G^* results, we conducted the analysis using a range of thresholds (1–48 hours; results are presented in Appendix A). Single detections were assigned a residence duration of 90 s (the mean transmission interval of the acoustic tags). To account for differences in the length of time receivers were deployed, the duration of residence events for each individual was scaled by the amount of overlap between receiver deployment and ice-free period (before freshwater return) in a given year. To account for differences in time of freshwater return, the duration of residence events for each individual at each receiver was also standardized by time from river break-up until freshwater return. The value chosen for d was 6000 m, which ensured that all receiver locations would have at least one neighbour, with the exception of four locations that had no neighbours that were similar in depth and coastal features. Similar to the distances used in network analyses, distances were calculated in `gdistance` to avoid land, but without the constraint of avoiding detection radii of other receivers. G^* was calculated using the function `localG_perm` in R package `spdep` version 1.2-8 (Bivand and Wong 2018). Weights were binary (1 for receivers within 6000 m of receiver i , 0 for receivers further than 6000 m from receiver i).

The three local metrics (node strength, restricted betweenness, G^* ; Table 3.1) were compared qualitatively between overwintering locations (above or below falls). High-use locations were identified by qualitatively comparing relative ranks of all three local spatial metrics. The receivers at the mouth of the Coppermine River were excluded, as they were not included in G^* calculations. As discussed above, two marine receivers had individual G^* values, but were combined to form one node for network analysis. To allow comparison of ranks among local metrics, the mean G^* value of these two marine receivers was calculated and used as a single location in comparisons. Locations were assigned a rank for each spatial metric, and the three ranks were summed for each location to form a combined rank.

3.3.7 Locations associated with absences

To identify locations associated with absences or lack of detections within the array, we counted the number of ice-free days (before freshwater return) that each fish was not detected either immediately preceding or immediately following detection at each receiver. Similar to the global metric of days undetected (see above), day was selected as the unit of time because 24 hours was used as the gap threshold for differentiating separate residence events. The number of undetected days associated with each receiver was standardized for differences in timing of freshwater return by dividing by the number of ice-free days before each individual returned to fresh water. The mean standardized values for each receiver were used to calculate G^* values using the same method as above. Statistical significance of G^* values (both hotspots and coldspots) was determined using 1000 conditional permutations (holding the value at the central location constant while shuffling remaining values without replacement), using the function `localG_perm` in R package `spdep` version 1.2-8 (Bivand and Wong 2018) and following Ord and Getis (Ord and Getis 1995).

3.3.8 Mapping and data visualization

Data visualization was conducted using the R packages `ggplot2` version 3.4.1 (Wickham 2016) and `ggalluvial` version 0.12.3 (Brunson and Read 2023). Networks were visualized with R package `ggraph` version 2.1.0 (Pedersen 2022). Shapefiles of waterbodies were obtained from the CanVec hydrographic series (Natural Resources Canada 2015). Maps were arranged with R package `patchwork` version 1.1.2 (Pedersen 2024) and annotated using R packages `ggspatial` version 1.1.7 (Dunnington 2022) and `geomtextpath` version 0.1.1 (Cameron and van den Brand 2022).

3.4 Results

Fifty-one fish met all four criteria to be included in analyses (complete record of marine migration, more than one marine residence event, identified date of freshwater return, and identified overwintering location) in at least one year of the study (2019–2022). Eighteen fish met the criteria in more than one year, yielding a sample size of seventy-three unique fish*year records. At the time of tagging, fork lengths of the fifty-one fish ranged from 539 to 857 mm, and weights ranged from 1850 to 5140 g. Tag burden was less than 1.8% of fish body weight. There were 34 343 detections recorded at the twenty-three marine receivers that were deployed consistently over the four years of the study (Figure 3.1).

3.4.1 Movement patterns in the marine environment

3.4.1.1 Return to fresh water

The date of fall return to fresh water was highly variable among individuals and years. Date of freshwater return ranged from 18 July to 15 September (Figure 3.2). Median date of freshwater return was 14 August.

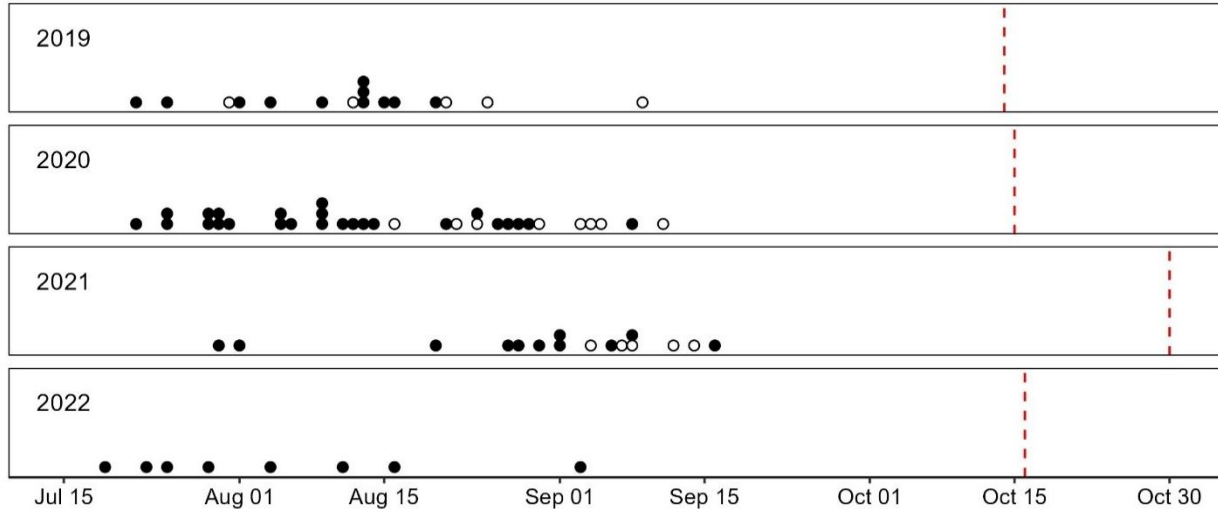


Figure 3.2: Dates of return to fresh water for fish that overwintered above (filled circles) and below (open circles) Kugluk/Bloody Falls. Red dashed lines indicate the dates of freeze-up in the Coppermine River. Break-up dates for river ice were 19 June 2019, 21 June 2020, 18 June 2021, and 15 June 2022.

3.4.1.2 Individual network metrics and minimum distances traveled

Metrics for individual networks were highly variable. Node density of the seventy-three records ranged from 0.04 to 0.70 (median = 0.35), or 1 to 16 (median = 8) of 23 possible nodes. Edge density ranged from 0 to 0.11 (median = 0.03), or 0 to 29 (median = 8) of 253 possible undirected edges, excluding self-edges. Diameter of observed networks ranged from 0 to 179.1 km (median = 55.8 km). Clustering coefficient ranged from 0 to 0.6 and was highly skewed (median = 0). The furthest distance that individuals were detected from the river mouth ranged from 13.6 to 78.8 km (median = 33.0 km). Approximately 40% of all individuals*years ($n = 29$) were detected at least once at the receiver located furthest from the mouth of the Coppermine River (i.e., 78.8 km). The total minimum distance that individuals were detected traveling in a single ice-free period ranged from 28.5 to 394.8 km (median = 162.9 km).

3.4.1.3 Cluster analysis

Silhouette analysis, the gap statistic, and the elbow method consistently indicated the optimal number of clusters was three. Ranking of internal and stability validation measures indicated that *K*-means clustering with three groups was the most appropriate clustering method. The first two axes of a PCA, which included node density, edge density, diameter, cluster coefficient, total distance, furthest distance, days undetected, and freshwater return (Table 3.1), explained 72% of the variation in the data (Figure 3.3). Three movement or detection patterns were identified when PCA results were compared with the *K*-means cluster analysis (with three clusters): intensive, far, and limited.

The intensive group was detected at locations relatively near the Coppermine River. Fish in this group had relatively early freshwater return and traveled intensively through a relatively restricted portion of the study area (high node and edge densities, high clustering coefficient, high minimum total observed distance; example network in Figure 3.4A). The intensive group had a relatively low proportion of days undetected in the array (mean = 0.46, standard deviation (SD) = 0.20). Fish in the far group had the latest dates of freshwater return, were observed traveling relatively long distances, and were detected at the receivers furthest from the Coppermine River (example network in Figure 3.4B). The far group had a relatively high proportion of days undetected in the array (mean = 0.77, SD = 0.10). Fish in the limited group had low observed node and edge densities, and were detected traveling short minimum distances (example network in Figure 3.4C). Individuals in this group had the highest proportion of days where they were undetected in the array (mean = 0.86, SD = 0.09). Proportion of days undetected differed significantly among groups (ANOVA, $F = 19.74$, $p < 0.0001$, $df = 2,46$). Pairwise comparisons using Tukey HSD indicated that proportion of days undetected was significantly higher for the limited and far groups than for the intensive group ($p < 0.0001$), and that proportion of days undetected for the limited group was not significantly different from the far group ($p = 0.26$).

All fish in the intensive movement group overwintered above Kugluk/Bloody Falls (Figure 3.3). There was no evidence that fish in the limited or far movement groups were associated with either overwintering location (above or below the falls); fish from both movement groups were observed overwintering in both locations. For fish that were observed in more than one ice-free season ($n = 18$), movement or detection pattern was not consistent among years (Figure 3.5).

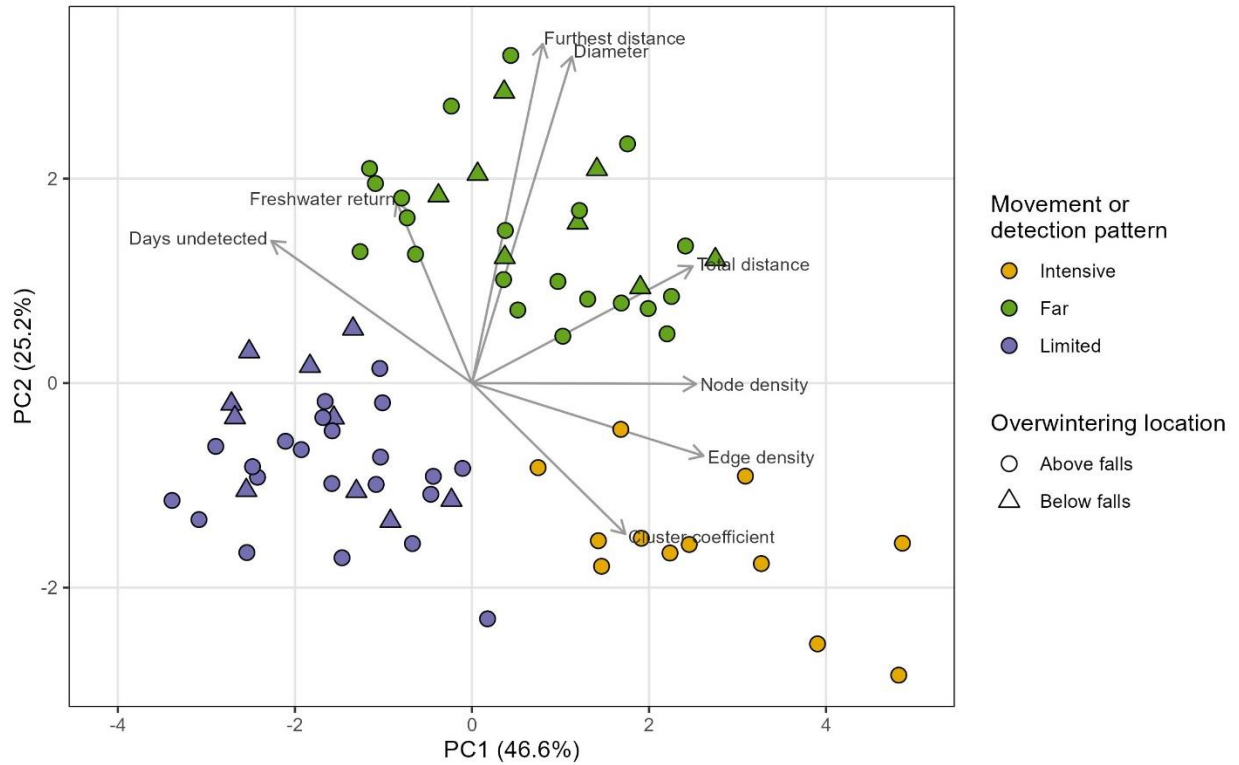


Figure 3.3: Principal components analysis of date of freshwater return (Freshwater return), proportion of days undetected (Days undetected), minimum total detected distance travelled (Total distance), distance of furthest detection (Furthest distance), and network metrics (Node density, Edge density, Diameter, Cluster coefficient; Table 3.1). Only the first two axes are displayed, as they explained a cumulative percentage of 71.8% of the variance and subsequent axes explained 12.3% or less of the variance. Colour indicates the movement or detection pattern observed, as inferred from *K*-means cluster analysis with three groups. Shape indicates overwintering location.

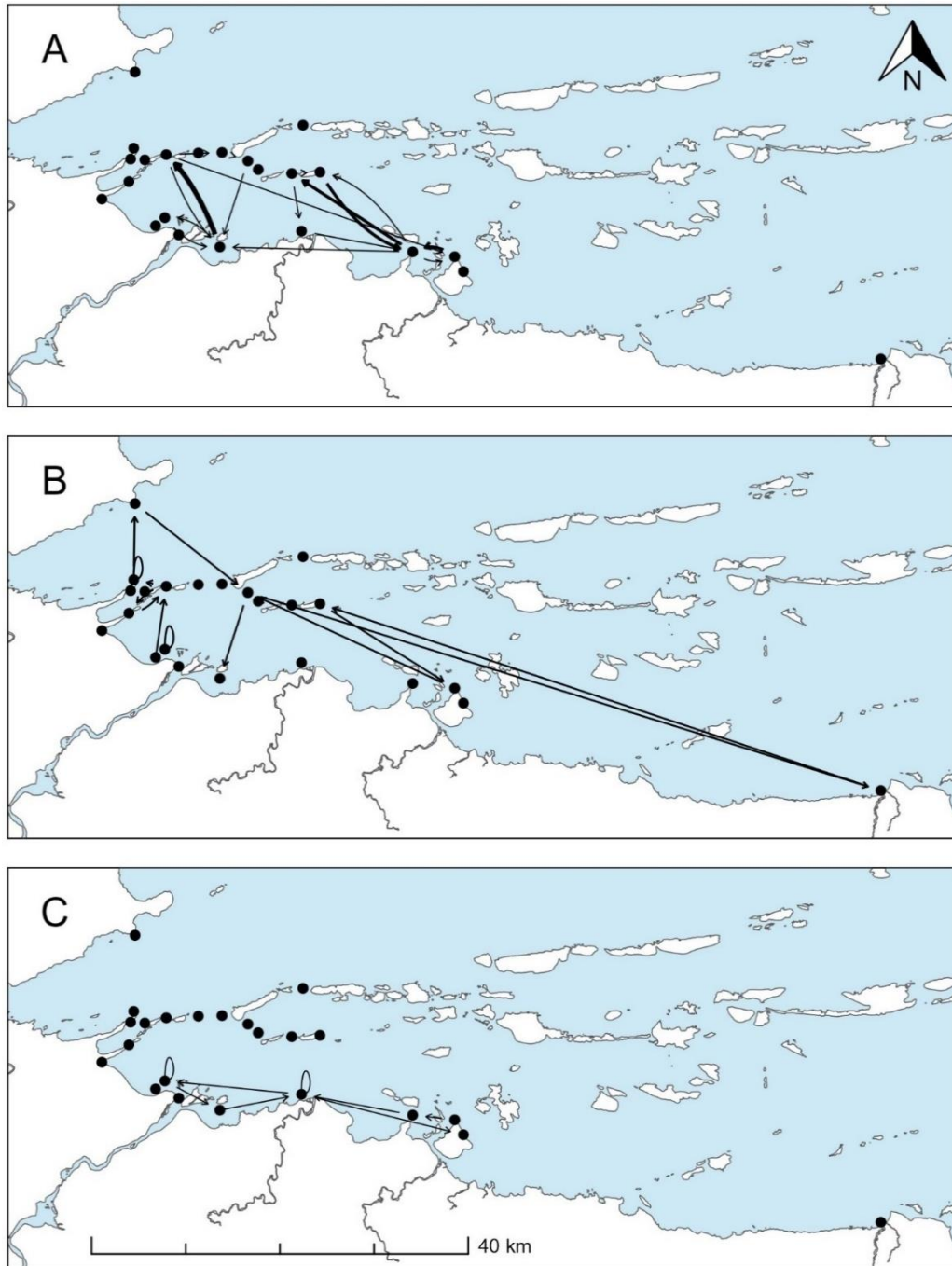


Figure 3.4: Examples of networks generated for the three observed movement or detection patterns, as identified by cluster analyses: A) Intensive; B) Far; and, C) Limited. Network nodes (receivers) are indicated by black points. Edge weights (i.e., number of movements) are indicated by line thickness. Note that network edges are drawn for illustration purposes only; lines do not represent paths and lengths do not represent minimum distances traveled. Self-edges are indicated by loops that leave and return to the same receiver location.

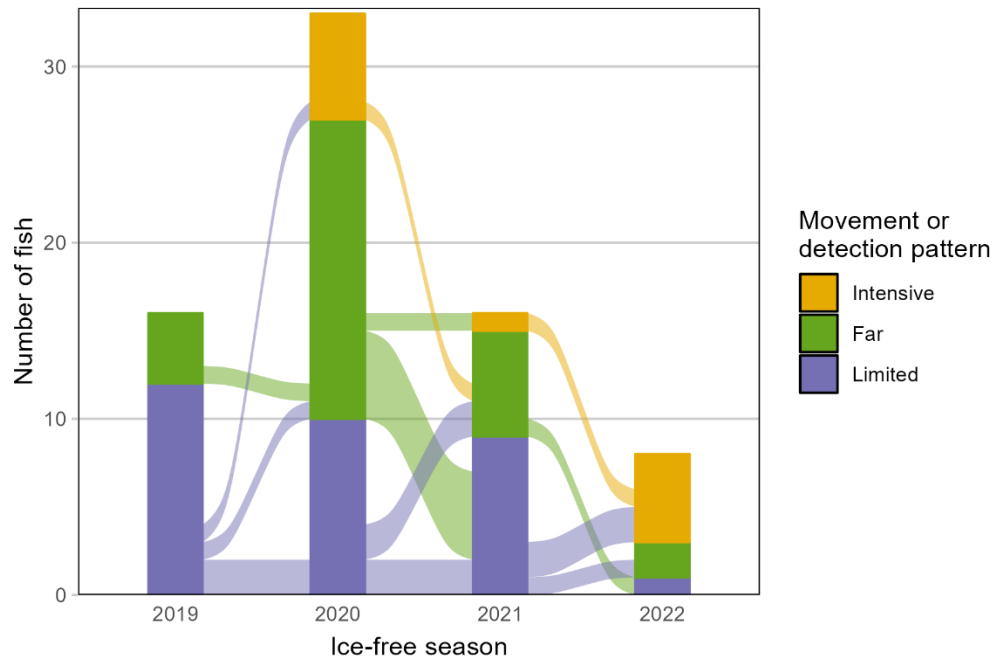


Figure 3.5: Observed movement or detection patterns of tagged fish in the marine environment during each ice-free season of the study. Colour connections between ice-free seasons indicate the pattern observed in the previous ice-free season (e.g., a yellow connection to a green bar represents an individual that exhibited the intensive pattern in one ice-free season and the far pattern in the following ice-free season).

3.4.1.4 Movement patterns and overwintering location

Date of freshwater return differed significantly both between overwintering locations and among years (ANOVA, $F \geq 11.103$, $p \leq 0.00178$, $df = 2, 43$). The interaction between overwintering location and year was not significant ($F = 0.097$, $p = 0.907$). Pairwise comparisons using Tukey HSD indicated that freshwater return in 2021 was significantly later than freshwater return in both 2019 and 2020 ($p < 0.0006$), and that freshwater return in 2019 was not significantly different from freshwater return in 2020 ($p = 0.51$). Fish that overwintered above the falls returned to fresh water significantly earlier than fish that overwintered below the falls ($p = 0.0014$). All other global metrics (Table 3.1) did not differ significantly between overwintering locations or among years (ANOVA, $F \leq 2.246$, $p \geq 0.118$, $df = 2, 43$).

Overwintering location was the best predictor of date of freshwater return and explained 19.3% of the variation when included in a linear mixed model as the sole explanatory variable (with year and fish ID as random factors; Table 3.2). Global network metrics (describing individual movement; Table 3.1) and

furthest detected distance were not good predictors of freshwater return and were ranked below or similar to the null model. When compared to the model with overwintering location alone, models that included both overwintering location and another explanatory variable had similar AICc scores, deviance (-2log-likelihood), and model fit (marginal R^2 , Table 3.2), indicating that other explanatory variables were noninformative (Anderson 2008).

Table 3.2: Subset of linear mixed models that related date of freshwater return to overwintering location, distance of furthest detection (furthest distance), node density, diameter, and clustering coefficient for fifty-one individuals. Eighteen individuals were observed in more than one year, for a total sample size of seventy-three observations. The null model includes only the random factors of year and fish ID. AICc scores were used to rank models, and models are presented in order of increasing AICc (decreasing rank). Marginal R^2 values represent the proportion of variance explained by the fixed factors. Conditional R^2 values represent the proportion of variance explained by both the fixed and random factors.

Model	AICc	Δ AICc	-2log-likelihood	Marginal R^2	Conditional R^2
Overwintering location	591.19	0	580.30	0.193	0.416
Overwintering location + Furthest distance	591.98	0.79	578.71	0.206	0.452
Overwintering location + Node density	592.53	1.33	579.25	0.212	0.492
Overwintering location + Diameter	592.80	1.61	579.53	0.202	0.419
Overwintering location + Clustering coefficient	593.13	1.94	579.86	0.204	0.409
Overwintering location + Node density + Diameter + Clustering coefficient + Furthest distance	597.55	6.35	576.69	0.240	0.570
Furthest distance	608.54	17.34	597.64	0.026	0.357
Null	608.68	17.48	600.09	0	0.309
Node density	609.73	18.53	598.83	0.015	0.339
Diameter	610.21	19.02	599.32	0.008	0.321
Clustering coefficient	610.58	19.39	599.69	0.006	0.263

3.4.2 High-use locations and space use

Local metrics (node strength, restricted betweenness, G^* ; Table 3.1), which were used to indicate movement corridors and high-use locations, were generally similar between groups of fish that differed in overwintering location (above or below the falls). Similar patterns in node strength were qualitatively observed between the two overwintering groups (Figure 3.6A), except that fish that overwintered above the falls made proportionally more movements to and from the receivers immediately to the west of the mouth of the Coppermine River. Restricted betweenness was generally similar between the two overwintering groups, although values at each receiver were consistently lower for fish that

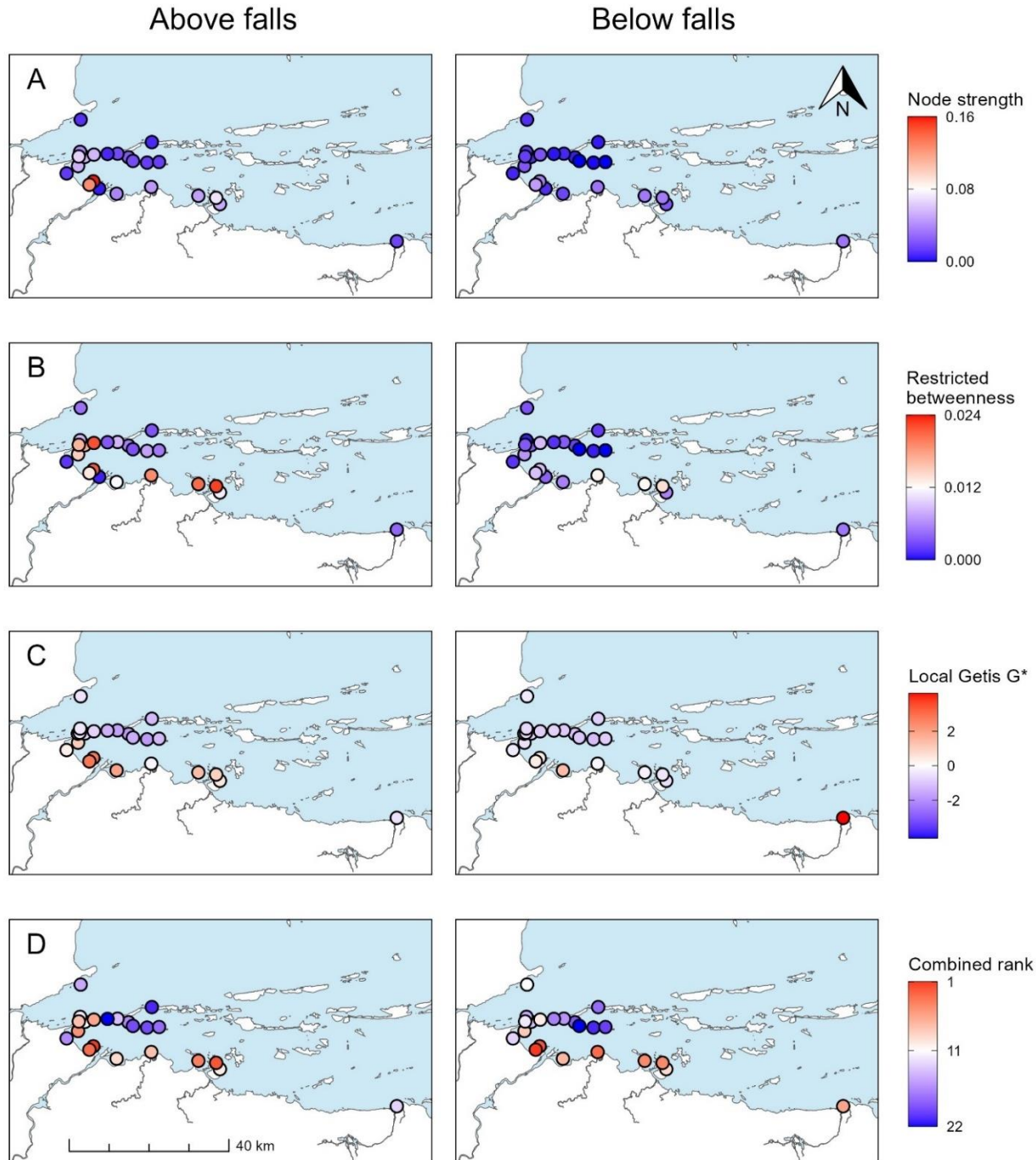


Figure 3.6: Values for local metrics: A) Node strength; B) Restricted betweenness; C) Local Getis G^* ; and, D) Combined rank for each receiver. For each measure, the scale is the same for fish that overwintered above the falls (left panels) and those that overwintered below the falls (right panels). Note that for local Getis G^* , a value of 0 indicates that relative activity at that location was equal to the mean value for the whole study area. Similarly, negative values indicate locations where activity was observed, but relative activity was less than the mean value for the study area.

overwintered below the falls (Figure 3.6B). Higher values of restricted betweenness were typically observed at receivers located along the coastline to the east of the Coppermine River, receivers immediately to the west of the river mouth, and receivers located between the islands to the northwest of the river mouth, which indicated that these locations were important movement corridors. Qualitative assessment of local Getis G^* values indicated that patterns in the relative time spent at locations across the study area were also largely similar between overwintering locations (Figure 3.6C), except for two regions. First, G^* values indicated the receivers immediately to the west of the mouth of the Coppermine River were greater hotspots for fish that overwintered above the falls. Second, G^* values indicated the receiver located furthest east in the study area was a greater hotspot for fish that overwintered below the falls.

When receiver locations were ranked based on all three local spatial metrics, combined ranks were qualitatively similar between overwintering locations (Figure 3.6D). Receivers that were located in deeper water (34–60 m), among offshore islands, typically had low combined ranks. Receivers that were located near the river mouth or along the coast typically had high combined ranks. The receiver with the greatest difference in combined rank between overwintering groups was the receiver located furthest east in the study. This location was ranked thirteenth for fish that overwintered above the falls and sixth for fish that overwintered below the falls.

3.4.3 Locations associated with absences

Qualitative assessment of local Getis G^* values, a measure of local spatial association, indicated that receivers associated with the highest number of undetected days were typically located along the coast (Figure 3.7). Conditional permutations indicated that positive spatial association (i.e., hotspot) was significant at one location, with a G^* value of 1.77 (star in Figure 3.7). The receiver located furthest east had the highest G^* value (2.83; Figure 3.7). This location did not have neighbours within 6000 m and, as conditional permutations keep the value at the central receiver constant and shuffle the remaining values, significance could not be assessed at this location.

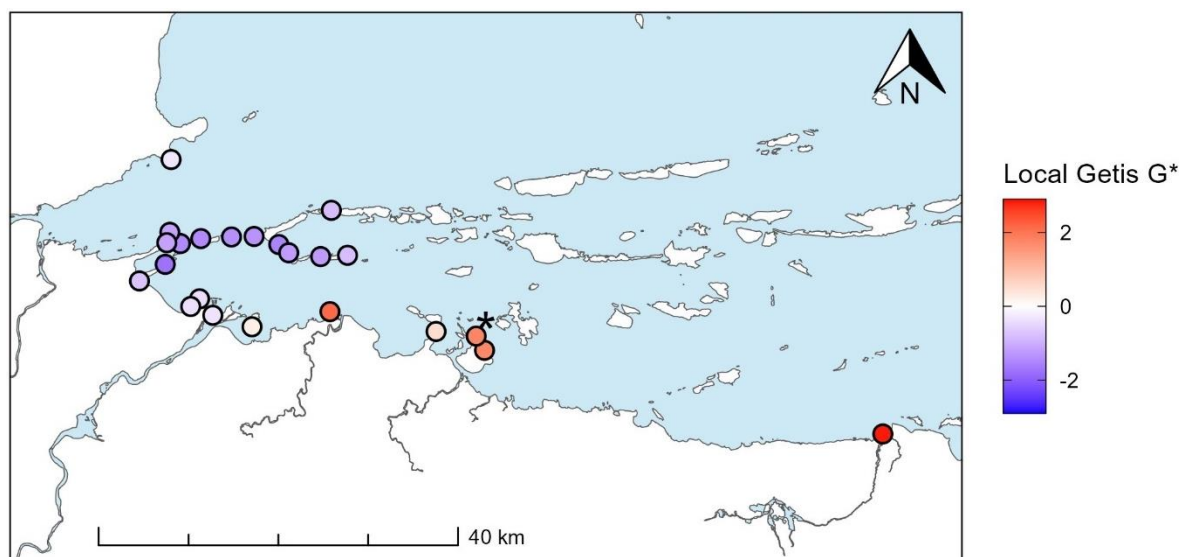


Figure 3.7: Local Getis G^* of the number of undetected days associated with each receiver (i.e., days when a fish was not detected either immediately before arriving at or immediately after leaving a receiver). Star indicates a location with statistically significant spatial association ($p < 0.05$). Note that the receiver located furthest to the east had the highest G^* value but did not have neighbours within 6000 m, so significance of spatial association could not be assessed through conditional permutation.

3.5 Discussion

3.5.1 Movement patterns in the marine environment

Date of freshwater return was the only global (individual) metric that differed significantly among years. Freshwater return was highly variable among fish and years, and was significantly later in 2021 than 2019 or 2020; mean freshwater return was twenty days later in 2021 than in 2019 and seventeen days later in 2021 than in 2020. The dates of river freeze-up were respectively sixteen and fifteen days later in 2021 than in 2019 and 2020. Climate change is causing earlier break-up and later freeze-up of both river and sea ice throughout the Arctic (Prowse et al. 2011; Onarheim et al. 2018). Changing ice conditions have impacted the migration patterns of both terrestrial (e.g., Leblond et al. 2016) and marine (e.g., Hauser et al. 2017) mammals, but similar impacts have not yet been observed in anadromous species of fish. Freeze-up likely does not directly affect timing of freshwater return in fall, because Arctic Char return to fresh water before freeze-up of either marine or river environments, but water temperature or other climatic factors that affect freeze-up may influence migration timing. Dempson and Kristofferson (1987) found a negative relationship between mean catch date and sea

temperature in commercial Arctic Char fisheries of Labrador, Canada. This suggests that water temperature influences migration timing, but environmental cues for freshwater return remain largely unknown for Arctic Char and Dolly Varden (but see Bond and Quinn 2013). Multi-year studies of multiple populations and geographic areas are necessary to understand migration cues and associated potential impacts of climate and other stressors.

Date of freshwater return was significantly later for fish that overwintered below the falls than for fish that overwintered above the falls. Inter-annual variability in overwintering location within individuals (i.e., the same fish overwintered in different locations in different years) has been observed in this system (Smith et al. 2022), which suggests that Arctic Char and Dolly Varden cannot be distinguished based on overwintering location (in relation to the falls). The difference in timing of freshwater return between overwintering groups is thus unlikely to be due to differences between Arctic Char and Dolly Varden in migration timing. Overwintering above the falls involves a longer migration route and a challenging ascent. The length and difficulty of freshwater migration routes have previously been associated with life history type (Finstad and Hein 2012) and choice in overwintering location (Moore et al. 2017) in Arctic Char, but have not been investigated for Dolly Varden. This is, to our knowledge, the first evidence that suggests the length and/or difficulty of the migration route affects the timing of freshwater return for either species. Linear mixed models that accounted for inter-annual differences and repeated measures indicated that fish that overwintered above the falls entered fresh water sixteen days earlier than those that overwintered below the falls. As the ice-free period available for rich marine foraging is brief (often < 3 months), this represents a substantial reduction in the time available for growth and improvements in body condition for fish overwintering above the falls, and may affect reproduction and survival.

We expected that individuals that overwintered above the falls would not travel as far or as extensively in the marine environment as those that overwintered below the falls, because individuals that overwintered above the falls returned to fresh water earlier. We were generally unable to detect differences in movement metrics or patterns between overwintering groups, but all fish that exhibited the intensive movement pattern overwintered above the falls. Fish in this group were detected making numerous movements, all relatively near the mouth of the Coppermine River. Movements over a relatively restricted area may be a tactic to conserve energy. While factors that affect overwintering locations used by fish within the Coppermine River system are unknown, there is no known spawning habitat below the falls, and previous researchers have suggested that overwintering location may be

related to spawning status or body condition (Smith et al. 2022). Arctic Char and Dolly Varden are iteroparous and intermittent (i.e., not every year) spawners. Some anadromous Arctic Char (Radtke et al. 1996) and Dolly Varden (Gallagher et al. 2018b) are known to skip marine migrations altogether in years that they spawn, perhaps as a tactic to conserve energy. Restricting movement in marine environments during the ice-free season could allow fish to conserve energy while still allowing exploitation of rich marine food sources. Fish in the intensive movement group may thus conserve energy before ceasing marine foraging relatively early and completing the longer and more challenging migration above the falls to spawn and/or overwinter. Further investigation of overwintering locations in the Coppermine River should include discrimination among locations at finer spatial scales, as well as assessments of fish spawning status and frequency.

The high proportion of days where individual fish were absent or not detected in the array suggests that the full extents of global (individual) metrics remain unobserved. The intensive movement or detection group had a significantly lower proportion of days undetected (mean 0.46) than the far or limited groups, suggesting that the array configuration is appropriate and characterization of movement patterns is reasonable for fish in the intensive group. Fish in the far movement group were observed at receiver locations furthest from the Coppermine River, where receivers had few or distant neighbours. It is logical that individuals in this group had a higher proportion of days undetected, as there was less opportunity for detections during transition periods to and around these areas of the array. Although the full extent of movement for these individuals was unobserved, it is reasonable to conclude that their movements in the marine environment differed from the intensive group.

Fish in the limited group had the highest proportion of days undetected. Given this detection pattern and the array configuration, it is impossible to ascertain if individuals in this group demonstrated unique movement characteristics, or if movement was actually similar to either the intensive or far groups (but was unobserved). Additional detection information, likely involving an increase in number and locations of receivers, is required to adequately describe the movement patterns of this group of fish.

There are many logistical and environmental challenges associated with conducting aquatic research in remote areas, and decisions that balance effort and resources against scope and coverage must often be made with very limited or no prior information. In this understudied region, even limited information is valuable. Although the high proportion of days undetected for some individuals demonstrates the shortcomings of the array in terms of comprehensive or detailed assessment of movement patterns, the

configuration and coverage of the array are not dissimilar from arrays in other studies that have attempted to describe marine migration of Arctic Char in the Canadian Arctic (Spares et al. 2012; Moore et al. 2016; Hollins et al. 2022). The locations of the receivers used in our analysis were consistent among study years, which allowed comparisons among study years. Fish entered and exited the marine environment from the same location and thus had equal opportunity to travel through (and be detected within) the study area each year, which allowed comparisons among individuals. While substantial uncertainty remains, particularly for fish in the limited group, movement or detection pattern was inconsistent among years for individuals with more than one complete year of summer movement data (i.e., the same individual exhibited different movement patterns in different years). This indicates that fish do not exhibit repeatable movement patterns or return to the same regions of the array each year. The inter-annual variability observed within individuals suggests that movement was not uniquely related to innate factors, such as species, sex, or population. For example, because fish in the intensive movement group exhibited other movement groups in other years, we can infer that fish of the same species (Arctic Char or Dolly Varden) do not all exhibit the intensive movement pattern. There may yet be interspecific differences, such as the intensive movement pattern only being exhibited by one of the two species and with additional factors causing inter-annual variability in movement pattern, but this requires further investigation. The fork lengths of tagged individuals in our study were relatively large and within a relatively narrow range (539–857 mm), and results of relationships assessed between fish length and migration history (reconstructed from otolith microchemistry) for Arctic Char and Dolly Varden captured in the Coppermine River and nearby marine environment suggest that all tagged fish were repeat migrants (R. Smith, unpublished data). A comprehensive assessment of movement patterns and the drivers of inter-individual and inter-annual differences will require tracking both sexually immature and mature fish that reflect a wider range of fork length and migration experience, collection of additional information on spawning status and body condition, distinguishing between Arctic Char and Dolly Varden using new morphometric and genotypic information generated for the system (Weinstein 2023), and greater receiver coverage in this remote and understudied region.

3.5.2 High-use locations and space use in the marine environment

Although individuals that overwintered above the falls left the marine environment earlier than individuals that overwintered below the falls, there were similarities in patterns of space use in the marine environment between overwintering groups. Although there may have been differences

between groups in space use during periods when fish were not detected, the similarities that were observed indicate that overlap does exist. This contrasts with the findings of Hollins et al. (2022), who found that Arctic Char migrating to different overwintering lakes used distinct migration pathways and marine foraging areas. Stock mixing of Arctic Char during the ice-free season has been observed in the marine environment elsewhere in the Canadian Arctic (Dempson and Kristofferson 1987; Moore et al. 2016; Hammer et al. 2022) and there is some evidence that *Salvelinus* spp. from other river systems overwinter at least occasionally in the Coppermine River (R. Smith, unpublished data; A. Dumond and E. Hitkolok, pers. obs.). Also, as discussed above, some of the tagged individuals may be Dolly Varden rather than Arctic Char, and the two species cannot be differentiated based on overwintering location alone. It is thus possible that patterns of space use are similar between overwintering groups because overwintering groups are composed of both species. Genetic analyses to confirm the species of tagged fish is necessary to investigate if space use in the marine environment differs between Arctic Char and Dolly Varden, and if space use differs between overwintering groups within each species.

Although some marine locations, such as near the mouth of the Coppermine River, were consistently identified as high-use locations for both overwintering groups, local Getis G* revealed key differences in the proportion of time that each overwintering group spent at other locations. For example, individuals that overwintered below the falls spent a greater proportion of time at the receiver located furthest to the east of the study area. Fish that overwintered above the falls also frequented the same eastern location, but spent proportionally more time at receivers near the mouth of the Coppermine River and at intermediate locations along the coast. The difference in time that the two overwintering groups spent at these locations may be due to differences in freshwater return and patterns in break-up of sea ice. Sea ice breaks up near the mouth of the Coppermine River soon after river ice (mid-June), and before break-up of sea ice along the coast (A. Dumond and E. Hitkolok, pers. obs.). Although Arctic Char have been observed under sea ice (Bégout Anras et al. 1999; Hammer et al. 2021; Smith et al. 2022), extensive travel under sea ice is uncommon. It is likely that both overwintering groups remained near the Coppermine River and moved further from the river and along the coastline as the sea ice cleared. Individuals overwintering below the falls returned to fresh water later, which allowed them to spend proportionally more time at distant locations before returning to fresh water.

Spatial patterns in break-up of sea ice may also explain which locations were highly used by anadromous Arctic Char and/or Dolly Varden. Local spatial metrics indicated that coastal locations were generally used more than locations offshore or near islands, in terms of both duration of activity (G*) and

movement through the study area (node strength and restricted betweenness). Coastal receivers were relatively farther apart than offshore or island receivers, and both the number of movements associated with these receivers (affecting local network metrics) and the grouped duration of detections (G^*) would be expected to be lower. Despite this spatial bias, estimates of local metrics were higher at coastal receivers. Our finding that coastal locations were highly used is consistent with previous research in Nunavut that showed that Arctic Char prefer nearshore environments (Moore et al. 2016). Sea ice close to land breaks up earlier than sea ice further offshore (A. Dumond and E. Hitkolok, pers. obs.), and fish may spend more time and make more movements in areas that are ice-free earlier. Further, Capelin (*Mallotus villosus*), which are commonly preyed upon by Arctic Char in the marine environment (Power and Reist 2018), spawn on beaches in the Arctic (Coad 2018) and are frequently observed along the coastline near Kugluktuk (A. Dumond and E. Hitkolok, pers. obs.). The preference for coastal areas that we observed may thus be a combination of environmental conditions and prey availability.

The true extent of offshore marine movement by Arctic Char has not been fully investigated. Although Arctic Char have been documented offshore (~ 25 km, Dempson and Kristofferson 1987; ~ 10 km, Moore et al. 2016), there were often very few or no receivers located offshore in previous studies that used acoustic telemetry (e.g., Spares et al. 2015; Moore et al. 2016; Mulder et al. 2020; Hammer et al. 2022). To our knowledge, no studies have used satellite tags to obtain location estimates of Arctic Char. Based on the locations where pop-off satellite tags have detached, Dolly Varden have been observed frequenting offshore environments (2–152 km; Courtney et al. 2018; Gallagher et al. 2021). A char was reported in the middle of Coronation Gulf (E. Hitkolok, pers. obs.), between Victoria Island and Kugluktuk, but it is unknown if the individual was an Arctic Char or a Dolly Varden. Although not ranked as high-use locations, tagged individuals were observed frequenting receiver locations near islands in Coronation Gulf. Complex bathymetry and lack of suitable environmental data make it challenging to determine if habitat use of tagged individuals near islands should be characterized as offshore or coastal. Further research is required to demonstrate both preference and full extent of movements of both Arctic Char and Dolly Varden in this and other areas.

3.5.3 Locations associated with absences

Absences or periods when individuals are undetected are often ignored in acoustic telemetry studies (but see Stehfest et al. 2015; Williamson et al. 2021), and may have important implications for data

analysis and interpretation. In this study, a high proportion of days undetected precluded us from determining if limited or far movement/detection groups represented distinct movement patterns, and from fully characterizing movement in the marine environment. Resolving uncertainties surrounding absences is also important for identifying potential high-use areas outside of the current array configuration.

Local Getis G^* , a local indicator of spatial association (LISA), was useful in identifying areas of the receiver array with a disproportionate number of absences. G^* is similar to other LISAs, such as Moran's I , in that it identifies local clustering or spatial associations. A key difference that makes G^* well-suited for acoustic telemetry applications is that high values of the G^* statistic indicate hotspots and low values indicate coldspots, whereas high values of local Moran's I indicate regions of high spatial autocorrelation (i.e., clusters of similar values, either high or low; Dale and Fortin 2014). It should be noted that a second local Getis statistic exists, G . G only considers the values at neighbouring locations and does not consider the value at the central location itself, whereas G^* considers the values at neighbouring locations and the central location (Getis and Ord 1992). Acoustic telemetry studies are typically concerned with values at a specific location, so G^* is likely more appropriate for most acoustic telemetry applications.

Local Getis G^* indicated that areas immediately preceding or following absences or periods of non-detection were located along the coast, near the edge of the array, or at locations with larger distances to other receivers. The areas with high G^* values could be prioritized for deployment of additional receivers to increase coverage and identify direction of travel during absences. Similarly, particularly for studies with limited resources, areas with low G^* values (coldspots) could be further investigated to identify receivers that may be removed without unduly impacting results.

3.6 Conclusions

We found that overwintering location was associated with date of freshwater return, providing the first evidence that length and/or difficulty affects migration timing of Arctic Char or Dolly Varden. Fish that had a longer and more challenging migration returned to fresh water earlier. Overwintering location within the Coppermine River system is known from a previous study to vary both among individuals and years (within individual) (Smith et al. 2022). We found that movement or detection patterns in the marine environment also varied among individuals and years, but there was limited evidence that marine movement or detection patterns were associated with overwintering location. Although

interannual variability in observed movement patterns suggests that species alone does not determine movement and space use in the marine environment, genetic analysis is required to ascertain the influence of species. A high proportion of absences or lack of detections in the array resulted in substantial uncertainty in some marine movement patterns and should be addressed in future research in this and other areas.

High-use locations, both in terms of movement and duration of detections, were largely similar between overwintering groups. Minor qualitative differences were observed in the proportion of time spent at key locations, likely due to differences in timing of freshwater return. Local (location-based) metrics revealed a preference for coastal locations for both overwintering groups, despite the array configuration likely biasing metrics towards offshore or island locations. Preference for coastal areas is likely due to the abundance of capelin observed in these areas, as well as patterns in break-up of sea ice. Similarities in space use between overwintering groups has implications for management and sustainability of the local fishery.

Although local indicators of spatial association have been used previously in aquatic acoustic telemetry (e.g., Biggs and Nemeth 2016; Smoothey et al. 2019; Rothermel et al. 2020), their use remains uncommon. To our knowledge, we are the first to incorporate both local Getis G* and network analysis. Network analysis of spatial networks typically assesses the occurrence of movements between receivers (Jacoby et al. 2012; Jacoby and Freeman 2016), whereas G*, as demonstrated here, is well-suited to assess the length of time spent at each receiver. If receivers have consistent and relatively high ranks using both local methods, it can be inferred with greater confidence that these locations are high-use locations. For these reasons, the two methods are complementary and, when used together, can provide a more comprehensive assessment of local spatial structure and space use in acoustic telemetry applications. We also demonstrated the usefulness of G* in identifying locations associated with absences or a lack of detections, which can be used to help focus future receiver deployments. We hope this approach will provide a useful example for future researchers.

Chapter 4

Environment influences migration timing of cold-adapted salmonids (*Salvelinus alpinus* and *S. malma malma*) in the Canadian Arctic

4.1 Abstract

Shifts in migration timing in response to climate change have implications for fitness and survival of cold-adapted species. We used acoustic telemetry to investigate and compare environmental influences on return to fresh water between sympatric anadromous Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma malma*), and between overwintering locations (above or below an obstacle – a substantial cascade). Both Arctic Char and Dolly Varden that overwintered below the cascade returned to fresh water later in the year, when sea surface temperature was warm and river temperature was cool, whereas Dolly Varden that overwintered above the cascade returned to fresh water earlier in the year, at cooler sea surface temperatures and during warm and likely stressful river temperatures. Ascension of the cascade by Dolly Varden (no Arctic Char were observed to ascend the cascade) was likely assisted by high tide but unaffected by other environmental factors, including temperature. Fish demonstrated plasticity in response to inter-annual variation in environmental conditions, but may experience decoupling of environmental cues and suitable migratory conditions, which could impact persistence of these ecologically and culturally important species.

4.2 Introduction

Identifying and understanding migration cues is essential in monitoring and predicting effects of climate change and other stressors on migratory species. Migration timing has implications for trophic relationships (e.g., Mayor et al. 2017), fitness (e.g., Gienapp and Bregnballe 2012), and abundance (e.g., Moller et al. 2008), and phenological shifts have been associated with observed increases in mortality rates in an anadromous fish (Hinch et al. 2012). Anadromous species of fish are particularly vulnerable because of potential decoupling between environmental cues and critical life history transitions, including migration, and because they can experience climate-induced impacts in multiple environments (fresh water, salt water, and along migratory pathways; Reist et al. 2006). Discerning relationships between climate change and shifts in migration timing of anadromous species, such as salmonid fishes, is complex, and may be obscured by other anthropogenic influences such as fishing pressure (Morita 2019; Tillotson et al. 2021). Even within regions that experience consistent warming, there can be

considerable variability in shifts in migration timing, both among species and within species (i.e., among populations; Kovach et al. 2015). Many fish species of cultural and economic importance are migratory (e.g., Myrvold et al. 2019; Tallman et al. 2019; Carothers et al. 2021), and improving understanding of the diverse drivers of migration timing and responses to changing environmental conditions is crucial for fisheries stewardship and management.

Anadromous Arctic Char (*Salvelinus alpinus*) and northern form Dolly Varden (*Salvelinus malma malma*) are critical to subsistence fisheries across the Canadian Arctic (Priest and Usher 2004; Lea et al. 2021). Assessments of distributions and predicted impacts of climate change have been conducted for Dolly Varden in Alaska (Murdoch et al. 2020) and Arctic Char in Canada (Bommersbach et al. 2024), but phenology was not considered. The seaward migration of Arctic Char is known to be influenced by sea-ice (e.g., Bégout Anras et al. 1999; Hammer et al. 2021), but environmental drivers of return migrations to fresh water are largely unknown. There is some evidence that timing of return to fresh water is correlated with date of river freeze-up for *Salvelinus* spp. (Smith et al. 2024; Chapter 3), but freeze-up cannot be a direct cue for return because return occurs well in advance of freeze-up. Knowledge regarding environmental influences on timing of return migration thus remains limited for both Arctic Char and Dolly Varden (but see Bond and Quinn 2013), despite the importance of these two species to northern ecosystems and their adaptation to cold, polar environments that are disproportionately affected by climate change (Rantanen et al. 2022).

Phenological adaptations in response to environmental stressors/conditions have been observed to occur, such as at Nulahugyuk Creek, Nunavut, Canada, where Arctic Char have adapted to low summer flow conditions by returning to fresh water extraordinarily early in the ice-free season – when higher water levels allow access to the upstream lake (Gilbert et al. 2016). Similarly, Arctic Char at Nauyuk Lake, Nunavut, undergo a two-step migration over two seasons in fresh water to access spawning habitats (Johnson 1989). These unusual migration patterns represent adaptations to local environmental conditions, but plasticity of migration timing in response to inter-annual variation in environmental conditions remains poorly understood. Migration cues and timing may differ among populations and systems due to local adaptation to different environmental conditions (Jonsson 1991), which underscores the need for location-specific studies.

The Coppermine River in Nunavut, Canada, is of interest in the study of migration cues because recent genetic evidence indicates that the surrounding area is used by both anadromous Arctic Char and Dolly

Varden (Weinstein 2023). There is a large cascade that poses an obstacle for migrating fish, and fish that migrate and overwinter above this obstacle have been observed to return to fresh water earlier than fish that overwinter below (Smith et al. 2024; Chapter 3). The same individual fish may overwinter above the cascade in some years and below in other years, which facilitates the investigation of plasticity in migration cues in relation to overwintering location. The cascade also presents an opportunity to assess influences of environmental factors on obstacle ascension. We used acoustic telemetry to investigate how environmental variables, including those shown to influence migration timing and/or obstacle ascension in other Salmonidae spp., relate to return to fresh water and obstacle ascension in Arctic Char and Dolly Varden. We also compared migration timing and cues between sympatric Arctic Char and Dolly Varden and between overwintering locations.

4.3 Materials and methods

4.3.1 Study location

The Coppermine River has an approximate watershed area of 50 800 km² and runs 520 km from subarctic tundra in the Northwest Territories, Canada, to the Arctic Ocean (Wedel et al. 1988). The Coppermine River flows into Coronation Gulf immediately to the east of the Hamlet of Kugluktuk, Nunavut, in the western Kitikmeot region of Nunavut, Canada (Figure 4.1). Mean discharge in the lower reaches during the ice-free season is 473 m³/s and mean peak discharge during spring freshet is 1330 m³/s (Coulombe-Pontbriand et al. 1998). Kugluk or Bloody Falls (hereafter referred to as “the falls”) is a large cascade located approximately 17 km upstream of the mouth of the Coppermine River (Figure 1.2). The cascade poses a substantial obstacle but is passable by fish migrating upstream. Between the falls and the river mouth, the wetted width of the river is ~ 200–600 m and the depth of the main river channel, measured opportunistically, is ~ 2–10 m.

4.3.2 Community involvement statement

The board of the Kugluktuk Hunters and Trappers Organization (HTO) is elected by (Inuit) beneficiaries of the Nunavut Land Claims Agreement Act (1993) who live in Kugluktuk, Nunavut. The HTO is responsible for the management of the char fishery near Kugluktuk. In 2017, board members raised concerns regarding migration timing and low harvest numbers of char, as well as low water levels and warm temperatures. This study arose out of those initial concerns. Research questions have evolved throughout the project, and are conceived and directed by questions and observations from community

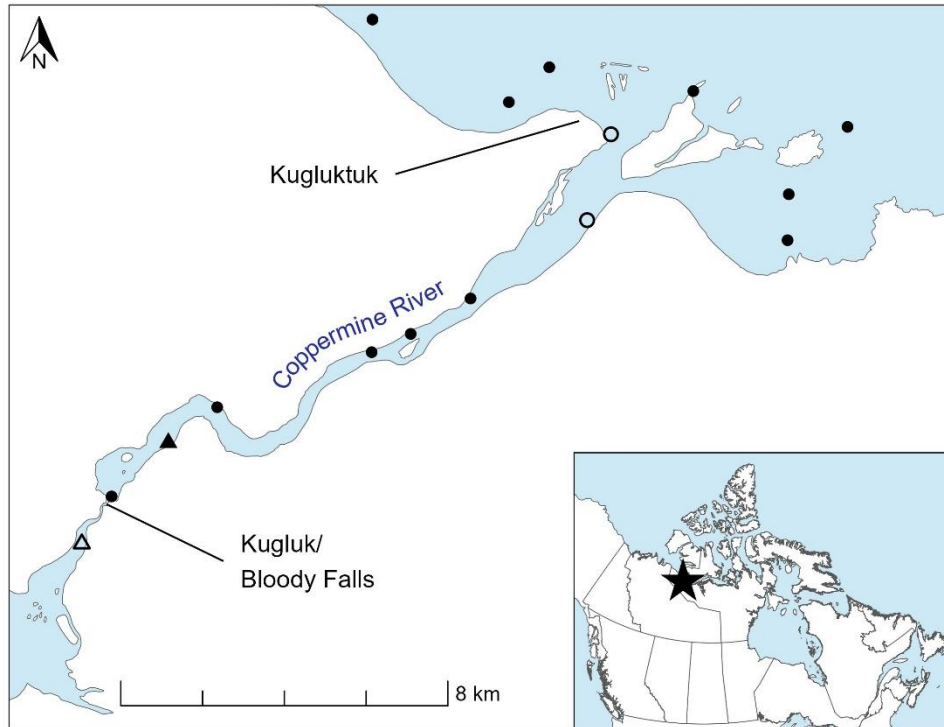


Figure 4.1: Map of study area and locations of acoustic telemetry receivers in and near the Coppermine River. Note that only marine receivers near the Coppermine River are displayed, because only movements into and within the Coppermine River were used for this study. Open circles indicate two receivers that were used to identify timing of return to fresh water. Open triangle indicates one receiver that was used to identify timing of passage above the falls. Closed triangle indicates the receiver location where river temperature was measured. See Figure B1 in Appendix B for locations where other environmental variables (discharge, sea surface temperature) were obtained. Shapefiles of Canada and United States boundaries were respectively obtained from Statistics Canada (2016) and the United States Census Bureau (2017). Shapefiles of water bodies were obtained from the CanVec hydrographic series (Natural Resources Canada 2015). Data are in WGS84 and unprojected.

members. Two Inuuk co-authors live in Kugluktuk and some non-Inuit co-authors live for extended periods (> 3 months) in Kugluktuk each year, which allows for continuous conversations to occur about project activities and results with interested and concerned community members. Inuit community members are involved in setting research priorities and study design, lead and conduct all field activities, review and interpret results, and are integral co-authors in publications and presentations.

4.3.3 Acoustic tagging and receivers

A total of 207 adult, anadromous char were live-captured in Coronation Gulf and the Coppermine River from 2018 to 2023. V16T acoustic tags (Innovasea, Halifax, NS) were surgically implanted into each fish, following methods in Smith et al. (2022). The fork length of each fish was measured to the nearest mm. The adipose fin was clipped for subsequent genetic analyses and was either stored in reagent alcohol and frozen or stored in filter paper and dried or frozen. To minimize stress and handling, fish were only weighed when conditions (i.e., wind) were favourable or when fork length was < 600 mm (to verify tag burden was less than 2% of body mass; Winter 1996).

An array of acoustic telemetry receivers was deployed to detect tag transmissions in both the marine environment of Coronation Gulf and the freshwater environment of the Coppermine River (Figure 4.1). Receiver hydrophones were located ~ 1–1.5 m above the bottom, at depths of 2–90 m in the marine environment and 3–14 m in freshwater environments. The number of receivers in the marine environment ranged from twenty-two (2018) to forty-seven (2021), and the number of receivers in the Coppermine River ranged from seven (2018) to nine (2019–2021). Only receivers in the Coppermine River and marine receivers within 5 km of the river mouth were used for this study, to identify movements into and within the river (Figure 4.1).

4.3.3.1 Ethics approvals

Fish captures, handling, and tagging were conducted under Animal Utilization Project Protocols 18–07, 30071, and 44099, which were approved by the University of Waterloo Animal Care Committee. All fieldwork was conducted under Nunavut Impact Review Board screening (File no. 18YN023), Kitikmeot Inuit Association Certificate of Exemption to access Inuit Owned Lands (Certificate no. KTX118N005), and Fisheries and Oceans Canada Licenses to Fish for Scientific Purposes (S-18/19-1025-NU, S-19/20-1023-NU, S-21/22-1034-NU, S-22/23-1008-NU, and S-23/24-1056-NU).

4.3.4 Species identification

Genotyping of fifty-eight tagged fish was previously done by Weinstein (2023) using the 87K *Salvelinus* SNP (single nucleotide polymorphism) chip developed by Nugent et al. (2019). Methods are available in Weinstein (2023). An additional seventy-two tagged fish were genotyped using TaqMan™ assays recently developed by Liu et al. (2023) to distinguish Arctic Char from Dolly Varden. DNA was extracted from fin clips collected from the seventy-two fish using a Qiagen DNeasy Blood and Tissue Kit (Qiagen,

Hilden, Germany), following the manufacturer's instructions and with the final optional step to increase DNA yield. DNA quantity was determined using broad range Qubit™ dsDNA Quantification Assay Kits (Thermo Fisher Scientific, Waltham, MA, USA). Genotypes were determined using both ACDV67-15 and ACDV72-24 TaqMan™ assays (Liu et al. 2023). Samples were genotyped in duplicate for each assay in a QuantStudio™ 3 Real-Time PCR System (Thermo Fisher Scientific) with a 96-well plate. Each well contained 4.5 µL diluted DNA (~4 ng DNA total), 0.5 µL 20x TaqMan™ assay working stock, and 5 µL 2x TaqMan™ Genotyping Master Mix (Thermo Fisher Scientific). Each plate had 6–8 wells with positive controls (3–4 wells with known Arctic Char and 3–4 wells with known Dolly Varden) which were determined by genetics, meristics, and morphometrics by Weinstein (2023). Each plate also had two wells with negative controls (molecular water). The qPCR conditions were set to hold at 95°C for 10 minutes, followed by 40 cycles of 95°C for 15 seconds and 60°C for 1 minute. QuantStudio™ Design & Analysis software version 2.8 (Thermo Fisher Scientific) was used to classify samples as homozygous Arctic Char, homozygous Dolly Varden, or heterozygous for each assay. Visual inspection of assigned genotypes of positive controls determined that both assays correctly genotyped all controls. Final genotypes were determined using results from both assays. There were no instances of disagreement between the two assays (e.g., homozygous Arctic Char at one SNP and homozygous Dolly Varden at the other SNP). In instances when an individual was heterozygous at one SNP and homozygous at the other SNP, we classified the individual as homozygous.

4.3.5 Detection data

Detection data were downloaded at least once per year; the final download was on 03 October 2023. Detection data were processed following Smith et al. (2024; Chapter 3). The R package `mort` version 0.0.1 (Smith et al. 2025; Chapter 2) was used to identify detections from potential mortalities or shed tags. Residence events were generated with a maximum gap in detections of 24 hours. The function `morts` was applied with 'all' methods, and with 'drift' (from upstream to downstream stations and from the river mouth to nearby coastal receivers) used when identifying mortalities (not when identifying thresholds). Seasonality was applied during the period that the river was ice-free each year, as determined by time-lapse cameras (Kugluktuk Ikaarvik youth group, unpublished data) and by personal observations by the authors. The function `morts` was also applied with the 'cumulative' method without seasonality. The function `infrequent` was applied using the 'recent' method, with a timeframe of 52 weeks and a threshold of 48 hours. In all cases, the 'backwards' option was used, to flag

residence events that were observed at the same station where subsequent residence event(s) exceeded a threshold (i.e., to flag the earliest possible time that a potential mortality could have been observed).

4.3.6 Return to fresh water, ascension of falls, and overwintering location

The timing of return to fresh water was determined using detection data at the two receivers near the mouth of the Coppermine River (Figure 4.1). A fish was considered to have returned to fresh water if it had been previously observed, either by tagging or detection, in the marine environment and if it was subsequently detected at receivers upstream of the river mouth. If multiple consecutive events were recorded at the river mouth (i.e., a fish was detected at the river mouth, then not detected elsewhere for ≥ 24 hours), the fish was considered to have approached but not returned to the river, and the approach was excluded from analyses. Similarly, the timing of ascension of the falls was recorded by a receiver that was located ~ 500 m above the uppermost rapid of the falls (Figure 4.1). A fish was considered to have ascended the falls if it had been previously observed in the Coppermine River below the falls and subsequently observed at the receiver above the falls; these fish were assigned the overwintering location of “Above falls” for that year. Fish that were detected during the ice-covered season by one or more receivers in the Coppermine River below the falls were assigned the overwintering location of “Below falls” for that year.

4.3.7 Environmental drivers of migration timing

Environmental variables that have been shown to influence return to fresh water and/or obstacle ascension in other Salmonidae spp. (e.g., Gowans et al. 1999; Dahl et al. 2004; Kovach et al. 2015; Goetz et al. 2021) were considered. Linear variables (sea surface temperature (SST), river temperature, discharge, changes in SST/river temperature/discharge) were assessed separately from cyclical or circular variables (lunar phase, tidal phase, time of day).

4.3.7.1 Linear environmental drivers

River discharge was measured by Environment and Climate Change Canada’s (ECCC) Hydrometric Station 10PC004, located ~ 70 km upstream of the falls (Figure B1 in Appendix B). Daily discharge data were obtained by direct request to ECCC for 2018–2021 and from Real-Time Hydrometric Data (Environment and Climate Change Canada 2024) for 2022 and 2023. River temperature data were extracted from acoustic receiver logs at the location where a receiver was deployed most consistently

(i.e., no gaps in deployment) during the ice-free seasons of the study (Figure 4.1). This location was in the main river channel in a section with relatively high velocity. Temperatures recorded by acoustic receivers may differ by $\sim 1^{\circ}\text{C}$ due to differences in calibration (Smith et al. 2022), so a linear offset was applied. The offset was determined by comparing temperatures from acoustic receivers to those from temperature loggers deployed between the falls and the river mouth ($n = 1\text{--}29$ each year) by the Ikaarvik Coppermine River Monitoring youth group (unpublished data); temperature data from Ikaarvik indicate that temperatures are consistent (with the exception of back eddies and deep pools) from the falls to the river mouth. Mean river temperature was calculated for each day of the ice-free seasons. Daily sea surface temperature (SST) data were obtained from the National Oceanic and Atmospheric Administration Daily Optimum Interpolation SST Version 2.1 high resolution dataset (Reynolds et al. 2007; Huang et al. 2021). The `griddap` function in the R package `rerddap` version 1.1.0 (Chamberlain 2024) was used to obtain SST observations from grid cells (Figure B1 in Appendix B) with longitudinal centres between -114.6°W and -112.9°W (spanning the study area) and a latitudinal centre of 67.88°N (corresponding to the grid cells closest to the coastline of the study area, where *Salvelinus* spp. have been observed to preferentially occupy marine habitat (Smith et al. 2024; Chapter 3)). The daily means of all grid cells were calculated to obtain a single daily SST measurement for the study area. Daily photoperiod data (hours from sunrise to sunset) were obtained from the National Research Council Canada Sunrise/Sunset calculator (National Research Council Canada 2020). Days of year were delineated as 24-hour periods that ended at midnight in local time. Weekly mean values and the weekly rate of change were calculated for river temperature, SST, and discharge.

To investigate return to fresh water for each fish and year, a dataset was generated of days available but unused (response of 0) and used (response of 1). Return to fresh water was considered available but unused on days when a fish was known or assumed to be in the marine environment and did not approach or return (see Section 4.3.6 – Return to fresh water – above) to the Coppermine River. For fish that were tagged in the marine environment, the response record started on the day of tagging. For fish tagged in a previous year, the record started on the day of the first marine detection following the break-up of river ice. If a fish was detected in the marine environment prior to break-up, the record started on the day of break-up. Some fish may have entered the marine environment without being detected in the spring, likely due to increased noise from dynamic break-up. For fish that were not detected on or within two weeks of break-up and subsequently detected in the marine environment, the record started two weeks (14 days) after the day of break-up. The response record of each fish

ended (i.e., no response was recorded) when that fish returned to the Coppermine River and was in fresh water. For fish that returned to fresh water and then re-entered the marine environment, the response record re-started on the day the fish re-entered the marine environment. Days when a fish approached but did not return to fresh water were excluded (i.e., no response was recorded).

Return to fresh water (1 = return, 0 = no return) was related to environmental variables, species, and overwintering location using generalized linear mixed models implemented with the R package `glmmTMB` version 1.1.9 (Brooks et al. 2017). Incomplete observations (e.g., unknown species or overwintering location, missing environmental data) were excluded and environmental variables were scaled (to standard deviation = 1) and centred (to mean = 0). Fish ID was included as a random factor. Year was not included as a random factor because we expected differences among years would be captured by environmental covariates. The deviance was compared between saturated models fit using a logit link and a complementary log-log link (Hardin and Hilbe 2018). Deviance values of models fit using a logit link were lower than those using a complementary log-log link, so the set of candidate models was fit using a logit link. To compare the potential effects of each environmental variable, candidate models included single environmental variables. An interaction with species was included. An interaction with overwintering location was also included, because the timing of return to fresh water is known to differ significantly between fish that overwinter above the falls and fish that overwinter below the falls (Smith et al. 2024; Chapter 3). The model set included a null model (random factor only), a model with day of year, and a model with photoperiod, which is invariant among years. Models were compared with Akaike's Information Criterion adjusted for small sample sizes (AICc). Environmental variables with different quantification methods (e.g., mean daily, mean weekly, and mean weekly rate of change) were compared; the best methods for each variable were used to generate additional candidate models with combinations of river temperature, SST, discharge, and photoperiod. A maximum of one quantification method for each variable was included in each model. Variance inflation factors (VIFs) were assessed using the `corvif` function from Zuur et al. (2009); all VIFs were < 3. Model fit was assessed using quantile-quantile plots, residual plots, and tests for residual distribution, dispersion, outliers, and zero-inflation implemented using the R package `DHARMa` version 0.4.6 (Hartig 2022). When a test for zero-inflation was significant, the model was refit as a zero-inflated model and re-assessed. Marginal and conditional R^2 values (determined using the delta method; Nakagawa et al. 2017) and AICc scores were computed using the R package `MuMIn` version 1.47.5 (Barton 2019). Experimental variograms of model residuals were generated with the R package `gstat` version 1.1-1 (Pebesma and

Graeler 2023) to check for temporal autocorrelation in the top model. One variogram was generated for all fish together, and separate variograms were generated for individual fish.

To investigate ascension of falls for each fish and year, a dataset was generated of days available but unused (response of 0) and used (response of 1). Falls ascension was considered available but unused on days when a fish had returned to fresh water and was known to be in the river. Ascension of falls (1 = ascent, 0 = no ascent) was related to environmental variables using generalized linear mixed models with a logit link. Environmental variables were the same as those used for models of return to fresh water, except SST was excluded. Species and overwintering location were not included, because only Dolly Varden were observed ascending the falls and all fish that ascended the falls overwintered above the falls. Fish ID was included as a random factor. Models were fit and assessed using the same methods as those for return to fresh water (above).

4.3.7.2 Cyclical environmental drivers

Return to fresh water and ascension of falls were related to the circular variables time, lunar phase, tidal phase, and light. Time was obtained directly from detection data (see above). Times of new and full moons were obtained from the United States Navy Astronomical Applications Department (2023). Lunar phase (°) was determined for each observation by interpolating between new (0°) and full (180°) moons. Similarly, times of high and low tides were obtained from the Canadian Hydrographic Service (2022b). Tidal phase (°) was determined for each observation by interpolating between low (0°) and high (180°) tides. Light was determined using sunrise, sunset, and nautical twilight times obtained from the National Research Council Canada (2020). Because some observations were made during polar day (i.e., 24 hours of daylight), light could not be measured in degrees. Each observation was assigned one of four light categories: day (sunrise to sunset), dusk (sunset to end nautical twilight), night (end nautical twilight to beginning nautical twilight), dawn (beginning nautical twilight to sunrise).

For return to fresh water, only fish with known overwintering locations (either above or below falls) were included. When more than one return was documented for an individual within a year, only the final return was included. When individuals were observed returning in more than one year, only one year was included. To improve balance in sample sizes among years, observations in 2021 and 2023 were preferentially included and observations in 2019 and 2020 were preferentially excluded.

Time, lunar phase, and tidal phase of return to fresh water were compared between Arctic Char and Dolly Varden that overwintered below the falls and between overwintering locations for Dolly Varden.

No Arctic Char were observed passing above the falls. Samples were compared using Watson's U^2 test (Watson 1962), which is consistently powerful relative to other tests in comparing distributions of two circular samples (Landler et al. 2021). Watson's U^2 test was implemented with the `watson.two.test` function in the R package `circular` version 0.5-0 (Agostinelli and Lund 2023). No significant differences were observed between Arctic Char ($n = 23$) and Dolly Varden ($n = 21$) that overwintered below the falls ($U^2 \leq 0.1729$, $p > 0.05$). Significant differences were observed between Dolly Varden that overwintered above ($n = 55$) and below ($n = 21$) the falls ($U^2 \geq 0.2304$, $p < 0.05$). Therefore, species were pooled and overwintering locations were assessed separately in subsequent analyses of return to fresh water.

Uniformity (randomness) of time, lunar phase, and tidal phase of return to fresh water was assessed for each overwintering location, as well as ascension of falls, using Rayleigh tests (Rayleigh 1880). Rayleigh tests were implemented with the R package `circular` (Agostinelli and Lund 2023). Because Rayleigh tests lack power for multimodal distributions, modified Hermans-Rasson tests (Landler et al. 2019), implemented with the R package `CircMLE` version 0.3.0 (Fitak and Johnsen 2017), were used to confirm uniformity when Rayleigh tests were not significant. When there was a significant departure from uniformity, the most likely model of circular orientation was selected and the confidence intervals of model parameters were calculated with the `circmle` and `ci_circmle` functions in the R package `CircMLE` (Fitak and Johnsen 2017). The model parameters that were extracted were circular means and concentration parameters (κ). Resultant lengths (a measure of concentration; Batschelet 1981) were calculated from κ values following the equations in Mardia and Jupp (2000).

To assess whether perceived patterns in return to fresh water in relation to lunar phase were due to differences in the lunar cycle and unequal sample sizes among years (e.g., a large sample size in a year when peak return coincided with a particular lunar phase), Watson's U^2 test was used to compare lunar phases of return to fresh water among years (for above and below falls separately). Comparisons were restricted to years with combined sample sizes > 17 . A Bonferroni correction was applied when multiple comparisons were made. As the `watson.two.test` function provides a range of p values, the Bonferroni correction was applied to the high end of the range.

The availability of the four light categories (day, dusk, night, dawn) varied greatly throughout the study period and not all categories were available each day (e.g., during polar day). To determine if fish were more likely to return to fresh water or ascend the falls in daylight than would occur randomly, Monte

Carlo analysis was performed with 10 000 random permutations. For each permutation, observations were assigned random times while retaining day of year. Light category was determined for the random times. The proportion of fish returning to fresh water or ascending the falls during day was calculated for each permutation and used as the test statistic. Exact p-values were calculated as the proportion of permutations with equal or greater test statistics than the observed test statistics.

4.4 Results

During the study (2018–2023), 130 of the 207 tagged fish were observed returning to the Coppermine River in at least one year and 79 individuals were observed ascending the falls in at least one year. Of the 130 fish that returned to the Coppermine River, 25 were genetically identified as Arctic Char, 98 were genetically identified as Dolly Varden, and 7 were of unknown species because genetic samples were not available. Of the 79 fish that ascended the falls, 77 were genetically identified as Dolly Varden and 2 were of unknown species. No Arctic Char were observed ascending the falls. Fork lengths at the time of tagging ranged from 560–725 mm for Arctic Char and 539–889 mm for Dolly Varden. The minimum weight at the time of tagging was 2200 g for Arctic Char and 1850 g for Dolly Varden. Tag burden was less than 1.9% of fish body weight for all fish.

4.4.1 Return to fresh water, ascension of falls, and overwintering locations

Fish of known species and overwintering location ($n = 106$) were observed returning to fresh water a total of 167 times, including 154 final returns (i.e., the fish stayed in the river system for the winter) and 13 temporary returns (i.e., the fish subsequently exited the river and later made a final return before freeze-up). Eight individuals (five Arctic Char and three Dolly Varden) had temporary returns. All fish with temporary returns overwintered below the falls. The number of temporary returns for a given individual*year ranged from 1–4 (median = 1). The dates of temporary returns ranged from 03 August (in 2019) to 03 October (in 2022), with a median of 06 September. The dates of exits into the marine environment following temporary returns ranged from 06 August (in 2023) to 10 October (in 2022), with a median of 08 September. The daily mean river temperature at the time of exit ranged from 2.9–12.6°C (median = 8.3°C). The dates of final returns (including returns of fish that only returned once, as well as final returns of fish that temporarily returned earlier in the season) ranged from 19 June (in 2023) to 12 October (in 2022), with a median of 16 August (Figure 4.2). The date of break-up of river ice in 2023 was 31 May, which allowed ~ 20 days of marine foraging for the individual that returned on 19 June 2023. Within a given year, the dates of final returns of Arctic Char that overwintered below the falls

were qualitatively similar to those of Dolly Varden that overwintered below the falls (Figure 4.2). Fish that overwintered above the falls returned to fresh water earlier than fish that overwintered below the falls, as previously observed in this study system (Smith et al. 2024; Chapter 3). Note that no Arctic Char or Dolly Varden were observed overwintering below the falls in 2023, likely due to fewer tagged fish surviving in the study area and the relatively low proportion of tagged fish that were Arctic Char.

Dolly Varden (n = 77) were observed ascending the falls a total of 115 times. No fish were subsequently observed descending the falls within the same year. The dates of ascension ranged from 13 June (in 2023) to 27 September (in 2022), with a median of 17 August. For fish that were detected both returning to fresh water and ascending the falls in the same year (n = 95 fish*years), the number of days between final return to fresh water and ascension ranged from 0.6–32.0 (median = 3.2, interquartile range = 1.9–9.6). Five fish returned to fresh water and ascended the falls when mean river temperatures (mean daily river temperatures between day of return and day of ascension) were $\geq 20^{\circ}\text{C}$. The number

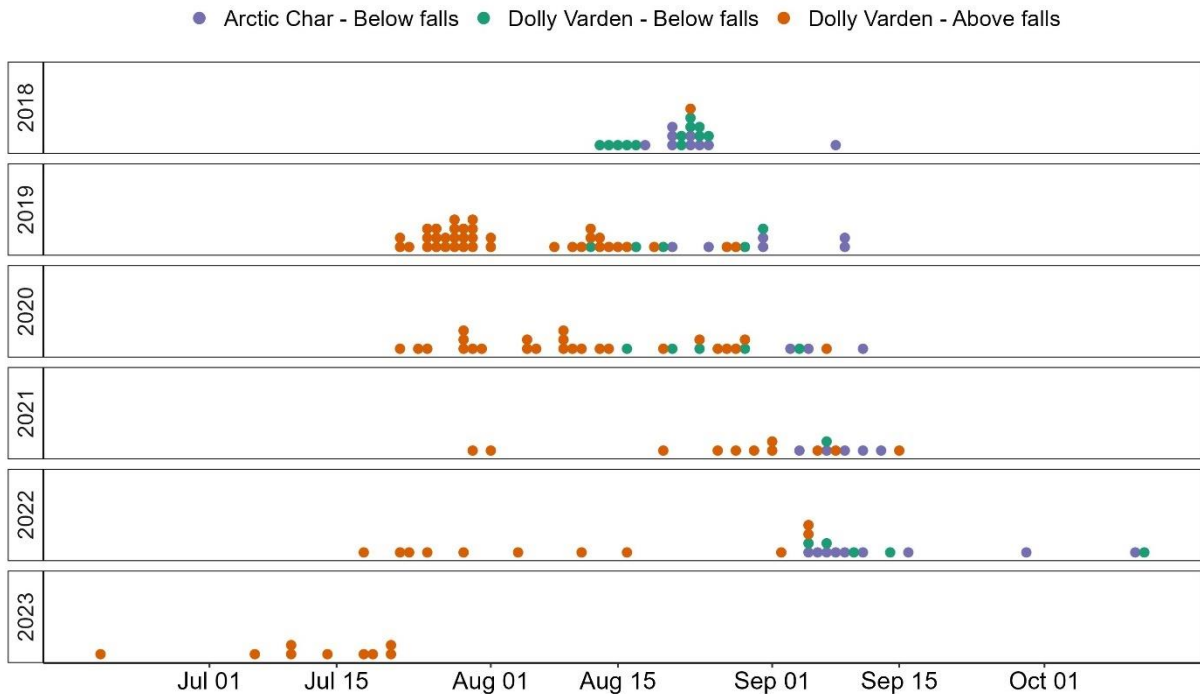


Figure 4.2: Dates of final return to fresh water of Arctic Char and Dolly Varden with known overwintering locations. Note that no Arctic Char were observed returning to the Coppermine River in 2023, likely due to a relatively low proportion of tagged fish that were Arctic Char and relatively low number of active tags.

of days between final return to fresh water and ascension ranged from 0.6–1.3 (median = 0.8) for these five individuals.

4.4.2 Linear environmental drivers of migration timing

4.4.2.1 Return to fresh water

All generalized linear mixed models relating return to fresh water to environmental variables had lower AICc scores (higher ranks) than the null model (random factor only; Table 4.1). Models that included an interaction between environmental variables and species had higher AICc scores (lower ranks) than the same models with the interaction term removed (see Table B1 in Appendix B for full set of model results). Mean weekly SST was the best SST predictor and the highest ranked model with a single environmental variable. Mean weekly SST was also the only model with a single environmental variable that ranked higher than the models with photoperiod (Table 4.1) or day of year (Table B1 in Appendix B). Marginal R^2 of the model with mean weekly SST was much higher (0.66) than that of the model with photoperiod (0.24) or day of year (0.21), which indicates that mean weekly SST was a better predictor of return to fresh water than day length or time of year. Mean daily river temperature was the best river temperature predictor. Both daily and weekly rates of change of discharge had similar AICc scores to the null model, which indicates there was little evidence that changes in discharge were cues for returning to fresh water. Mean daily discharge was the best discharge predictor of return to fresh water when discharge was the sole environmental variable, although AICc and deviance were almost identical to mean weekly discharge (Table 4.1).

The highest ranked model included mean weekly SST, mean daily river temperature with an interaction with overwintering location, mean daily discharge, photoperiod with an interaction with overwintering location, and species (Table 4.1). The model coefficients for mean weekly SST were positive in all models that included mean weekly SST as a covariate (Table 4.1); fish had a higher probability of returning to fresh water when mean weekly SST was warmer (Figure 4.3A). The model coefficients for mean daily river temperature were consistently negative (Table 4.1), and fish that overwintered below the falls had a higher probability of returning to fresh water when river temperatures were colder. The positive association between return and mean weekly SST and the negative association between return and river temperature was due to a lag between changes in SST and changes in river temperature; river temperatures increased (above 0°C) earlier each year than SST, warmest river temperatures typically occurred when SST was relatively cold, and river temperatures decreased when SST was either relatively

Table 4.1: Generalized linear mixed models (logit link) relating return to fresh water to environmental variables. The null model includes only the random factor of fish ID. AICc scores were used to rank models. Models are presented in order of increasing AICc or decreasing rank. Model deviance (-2l) is -2log-likelihood. Coefficients apply to scaled and centred variables. Marginal R² only considers fixed factors and conditional R² considers both fixed and random factors. Models with day of year are not shown because day of year was highly correlated with photoperiod (Pearson's r = -0.975). See Table B1 in Appendix B for full set of model results.

Model	AICc	ΔAICc	-2l	Coefficient estimates (± standard error)								Marginal R ²	Conditional R ²
				Discharge	Temperature	SST	Photoperiod	Species (Dolly Varden)	Overwintering location (Above falls)	*Overwintering location	Zero-inflation intercept		
Temperature*Overwintering location + SST (weekly) + Discharge + Photoperiod*Overwintering location + Species	1054.56	0	1032.49	0.60 (0.28)	-3.18 (1.50)	4.23 (1.18)	-5.62 (2.69)	9.22 (3.77)	6.56 (3.05)	Temperature: 3.86 (1.55) Photoperiod: 4.83 (2.70)	1.79 (0.12)	0.85	0.85
Temperature*Overwintering location + SST (weekly) + Photoperiod + Species	1060.49	5.93	1042.44	—	-2.31 (0.87)	3.85 (1.21)	-1.50 (0.37)	7.78 (3.05)	1.76 (1.09)	3.19 (0.98)	1.81 (0.11)	0.73	0.73
SST (weekly) + Photoperiod*Overwintering location + Species	1064.19	9.63	1048.15	—	—	4.32 (1.26)	-11.24 (4.4)	7.04 (2.96)	12.33 (4.76)	9.91 (4.37)	—	0.90	0.90
Temperature*Overwintering location + SST (weekly) + Discharge + Species	1066.22	11.66	1048.17	0.97 (0.27)	-2.04 (0.75)	5.55 (1.43)	—	7.26 (2.94)	1.39 (0.95)	2.74 (0.83)	1.82 (0.11)	0.73	0.73
Temperature*Overwintering location + SST (weekly) + Species	1081.96	27.40	1065.92	—	-1.89 (0.72)	4.06 (1.40)	—	6.11 (3.00)	1.13 (0.88)	2.59 (0.79)	1.80 (0.12)	0.31	0.31
SST (weekly)*Overwintering location + Species	1095.87	41.31	1081.84	—	—	5.35 (2.92)	—	4.64 (3.51)	0.74 (1.69)	-0.79 (3.20)	1.89 (0.12)	0.66	0.66
SST*Overwintering location + Species	1110.72	56.16	1096.69	—	—	11.09 (6.39)	—	5.64 (5.40)	-3.15 (3.09)	-9.07 (6.39)	1.92 (0.12)	0.79	0.79
Photoperiod*Overwintering location + Species	1128.48	73.92	1114.45	—	—	—	-2.72 (0.68)	1.14 (0.70)	2.04 (0.76)	1.13 (0.58)	-0.10 (0.88)	0.24	0.34
Temperature*Overwintering location + Species	1240.14	185.58	1226.11	—	-2.02 (0.39)	—	—	1.00 (0.44)	0.52 (0.39)	2.05 (0.41)	1.06 (0.30)	0.11	0.11
Discharge*Overwintering location + Species	1250.51	195.96	1238.49	-1.19 (0.16)	—	—	—	0.70 (0.29)	-0.33 (0.26)	0.81 (0.19)	—	0.04	0.05
Discharge (weekly)*Overwintering location + Species	1251.01	196.45	1238.99	-1.12 (0.15)	—	—	—	0.67 (0.28)	-0.34 (0.25)	0.73 (0.18)	—	0.04	0.04
Temperature (weekly)*Overwintering location + Species	1258.42	203.87	1246.40	—	-1.05 (0.16)	—	—	0.32 (0.41)	-0.06 (0.34)	1.30 (0.20)	—	0.03	0.09
SST (weekly rate)*Overwintering location + Species	1275.08	220.52	1263.06	—	—	-0.50 (0.23)	—	0.00 (0.38)	-0.87 (0.31)	0.99 (0.24)	—	0.03	0.07
Temperature (weekly rate)*Overwintering location + Species	1284.88	230.33	1272.86	—	-0.53 (0.14)	—	—	0.05 (0.39)	-0.50 (0.31)	0.08 (0.18)	—	0.02	0.07
Discharge (daily rate)*Overwintering location + Species	1315.25	260.70	1303.23	-0.15 (0.16)	—	—	—	-0.05 (0.42)	-0.83 (0.32)	0.10 (0.20)	—	0.01	0.08
Discharge (weekly rate)*Overwintering location + Species	1315.85	261.29	1303.83	0.01 (0.16)	—	—	—	-0.08 (0.42)	-0.79 (0.32)	0.07 (0.20)	—	0.01	0.08
Null	1318.56	264.00	1314.56	—	—	—	—	—	—	—	—	0.00	0.08

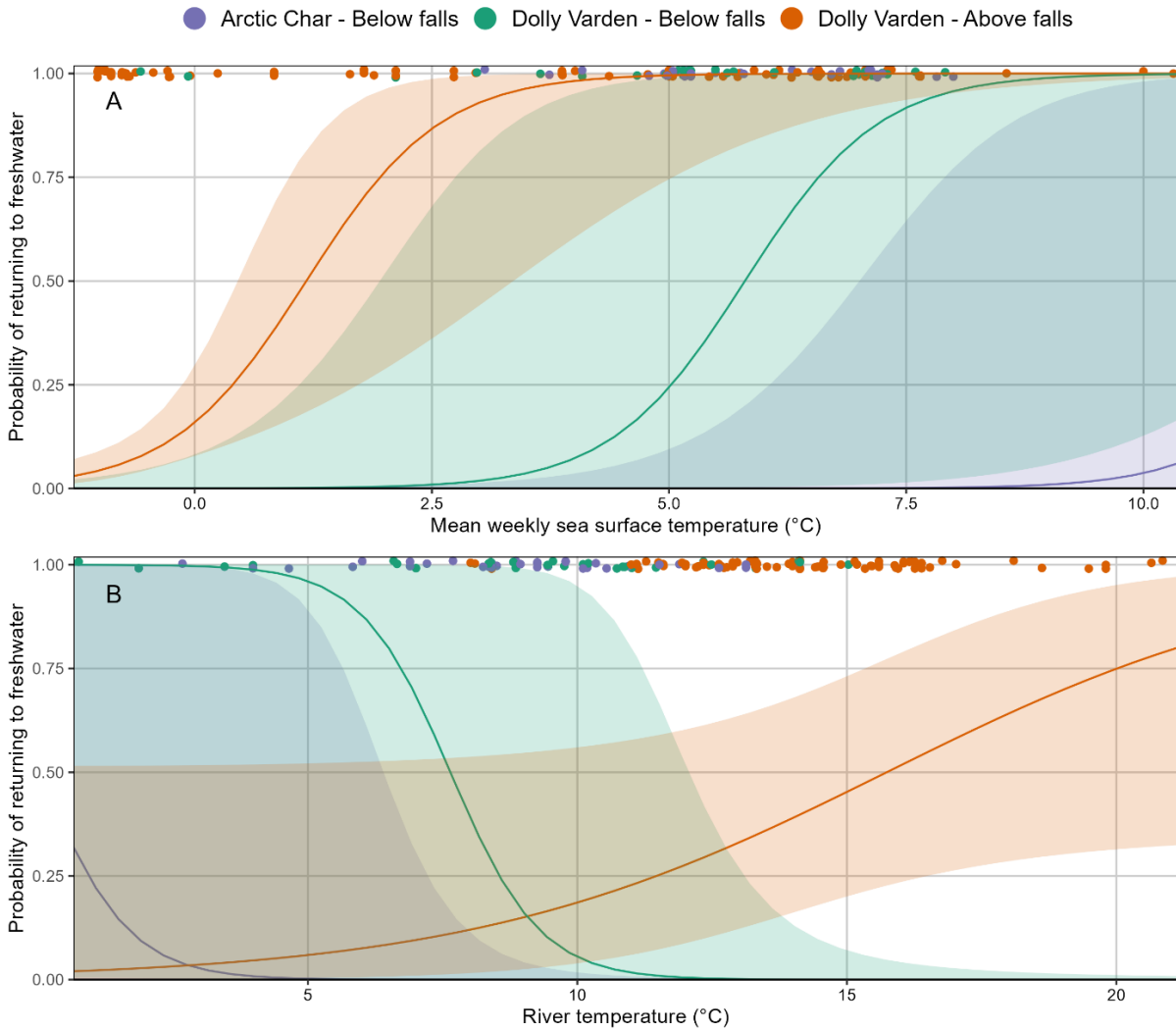


Figure 4.3: The relationship between probability of returning to fresh water (1 = return, 0 = no return) and A) Sea surface temperature and B) River temperature. Relationships are for the highest ranked model ($\text{Return} \sim \text{SST (weekly)} + \text{River temperature (daily)} * \text{Overwintering location} + \text{Discharge (daily)} + \text{Photoperiod} * \text{Overwintering location} + \text{Species}$) with other variables held at the mean value (e.g., the mean values of River temperature, Discharge, and Photoperiod were held constant for the plot of SST in A). The effects of random factor (individual ID) and zero-inflation are not shown. Shaded areas indicate 95% confidence intervals. Points indicate the conditions when fish were observed returning to fresh water. Note that points are jittered (height = 0.01) around the y-axis. The ranges of the x axes indicate the minimum and maximum values of SST (A) and river temperature (B) that were observed during the study periods.

warm or warming (Figure B2 in Appendix B). The highest ranked model included an interaction between mean daily river temperature and overwintering location, which resulted in a positive relationship between river temperature and probability of return to fresh water for Dolly Varden that overwintered above the falls (Figure 4.3B). Fish that overwintered above the falls thus had a higher probability of returning to fresh water when river temperatures were warmer, while fish that overwintered below the falls had a higher probability of returning to fresh water when river temperatures were colder. There was a positive relationship between mean daily discharge and probability of returning to fresh water in the highest ranked model, but the relationship was inconsistent in other models that included mean daily discharge (Table 4.1), likely due to drastic differences in discharge among years (Figure B3 in Appendix B). The model coefficients for photoperiod were consistently negative (Table 4.1); fish had a higher probability of returning when photoperiod was shorter (i.e., later in the year, because all observations occurred after the summer solstice each year). The highest ranked model included a positive interaction between photoperiod and overwintering location; fish that overwintered above the falls had a higher probability of return when photoperiod was longer (i.e., earlier in the year) than fish that overwintered below the falls.

4.4.2.2 Ascension of falls

The AICc scores of the generalized linear mixed models with photoperiod or day of year were similar to that of the null model, which indicated there was little evidence that day length or time of year were cues to ascend the falls. Daily mean discharge was the best discharge predictor of ascension of falls in generalized linear mixed models (Table 4.2). Weekly rate of change of river temperature was the best temperature predictor. The model with the highest rank (lowest AICc score) included both daily mean discharge and rate of change of river temperature. The ΔAICc between the highest and second highest ranked models was 11.05, which indicated a clear top model. The coefficient for daily mean discharge was negative (Table 4.2), both in the top model and in the model with daily mean discharge as the single environmental variable, which suggested that fish were more likely to ascend the falls when discharge was lower, although we observed Dolly Varden ascending the falls at both the minimum ($178 \text{ m}^3\text{s}^{-1}$) and maximum ($1020 \text{ m}^3\text{s}^{-1}$) discharge values observed during the study period. The coefficient for weekly rate of change of river temperature was negative (Table 4.2), which suggested that fish were more likely to ascend the falls during periods of cooling river temperatures. Despite the low AICc score of the highest ranked model, the marginal R^2 was only 0.036 (Table 4.2), which suggested that none of the models adequately explained the likelihood of fish ascending the falls.

Table 4.2: Generalized linear mixed models (logit link) relating ascension of falls to environmental variables. The null model includes only the random factor of fish ID. AICc scores were used to rank models. Models are presented in order of increasing AICc or decreasing rank. Model deviance (-2l) is -2log-likelihood. Coefficients apply to scaled and centred variables. Note that only marginal R² (fixed factors only) values are provided because conditional R² (both fixed and random factors) values were effectively equivalent to marginal R² values (i.e., negligible effect of random factor).

Model	AICc	Δ AICc	-2l	Coefficient estimates ($\pm$ standard error)			Marginal R ²
				Discharge	Temperature	Photoperiod/ Day of year	
Discharge (daily) + Temperature (weekly rate)	640.57	0	632.52	-0.45 (0.12)	0.37 (0.10)	—	0.036
Discharge (daily)	651.62	11.05	645.59	-0.45 (0.12)	—	—	0.022
Discharge (weekly)	653.47	12.90	647.44	-0.42 (0.11)	—	—	0.019
Temperature (weekly rate)	654.29	13.72	648.26	—	0.39 (0.11)	—	0.016
Temperature (daily)	663.22	22.65	657.19	—	0.23 (0.10)	—	0.006
Discharge (weekly rate)	664.13	23.56	658.10	-0.21 (0.11)	—	—	0.005
Discharge (daily rate)	665.40	24.83	659.37	-0.18 (0.11)	—	—	0.004
Photoperiod	665.74	25.17	659.71	—	—	0.16 (0.10)	0.003
Null	666.10	25.53	662.09	—	—	—	0
Day of year	666.77	26.20	660.74	—	—	-0.12 (0.10)	0.002
Temperature (weekly)	667.14	26.57	661.11	—	0.10 (0.10)	—	0.001

4.4.3 Cyclical environmental drivers of migration timing

4.4.3.1 Return to fresh water

Fish that overwintered below the falls were more likely to return to fresh water at certain times of day, tidal phase, and lunar phase, whereas fish that overwintered above the falls were more likely to return to fresh water only at certain lunar phases. Rayleigh tests of uniformity indicated that time of day, tidal phase, and lunar phase of return to fresh water of fish that overwintered below the falls ($n = 44$) were significantly different from uniform (i.e., non-random; resultant length (r) ≥ 0.348 , $p \leq 0.004$; Figure 4.4). For Dolly Varden that overwintered above the falls ($n = 55$), only lunar phase of return to fresh water was significantly different from uniform ($r = 0.238$, $p = 0.044$); both Rayleigh and modified Hermans-Rasson tests indicated that time of day and tidal phase were not significantly different from uniform (Rayleigh: $r \leq 0.096$, $p \geq 0.60$; Hermans-Rasson: $T \leq 2.35$, $p \geq 0.68$).

Fish that overwintered below the falls were more likely to return to fresh water at two times of day (early evening and mid-morning) and at flooding high tide; patterns in lunar phase of return to fresh water were less defined for fish of both overwintering locations (Figure 4.4). For fish that overwintered

below the falls, homogenous bimodal (two modes with different sizes but equal concentrations) was the most likely model of circular orientation for time of day that fish returned to fresh water (Table 4.3). There was little support for a bimodal (two modes with different sizes and concentrations) model, which was the second most likely model. The circular means of the two modes were 8:23 and 17:36 (Figure 4.4). Symmetric modified unimodal (half oriented in the same direction and half oriented uniformly or randomly) and unimodal were the most likely models for tidal phase (Table 4.3). The circular mean was 170° (flooding high tide; Figure 4.4). Bimodal and homogenous bimodal were the most likely models for lunar phase (Table 4.3). Circular means of the two modes were 32° (waxing crescent) and 155° (waxing gibbous; Figure 4.4). For Dolly Varden that overwintered above the falls, the most likely models for lunar phase ($\Delta\text{AICc} \leq 2$) included both bimodal and unimodal models. Circular means of the two modes in the highest ranked bimodal model were 126° (waning crescent) and 306° (waxing gibbous; Figure 4.4). The circular mean of the highest ranked unimodal model was 304°. Watson's U^2 test indicated that differences in lunar phase of return to fresh water did not differ significantly among years for either overwintering location ($U^2 \leq 0.1861$, $p \geq 0.15$), although lunar phase of return of Dolly Varden overwintering above the falls would have differed significantly between 2019 and 2020 without the application of a Bonferroni correction ($U^2 = 0.2868$, $p = 0.08$ after correcting for 8 comparisons).

Table 4.3: Most likely models of circular orientation for variables that were significantly different from uniform. Models are presented in order of increasing AICc or decreasing rank within each variable and group. The highest ranked model for each variable and group is shown, along with the second highest ranked model and any models with ΔAICc values ≤ 2 .

Response	Group	Variable	Model	AICc	ΔAICc
Return to fresh water	Below falls	Time of day	Homogenous bimodal	151.05	0
			Bimodal	153.59	2.54
		Tidal phase	Symmetric modified unimodal	154.72	0
			Unimodal	154.74	0.02
	Dolly Varden, Above falls	Lunar phase	Bimodal	143.46	0
			Homogenous bimodal	143.58	0.12
			Homogenous axial bimodal	198.06	0
			Symmetric modified unimodal	198.64	0.57
		Lunar phase	Axial bimodal	199.15	1.09
			Symmetric bimodal	199.58	1.52
		Time of day	Unimodal	260.42	0
			Symmetric modified unimodal	261.29	0.87
Falls ascension	Dolly Varden, Above falls	Tidal phase	Symmetric modified unimodal	260.87	0
			Unimodal	261.26	0.39

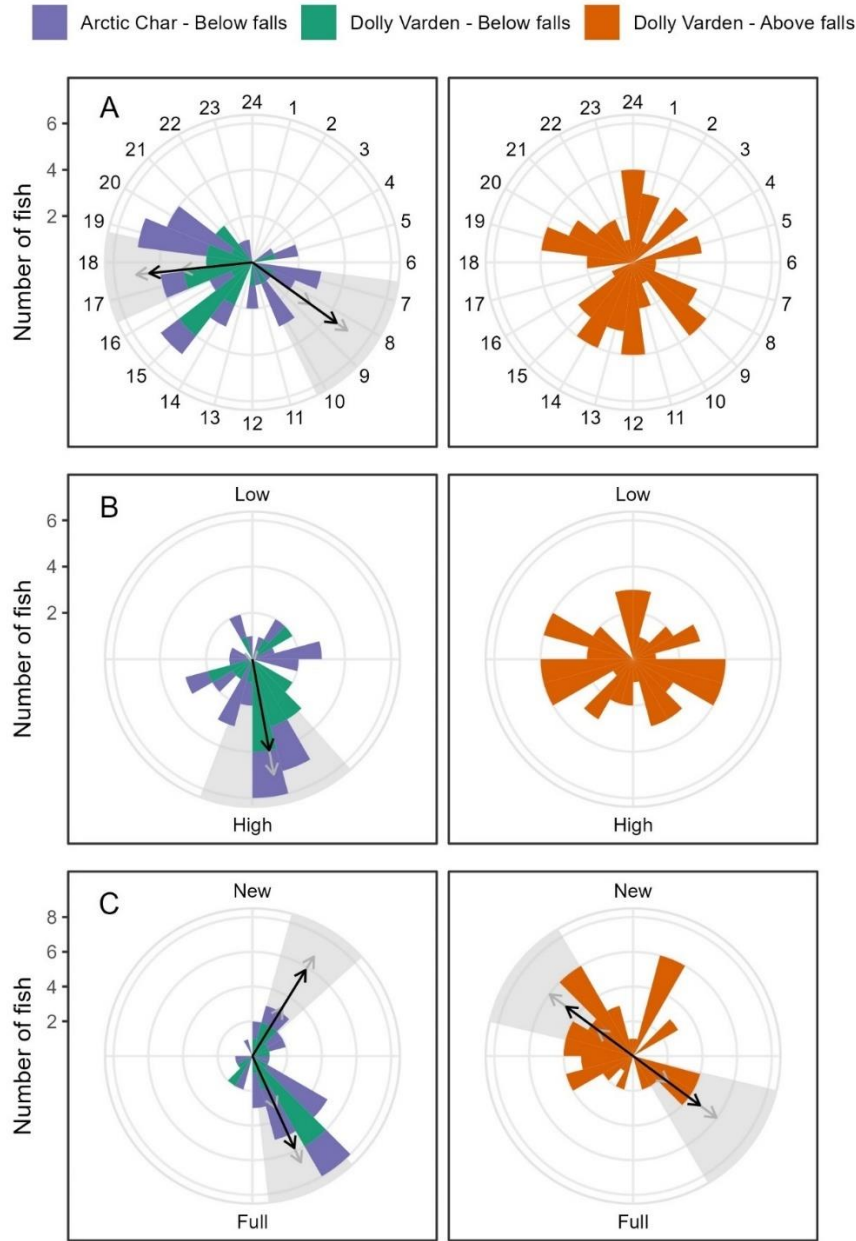


Figure 4.4: Circular histograms of return to fresh water at A) Time of day; B) Tidal phase; and, C) Lunar phase. Grey shading indicates 95% confidence intervals of the directional means. Black arrows indicate the resultant lengths of the directional means and grey arrows indicate the 95% confidence intervals of the resultant lengths. Note that means and resultant lengths are only displayed when observations differed significantly from uniform (i.e., observations were non-random).

Monte Carlo analysis indicated that fish that overwintered below the falls were not significantly more likely to return to fresh water in daylight than would occur randomly ($p = 0.07$). Conversely, Dolly Varden that overwintered above the falls were significantly more likely to return to fresh water in daylight than would occur randomly ($p = 0.008$).

4.4.3.2 Ascension of falls

Dolly Varden were more likely to ascend the falls in late evening and at ebbing high tide. Rayleigh tests of uniformity indicated that time of day and tidal phase of falls ascension ($n = 77$) were significantly different from uniform ($r \geq 0.402$, $p \leq 0.001$; Figure 4.5). Both Rayleigh and modified Hermans-Rasson tests indicated that lunar phase was not significantly different from uniform (Rayleigh: $r = 0.193$, $p = 0.06$; Hermans-Rasson: $T = 4.55$, $p = 0.22$). Unimodal and symmetric modified unimodal were the most likely models of circular orientation for time of day that fish ascended the falls (Table 4.3). The circular mean was 20:20 (Figure 4.5). Similarly, symmetric modified unimodal and unimodal were the most likely models for tidal phase. The circular mean was 220° (ebbing high tide; Figure 4.5). Monte Carlo analysis indicated that fish were not significantly more likely to ascend the falls in daylight than would occur randomly ($p = 0.40$).

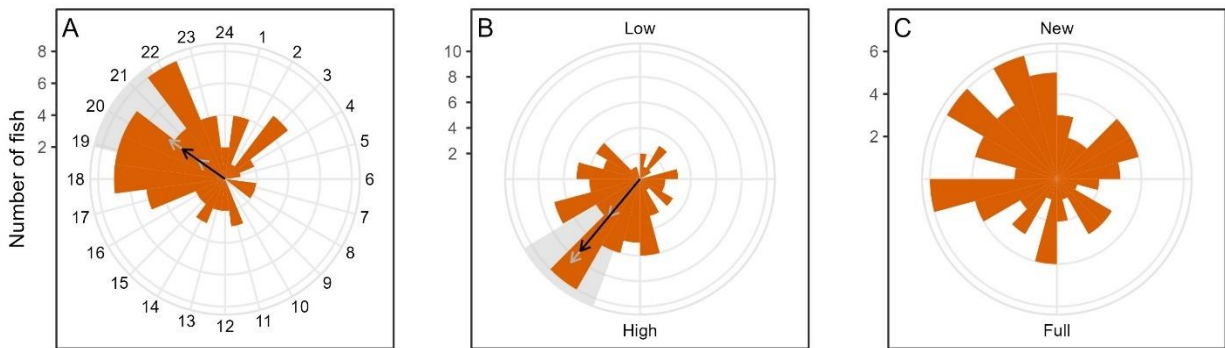


Figure 4.5: Circular histograms of falls ascension at A) Time of day; B) Tidal phase; and, C) Lunar phase. Grey shading indicates 95% confidence intervals of the directional means. Black arrows indicate the resultant lengths of the directional means and grey arrows indicate the 95% confidence intervals of the resultant lengths. Note that means and resultant lengths are only displayed when observations differed significantly from uniform (i.e., observations were non-random).

4.5 Discussion

4.5.1 Linear environmental drivers of migration timing

4.5.1.1 Return to fresh water

Mean weekly sea surface temperature was the best single environmental predictor of return to fresh water. SST was a substantially better predictor of return to fresh water than photoperiod. As photoperiod is invariant among years, these results suggest that timing of return varies among years in response to environmental conditions, which is consistent with our observation that fish returned to fresh water considerably earlier in 2023 than in other years; in 2023, break-up of river ice and warming of SST occurred earlier. Mean weekly SST was positively associated with return to fresh water (i.e., fish were more likely to return when mean weekly SST was warmer), but the threshold differed between species and overwintering locations. Dolly Varden that overwintered above the falls returned to fresh water at colder SST than fish that overwintered below the falls. To our knowledge, return to fresh water has not been associated with SST for Arctic Char, although Inuit knowledge in the eastern Canadian Arctic indicates that Arctic Char move upstream when ocean temperatures cool (Dubos et al. 2023). The only study of SST and migration timing of Dolly Varden was conducted in six Alaskan river systems (Bond and Quinn 2013). Relationships between SST and return to fresh water of southern form Dolly Varden (*S. m. lordi*) were inconsistent (two positive, two negative), and no relationship was observed between SST and return of northern form Dolly Varden (note that we inferred subspecies from geographical information in Bond and Quinn (2013) and distribution information in the recent review by Weinstein et al. (2024)). SST as a cue for return to fresh water thus appears variable among systems but remains understudied for *Salvelinus* spp. Previous researchers who used long-term datasets (20+ years) of Atlantic Salmon and Pacific salmon (*Oncorhynchus* spp.) returns found that fish returned earlier when SST was warmer (Rivinoja et al. 2001; Dahl et al. 2004; Mundy and Evenson 2011; Kovach et al. 2015), but others found inconsistent relationships (Summers 1995; Juanes et al. 2004; Hodgson et al. 2006). Pacific salmon are typically semelparous (i.e., return to fresh water once before dying) and migration timing is highly heritable (McClure et al. 2008). Shifts in migration timing of these species with SST, particularly over long-term studies, may therefore represent adaptive selection. Conversely, our data indicate short-term plasticity in response to inter-annual variability of SST; further investigation is required to ascertain if the observed plasticity is adaptive.

Photoperiod was the second-best single environmental predictor of return to fresh water (after SST) and was also included in the highest ranked model as an interacting factor with overwintering location. The negative relationship we observed between probability of returning to fresh water and photoperiod was not surprising, because all fish returned to fresh water after the summer solstice (when photoperiod was negatively correlated with day of year). The interaction between photoperiod and overwintering location indicated that fish that overwintered above the falls had a higher probability of returning to fresh water when photoperiod was longer compared to fish that overwintered below the falls. This result is consistent with our previous observation that fish that overwintered above the falls in this system returned to fresh water earlier than fish that overwintered below the falls, and may reflect differences in the length and difficulty of migration paths (Smith et al. 2024; Chapter 3). Arctic Char may overwinter in locations with shorter or less difficult migration paths in non-spawning years (Moore et al. 2017). Spawning and/or overwintering locations above the falls are unknown, but early return to fresh water may be “making the best of a bad situation” (Quinn et al. 2016), wherein fish return early to avoid inaccessible environmental conditions. For instance, Arctic Char have adapted to return to fresh water early at Nulahugyuk Creek, Nunavut, where low water levels later in the season prevent access to spawning grounds (Gilbert et al. 2016). If fish overwinter above the falls in spawning years, photoperiod may act as a cue for spawning individuals to return to fresh water early, thus allowing more time to ascend the falls and migrate longer distances, as well as avoid potential inaccessible conditions.

The highest ranked model included an interaction between river temperature and overwintering location. Although SST was the primary driver for return to fresh water, both Arctic Char and Dolly Varden that overwintered below the falls were more likely to return to fresh water when river temperatures were colder (later in the year), whereas Dolly Varden that overwintered above the falls were more likely to return when river temperatures were warmer (earlier in the year). Temperature has been associated with the outmigration of juvenile Dolly Varden to the ocean (Kovach et al. 2013) and with the upstream migration of riverine (non-anadromous) adult Dolly Varden (Koizumi and Maekawa 2003), but not with adult anadromous Dolly Varden. No relationship was found between number of upstream migrant Arctic Char and temperature in Labrador, Canada (Dempson and Green 1985), but the measurement location was 65 km upstream and migrant arrival may have reflected swimming conditions in the river rather than cues for return to fresh water. Berg and Berg (1993) observed a relationship between temperature and duration of marine residency of Arctic Char, but it is unclear if the relationship was due to earlier entry into the marine environment or later return to fresh water. To

our knowledge, our findings thus represent the first description of return to fresh water and river temperature for anadromous Arctic Char and Dolly Varden, although tracking return to fresh water over additional years with similar SST but varying river temperatures is necessary to definitively illustrate the relationship between return to fresh water and river temperature.

River temperature may cause adverse conditions that influence return migration. It has been suggested that Bull Trout (*Salvelinus confluentus*; Goetz et al. 2021) and Sockeye Salmon (*Oncorhynchus nerka*; Hodgson and Quinn 2002) adjust the timing of return migration to avoid warm river temperatures. Thermal tolerance of Dolly Varden is unstudied but is likely similar to that of Arctic Char. Previous researchers have observed cardiac arrhythmia in migrating adult Arctic Char at 15°C (Mottola et al. 2020) to 21°C (Gilbert et al. 2020), and impairment of post-exercise recovery at 16°C (Gilbert et al. 2020). Acclimation to warmer temperatures can improve performance of Arctic Char at elevated temperatures (Gilbert et al. 2022), but even extended acclimation periods at 18°C can result in mortality (Gilbert and Farrell 2021). Dolly Varden that overwintered above the falls thus returned to fresh water at river temperatures that were likely stressful; some individuals were in the river when temperatures exceeded 20°C in 2023, the same year that SST increased earlier than in other study years and likely caused early return to fresh water. High mortality rates have been observed for Sockeye Salmon in the Fraser River, Canada, due to earlier timing of return migration and warmer river temperatures (Hinch et al. 2012), and a warning of similar impacts has been issued for Pink Salmon (*Oncorhynchus gorbuscha*) in Alaska (Taylor 2008). Dolly Varden that overwinter above the falls in the Coppermine River may also experience higher mortality rates if SST is the primary cue to return to fresh water, if river temperatures warm earlier and to a greater extent, and if SST becomes further decoupled from suitable river temperatures.

Fish were more likely to return to fresh water when discharge was higher, although the relationship was weak and inconsistent among models. Inuit knowledge in the eastern Canadian Arctic indicates that Arctic Char wait for higher water levels to facilitate access to upstream locations (Dubos et al. 2023) and riverine Dolly Varden have been observed moving into upstream tributaries when discharge increases (Koizumi and Maekawa 2003). The return of anadromous Dolly Varden to salmon-bearing systems, however, was most closely associated with the return of Pacific salmon and the associated food source of salmon eggs, rather than discharge or river temperature (Sergeant et al. 2015; Bell et al. 2017). There has been great historical interest in the response of salmonids to flooding, and artificial floods have even been used to trigger the upstream migration of Atlantic Salmon (see Banks 1969). Return migration has

been positively related to high discharge (or precipitation as a proxy for discharge) for other species in the family Salmonidae (e.g., MacCrimmon and Gordon 1981; Quinn and Adams 1996; Kovach et al. 2015), but inconsistent relationships have been observed (e.g., Jonsson and Jonsson 2002; Dahl et al. 2004; Juanes et al. 2004; Davidsen et al. 2013). The relationship between discharge and return to fresh water may depend on the size of the river. In smaller rivers, fish may need to wait for higher discharge to access upstream locations (Jonsson et al. 2007) and homing may be facilitated when discharge is higher and there is a larger freshwater signal for olfactory navigation, which has largely been established as the mechanism for homing of salmonids (Bett and Hinch 2016). In large rivers such as the Coppermine, the relationship between discharge and return to fresh water may be weaker if baseline discharge is typically sufficient for access and olfactory navigation. We observed highly variable discharge values among years and there are concerns from community members in Kugluktuk that water levels are decreasing (E. Hitkolok and A. Dumond, pers. obs.). Discharge may become more important for return migration if water level and discharge decrease in the future.

The highest ranked models were best fit and passed residual tests when zero-inflation was included. For results of zero-inflated models to be meaningful, there must be a proposed process that generated the number of zeros in the dataset (Zuur and Ieno 2021). We suggest that the zero-inflation reflects days when conditions were suitable for returning to fresh water but the fish did not return on those days and instead returned later in the year. Fish may not have returned immediately upon occurrence of a given cue if they were simply too far from the river to detect the cue (for river temperature or discharge) or if it took a long time to travel to the river once the cue was received (for SST or photoperiod). An alternative explanation is that fish received environmental cues but did not return because body condition was low. Migration timing likely involves balancing risks and benefits, where fish in poor condition stay in the marine environment longer to feed (Quinn et al. 2016). Jorgensen and Johnsen (2014) suggested that Arctic Char return to fresh water when they receive physiological cues of body condition. If the decision to spawn is also triggered by body condition early in the season, as suggested by Dutil (1986), and if spawners migrate above the falls (as discussed above), then body condition could also be related to timing of return migration indirectly through spawning status. Todd et al. (2012) observed that Atlantic Salmon returned to fresh water later when body condition was lower. Similarly, Moore et al. (2016) observed a negative relationship between body condition and marine duration of Arctic Char, but did not observe a relationship between body condition and date of marine entry or date of return to fresh water, and Hollins et al. (2022) did not observe a relationship between body condition

and time that Arctic Char left their marine feeding grounds (to return to fresh water). Both these studies (and the current study) only measured body condition at the time of tagging. The weight of Arctic Char may almost double within a single season of marine foraging (e.g., Mathisen and Berg 1968; Jørgensen et al. 1997), and measurements of body condition are likely to be invalid relatively soon after tagging. A comprehensive evaluation of the effect of body condition, spawning status, or other physiological processes on migration timing would likely require advancements in biologging technology.

4.5.1.2 Ascension of falls

Environmental variables did not satisfactorily explain the probability of Dolly Varden ascending the falls. Weak relationships were observed between ascension of the falls and each of discharge and temperature; AICc values indicated that models with these variables were better than the null model, but R^2 values suggested that all models fit the data poorly. To our knowledge, no studies of Arctic Char or Dolly Varden ascending obstacles have been conducted, but our results contrast with findings that discharge influenced the ascension of some obstacles by Atlantic Salmon (Jensen et al. 1986; Erkinaro et al. 1999; Lennox et al. 2018). We observed Dolly Varden ascending the falls at both the minimum and maximum discharge values observed during the study period. In the Coppermine River, higher discharge rates may both hinder and benefit Dolly Varden in ascending the falls. It may be more challenging to ascend against higher discharge, but higher discharge also coincides with higher water levels, which makes additional resting habitats available along the margins of the falls. Additional space in the water column may also prevent traumatic injuries from fish colliding with the substrate (E. Hitkolok, pers. obs.). This trade-off may obscure or negate the relationship between discharge and ascension.

River temperature has been shown to be important for other salmonids ascending obstacles such as waterfalls, fish ladders, dams, and weirs. Atlantic Salmon (Gerlier and Roche 1998; Gowans et al. 1999; Kennedy et al. 2013; Kristinsson et al. 2015) and Brown Trout (*Salmo trutta*; Rustadbakken et al. 2004) ascended obstacles when river temperatures exceeded thresholds of 8.4–10.5°C, likely due to physiological constraints at colder temperatures. Conversely, Atlantic Salmon have been observed to halt or delay migration when river temperatures were too warm (Baisez et al. 2011). Dolly Varden that overwintered above the falls returned to fresh water when temperatures were typically above the minimum thresholds observed for other species (range = 8.0–20.9°C, median = 14.0°C). All fish that experienced mean daily temperatures $\geq 20^\circ\text{C}$ ascended the falls within 1.4 days (less than the first quartile) of returning to fresh water, which suggests that warm river temperatures did not delay

migration. The high correlation and short interval that we observed between date of return to fresh water and date of falls ascension suggests that once fish have returned to fresh water, they make directed upstream movements that are largely unhindered by temperature or other environmental variables.

4.5.2 Cyclical environmental drivers of migration timing

4.5.2.1 Return to fresh water

Fish that overwintered below the falls returned to fresh water at non-random times of day and tidal phases. During the study period, there was typically a single high tide each day, with a circular mean time of $\sim 17:00$ ($r = 0.6477$, $p < 0.001$). The best model of circular orientation for time of day was bimodal, whereas the best model for tidal phase was unimodal. Tidal phase is thus likely a stronger predictor of timing of return to fresh water. Arctic Char exhibit changes in uptake of ions by the gills in preparation for return to fresh water (Bystriansky et al. 2007) and may adjust movements in response to salinity (Spares et al. 2012). The effect of tides on salinity in the study area is unknown because salinity measurements and/or modeling is not available, but large inputs of fresh water from the Coppermine River result in a surface layer of fresh water (E. Hitkolok, pers. obs.) that is available for acclimation of migrating fish before returning to the river. It is thus likely that association of return with tidal phase is due to changes in water level and direction or strength of water movement, rather than salinity. Return to fresh water of fish overwintering below the falls was more likely to occur at flooding high tide, which is consistent with other reports that Arctic Char returned to fresh water at high tide (Andrews and Lear 1956; Dubos et al. 2023). In contrast, Dolly Varden that overwintered above the falls returned to fresh water at random times of day and tidal phases. Timing of falls ascension was highly correlated with timing of return to fresh water, which suggests that Dolly Varden that overwintered above the falls returned to fresh water with intent to migrate above the falls. It may be that the drive to migrate above the falls superseded daily environmental cues such as tide, whereas fish that overwintered below the falls returned to fresh water more passively and were directed towards the river by flooding tidal currents. The observation that all fish that returned temporarily to fresh water subsequently overwintered below the falls is also consistent with the suggestion that fish that overwintered below the falls made more passive movements and fish that overwintered above the falls made more directed movements.

Dolly Varden that overwintered above the falls preferentially returned to fresh water in daylight. Fish that overwintered below the falls did not preferentially return to fresh water in daylight, which again suggests that fine-scale timing of return was more passive for these individuals. There was no relationship between light and return to fresh water of southern form Dolly Varden in Alaska (Bond and Quinn 2013), but Sockeye Salmon have been observed to return to fresh water at night to avoid predators (Bentley et al. 2014). Predation by Grizzly Bears (*Ursus arctos horribilis*) is uncommon, and individuals returning to the Coppermine River were sufficiently large that their only marine predators were likely Ringed Seals (*Pusa hispida*), which have been observed in and near the Coppermine River but are unlikely to be present in high numbers (E. Hitkolok and A. Dumond, pers. obs.). It may be that, in the absence of notable predation pressure, fish that overwintered above the falls were more likely to return to fresh water in daylight when visibility facilitated navigation.

The moon can also provide light for navigation. Lunar phase of return to fresh water was significantly non-random for both overwintering groups, but observations were bimodal and modes did not align with possible explanations, such as light. The bimodal relationship may be due to the interaction between lunar phase and height of tides; spring tides (i.e., tides with higher ranges) occur around the new and full moons. Although comparisons of observations among years indicated there were no significant differences in lunar phase of return to fresh water among years, sample sizes for comparisons were small; larger sample sizes may reveal that significance of lunar phase was due to arbitrary coincidence with peak return in years with more observations. Increased sample sizes and a longer-term dataset is required to better understand the relationship between light, lunar phase, tidal height, and timing of return to fresh water.

4.5.2.2 Ascension of falls

Time of day and tidal phase that Dolly Varden ascended the falls were non-random. Due to the correlation between time of day and tidal phase, it is difficult to determine which was the cause of the observed pattern. The observed pattern for time of day was not likely due to available light; most Dolly Varden ascended the falls in daylight, but not statistically more than would be expected given the amount of daylight available. There were no major predators near the falls that may have affected the timing of migration, with the potential exception of local fishers who catch fish by snagging as they ascend the falls. Fishing pressure is possible but unlikely to be the cause of the observed pattern in time of day, because fishing pressure is typically higher in the evening, at a similar time to when fish were

observed ascending the falls. The observed patterns for time of day were likely due to the correlation between tidal phase and time of day.

A section of rapids is located between the falls and the receiver that recorded the time of falls ascension, so we could not identify the exact time that fish succeeded in ascending the falls. We also could not identify when the fish began ascent because the receiver located at the base of the falls did not capture detections (i.e., departure times) from all fish that migrated upstream, likely due to the large amount of noise from the falls. It is reasonable to assume there was a delay between ascending the falls and reaching the upstream receiver, so the times of ascension were probably earlier than what was recorded. Ascension thus likely occurred at flooding high tide. Arctic Char in the Sylvia Grinnell River have been reported to stage below a waterfall before ascending at high tide (VanGerwen-Toyne et al. 2013). Although the tidal amplitude is much lower in Coronation Gulf (Coppermine River, maximum range of 0.54 m) than Frobisher Bay (Sylvia Grinnell River, minimum range of ~ 3.5 m; Canadian Hydrographic Service 2022b) and salt water is rarely observed upstream of the river mouth (A. Dumond and E. Hitkolok, pers. obs.), there is a measurable tidal signal below the falls (Ikaarvik Coppermine River Monitoring youth group, unpublished data; pers. obs.). The increase in water level at high tide may facilitate ascension and create more accessible resting habitat along the margins of the falls.

4.5.3 Conclusions

Overwintering location (above or below the falls) had an important influence on return migration. Fish that overwintered below the falls, regardless of species, exhibited similar relationships to both linear and circular environmental drivers of return to fresh water. Fish that overwintered below the falls returned to fresh water later in the year, when SST was warm and river temperatures were cold. Return to fresh water of Dolly Varden that overwintered above the falls was also influenced by SST, but the cue was lower (i.e., colder, earlier in the year) than for fish that overwintered below the falls, which suggests that an internal cue also existed. Once the physiological and environmental cues to return to fresh water have been received by fish that overwinter above the falls, they may make directed movements towards the river and upstream; return to fresh water is largely unaffected by fine-scale temporal factors, such as tide. Conversely, the return to fresh water of fish that overwintered below the falls may be more passive; return to fresh water was influenced by tide.

Overwintering location has been shown to vary among years (i.e., some fish overwinter above the falls in one year and below the falls in another year (Smith et al. 2022)). The internal factors regulating the

SST cue for fish that overwintered above the falls were thus likely physiological rather than inherited, and could be associated with spawning status or body condition. Returning to fresh water at lower SST coincided with warmer river temperatures, at levels that were likely stressful for cold-acclimated fish navigating a challenging freshwater migration path. Warm river temperatures may have important implications for the survival and fitness of Dolly Varden that overwinter above the falls, particularly if spawning habitats are located above the falls and if river temperatures continue to warm from climate change. Despite warm river temperatures, neither environmental variables nor day of year explained ascension of the falls, although high tides may assist fish in ascending the falls. It is possible that environmental conditions prevented some individuals from ascending the falls altogether and they subsequently overwintered below the falls. Further research is required to identify the drivers of overwintering location, if overwintering location is pre-determined each year (e.g., based on spawning status), and if other movement characteristics (e.g., marine movements, staging periods) are consistent with the evidence for directed and passive movements that we observed.

Chapter 5

Return migration to fresh water and overwintering locations used by sympatric anadromous populations of Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma malma*)

5.1 Abstract

Anadromous Arctic Char (*Salvelinus alpinus*) and northern form Dolly Varden (*Salvelinus malma malma*) are highly valued by Indigenous communities in northern Canada. Rapid, ongoing environmental changes are affecting populations of both of these iteroparous species, and understanding variability in life history tactics is essential for assessment of current and future impacts. The Coppermine River, Nunavut, provides a unique opportunity to study anadromous life history types of Dolly Varden and Arctic Char that occur in sympatry in fresh water and have documented inter- and intra-specific variability in overwintering location. We used acoustic telemetry and physical samples from community collection programs to infer that Arctic Char overwintered in easily accessible habitats in the lower reaches of the Coppermine River, likely in non-spawning years, and that spawning likely occurs in rivers other than the Coppermine. Younger and smaller Dolly Varden overwintered in the river below a substantial obstacle (a large cascade), along with some larger adults that we suggest skipped spawning. Larger Dolly Varden, including potential spawners, migrated above the cascade and overwintered in the upper reaches of the Coppermine River. Arctic Char exhibited distinct patterns of return migration to fresh water that were consistent with intent to overwinter below the cascade. Dolly Varden that overwintered above the falls exhibited distinct patterns of return migration that were consistent with directed movements. Patterns of return migration to fresh water for Dolly Varden that overwintered below the cascade suggested some individuals intended to overwinter below the cascade, whereas others may have attempted to overwinter in the upper reaches of the river but failed to ascend the cascade. The patterns and variability we observed in overwintering location and return migration to fresh water have important implications for community-based management of the local fishery, provide insights into the ecology and adaptability of Arctic Char and Dolly Varden, and highlight a need for additional information regarding spawning locations and spawning frequency in this unique system.

5.2 Introduction

The Arctic is experiencing rapid and disproportionate environmental change (Rantanen et al. 2022). Concurrent shifts may be observed in life history traits such as iteroparity, which could become less favourable relative to semelparity if environmental changes result in a reduction in adult survival relative to juvenile survival (Charnov and Schaffer 1973; Hutchings 2021). Species that employ conditional strategies may experience particularly profound impacts of environmental change because their life history is determined by physiological state (Gross 1996), which, in turn, is influenced by environment. For instance, a shift in the prevalence of anadromous life histories (relative to freshwater-resident life histories) may be observed in Arctic environments because anadromy has been associated with high marine productivity relative to freshwater productivity (Gross et al. 1988) and/or characteristics of migratory pathways (Finstad and Hein 2012). Many Arctic species of fish are both iteroparous and anadromous (e.g., Arctic Char (*Salvelinus alpinus*), Arctic Cisco (*Coregonus autumnalis*), Broad Whitefish (*C. nasus*), Inconnu (*Stenodus leucichthys*); Scott and Crossman 1973; Coad and Reist 2018), and are also of cultural and economic importance (e.g., Van Oostdam et al. 2005; Tallman et al. 2019). There may be considerable variability in life history tactics within anadromy (e.g., frequency of migration, timing of return migrations) and iteroparity (e.g., repeat vs. skipped spawning). To evaluate the implications of environmental change on these important anadromous species in the Arctic and to inform fisheries management and conservation efforts, it is critical to understand the drivers and variability in life history tactics.

Arctic Char and northern form Dolly Varden (*Salvelinus malma malma*) are two closely related and iteroparous species. Both species are facultatively anadromous and the anadromous life history types are of particular importance for Indigenous communities in the Arctic in Canada (Priest and Usher 2004; Byers et al. 2019). Individuals from anadromous or partially anadromous populations of both species exhibit considerable variability in tactics and migration patterns among years, including skipped migrations (e.g., Radtke et al. 1996; Gallagher et al. 2018b) or cessation of anadromy (Bond et al. 2015), alternate-year or skipped spawning (Armstrong and Morrow 1980; Johnson 1980), and overwintering in non-natal habitats (e.g., Moore et al. 2013; Gilbert et al. 2016; Brown et al. 2019). The variability in life history tactics exhibited by Arctic Char and Dolly Varden is fascinating, and has allowed the two species to persist in diverse aquatic environments, but presents substantial challenges for conservation and fisheries management and necessitates location-specific data (e.g., Roux et al. 2011). Variability in overwintering location is of particular interest because spawning typically occurs shortly before

freeze-up in freshwater environments, environmental conditions may pose challenges for fishes attempting to access overwintering habitats, and the length and difficulty of migratory pathways have implications for fitness and survival through expenditure of energy reserves.

The Coppermine River in Nunavut, Canada, offers a unique opportunity to study drivers and variability in overwintering locations used by iteroparous, anadromous species of fish. The river (Chapter 4) and surrounding marine environment (Weinstein 2023) provide habitat for anadromous individuals of both Arctic Char and northern form Dolly Varden. The co-occurrence of anadromous life history types of both species is rare. In other documented sympatric populations (1200+ km west of the Coppermine River), Arctic Char are freshwater-resident and Dolly Varden are anadromous (DeLacy and Morton 1943; Craig 1977; Taylor et al. 2008; May-McNally et al. 2015; Dennert et al. 2016), with two possible exceptions (Becharof Lake drainage, Alaska: Scanlon 2000; Darnley Bay, Northwest Territories, ~ 400 km west of the Coppermine River: McNicholl et al. 2020). Findings from previous research indicate that anadromous Dolly Varden overwinter in both the upper reaches (above a large cascade) and the lower reaches (~ 17 km between the river mouth and the cascade) of the Coppermine River, and that overwintering location can vary among years for the same individual (Smith et al. 2022; note that Smith et al. refer to Arctic Char, but species was later confirmed to be Dolly Varden). Arctic Char have also been observed to overwinter in the lower reaches of the Coppermine River (Chapter 4). Whereas overwintering in fluvial environments is typical for Dolly Varden (Armstrong and Morrow 1980), it is uncommon for Arctic Char (Harwood and Babaluk 2014) in North America.

The fluvial environment in the lower reaches of the Coppermine River is unusual overwintering habitat for both species in that there are no known groundwater inputs (Smith et al. 2022). There is also no known spawning habitat in the lower reaches (i.e., below the cascade) of the Coppermine River; proximity to marine foraging (including under ice) and avoidance of a long, difficult migratory pathway in non-spawning years have been suggested as potential benefits of overwintering in the lower reaches (Smith et al. 2022). Failure to ascend the cascade may also explain why both species have been found overwintering in the lower reaches of the river, but drivers of overwintering in this unusual habitat, as well as drivers of inter-individual and inter-annual variability in overwintering location, are unknown.

Understanding inter-specific differences in return migration to fresh water and drivers of variability in overwintering locations used by Arctic Char and Dolly Varden is crucial to harvesters and fisheries managers in monitoring and ensuring the sustainability of this essential food source. Our overarching

objectives were to describe the variability in overwintering locations used by Arctic Char and Dolly Varden in the Coppermine River, and investigate potential explanations for why some fish overwinter in the fluvial environment (below the cascade) in some years. We proposed three hypotheses to explain why some fish in some years overwintered below the cascade: 1) fish overwintered below the cascade in years when they did not spawn because the migration is shorter and there is easier access (i.e., individuals that overwintered below the cascade were sexually immature or skipped spawning); 2) fish overwintered below the cascade because of closer proximity to feeding opportunities in the marine environment; and, 3) fish were unable to ascend the cascade due to swimming ability and/or environmental conditions. To assess the evidence for the first two hypotheses (spawning status and foraging opportunities), we used physical samples to: A) compare ages and lengths (as proxies of sexual maturity) of char that overwintered in the lower reaches (below the cascade) of the Coppermine River to those captured in the Coppermine River and surrounding marine environment during ice-free periods; B) examine fish captured in the lower reaches of the Coppermine River for evidence of spawning; and, C) assess potential for marine foraging during ice-covered periods. We used acoustic telemetry to evaluate patterns in return migrations to fresh water to ascertain whether fish that overwintered in the lower reaches of the Coppermine River intended to do so (hypotheses 1 and 2; spawning status and/or foraging opportunities), or whether they failed to ascend the cascade (hypothesis 3).

5.3 Methods

5.3.1 Study location

The Coppermine River flows into Coronation Gulf (Arctic Ocean), adjacent to the Hamlet of Kugluktuk (67.827° N, 115.093° W) in the Kitikmeot Region of Nunavut, Canada (Figure 5.1). Kugluk or Bloody Falls (hereafter, “the falls”) is located approximately 17 km upstream of the river mouth and is a large cascade that represents a challenging but passable obstacle for migrating species of fish (Figure 1.2). Date of river break-up ranged from 31 May to 21 June during the study period (2018 to 2023) and date of river freeze-up ranged from 01 October to 31 October (pers. obs.; Kugluktuk Ikaarvik youth group, unpublished data). There are no known inputs of groundwater between the falls and the river mouth (Smith et al. 2022). During the ice-covered season, there is no open water between the falls and the river mouth, but a mean winter discharge of $118 \text{ m}^3 \text{ s}^{-1}$ is maintained (Coulombe-Pontbriand et al. 1998). Although year-round data on the extent of the river plume are not available, the mean summer

discharge is $479 \text{ m}^3 \text{ s}^{-1}$ (Coulombe-Pontbriand et al. 1998), which represents a substantial input of fresh water to the nearby marine environment.

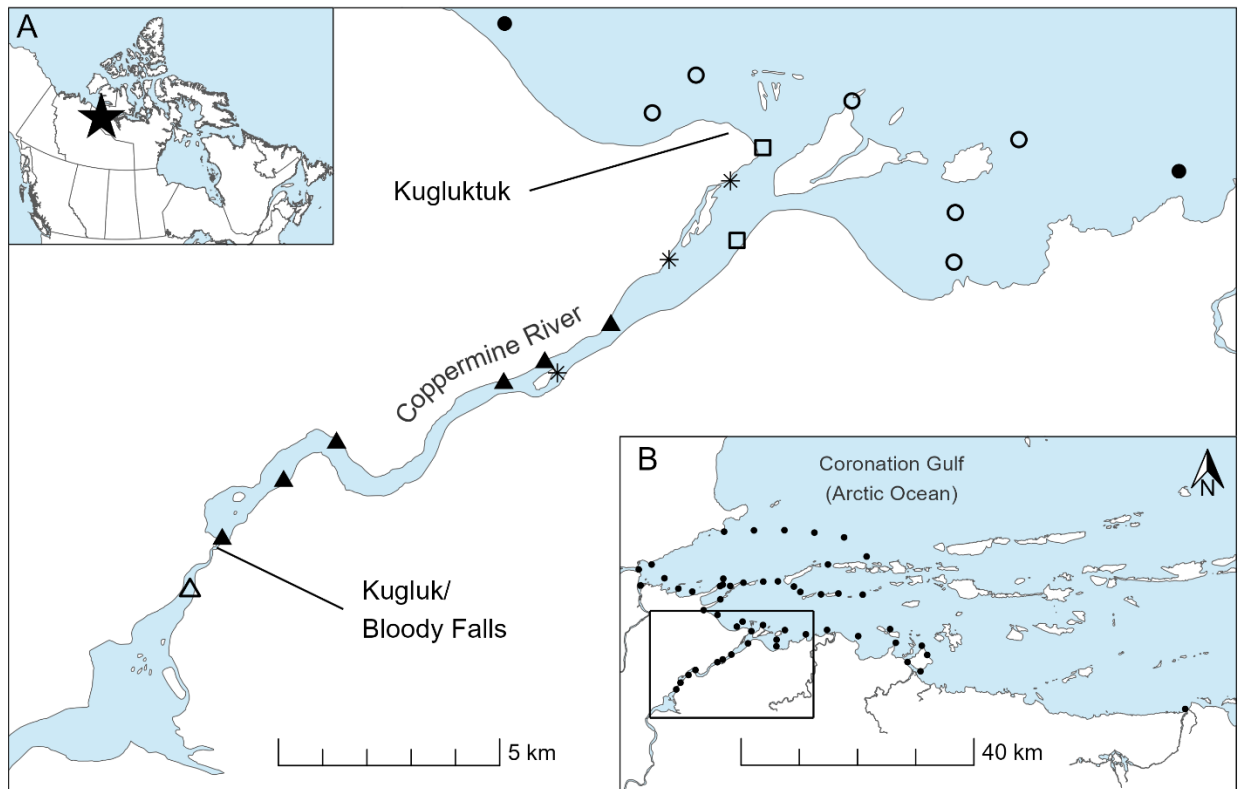


Figure 5.1: Map of acoustic telemetry receivers in and near the Coppermine River. Filled circles represent receivers located in marine waters, open circles represent receivers located within the river plume, open squares represent receivers located in fresh water at or near the mouth of the Coppermine River, filled triangles represent river receivers located below the falls, and the open triangle represents a receiver located above the falls. The asterisks represent the locations where fish ($n = 95$) were harvested by gillnets set below the ice in November–December 2021. Insets show location of the study area within Canada (A) and extended array of acoustic telemetry receivers (B; see Table C1 in Appendix C for complete details of receiver deployment). The geographic extent represented by inset (B) also indicates the area where samples from community collection programs were obtained. Shapefiles of Canada and United States boundaries were obtained from Statistics Canada (2016) and the United States Census Bureau (2017), respectively. Shapefiles of water bodies were obtained from the CanVec hydrographic series (Natural Resources Canada 2015). Data are in WGS84 and unprojected.

5.3.2 Physical sample collection

Physical samples were collected from 95 char that were harvested using monofilament gillnets (mesh size 127 mm or 5 inches) set under the ice in the Coppermine River from 7 November to 18 December 2021 (Figure 5.1). Otoliths were extracted for ageing and adipose fins were collected and stored at -20°C for genotyping (see Section 5.3.3 – Species identification – below). Fork lengths (mm) and weights (g) of whole fish were measured. Stomachs were dissected in the lab to discern contents. Gonads were weighed and visually examined to assess evidence of spawning activity earlier in the season (e.g., spawning colours, prominent kype, and/or large flaccid/empty testes for males; atretic or mature eggs, and/or large flaccid/empty ovaries for females; Núñez and Duponchelle 2009; Brown-Peterson et al. 2011).

Samples from a further 637 fish were obtained from various community collection programs operated by the Kugluktuk Hunters and Trappers Association, Fisheries and Oceans Canada, and University of Waterloo. All fish used in this study were harvested within the study area (Figure 5.1B), including 630 samples collected during the ice-free season in Coronation Gulf and Coppermine River and 7 collected during the ice-covered season in the Coppermine River. Capture method was not recorded for most of the samples but was assumed to be largely gillnet; most fish harvested by community members are captured by gill net (A. Dumond and E. Hitkolok, pers. obs.). Typical mesh sizes of gillnets used in the area are 114 or 127 mm (4.5 or 5 inches; A. Dumond and E. Hitkolok, pers. obs.). Otoliths were extracted for ageing. Adipose fins were collected from whole or fileted fish and samples of skin/tissue were collected along the cut edge of fish heads for genotyping. Samples for genotyping were either frozen at -20° C, dried, or stored in reagent alcohol, depending on the tissue type and collection program. Fork length, weight, and sex were recorded when possible. Many samples (n = 358) were collected from fish heads, so measurements of length and weight were not possible and sex could not be consistently discerned.

5.3.3 Species identification

Samples from 861 individual fish, including 79 from under-ice sampling, 637 from community collection programs, and 145 from tagged fish (see Section 5.3.5 – Acoustic telemetry – below) were genotyped. Genotyping of 205 fish was previously conducted by Weinstein (2023) using the 87K *Salvelinus* SNP (single nucleotide polymorphism) chip developed by Nugent et al. (2019). Methods are available in Weinstein (2023). DNA was extracted from the remaining 656 samples using Qiagen DNeasy Blood and

Tissue Kits (Qiagen, Hilden, Germany) or salt precipitation (see detailed methods in Appendix C). Samples were genotyped using TaqMan™ assays developed by Liu et al. (2023) to distinguish Arctic Char from Dolly Varden, as described in Chapter 4.

5.3.4 Age analysis

One otolith from each of 220 fish was embedded in Cold Cure epoxy (System Three Resins, Lacey, Washington) in preparation for ageing. The left sagittal otolith was preferentially used; the right sagittal otolith was used when the left was broken or unavailable. Epoxy was allowed to cure for at least 72 hours at room temperature before a transverse section was made through the core of each otolith with a low-speed precision saw (IsoMet, Buehler Ltd., Lake Bluff, Illinois). Otoliths from another 338 fish were prepared for ageing by AAE Tech Services (La Salle, Manitoba) using similar methods. Otolith sections were photographed under reflected light using Leica Application Suite X (version 5.0.3) and a Leica IC80 HD camera mounted on a Leica M80 microscope (Leica Microsystems, Wetzlar, Germany). A single ager used the photographs to determine ages visually by counting translucent bands (which appeared dark under reflected light) that indicated periods of reduced growth (i.e., winter; Chilton and Beamish 1982). Recorded ages were the number of winters since emergence. Winter bands present along the otolith margin (e.g., for fish captured early in the ice-covered season) were not counted. Photographs were assigned random names before ageing to prevent bias. A subset of 100 photographs was randomly selected to be aged in duplicate to ensure consistency (age difference ≤ 1 year).

To determine if younger fish were more likely to overwinter in the Coppermine River below the falls, median ages were compared between two periods of capture – ice-free or ice-covered – in Monte Carlo analyses that were conducted separately for each species. Fish captured during ice-covered periods were known to be overwintering below the falls (the falls are believed to be impassable after river freeze-up), whereas fish captured during ice-free periods were assumed to be representative of all fish migrating to the ocean. Period of capture was shuffled randomly for 10 000 permutations. For each permutation, the test statistic was calculated as the difference in median age between ice-free and ice-covered captures ($\text{age}_{\text{ice-free}} - \text{age}_{\text{ice-covered}}$). Exact, one-tailed p-values were calculated as the proportion of permutations with equal or greater test statistics than the observed test statistic. To determine if smaller fish were more likely to overwinter in the Coppermine River below the falls, the same analyses were conducted with median fork length. These, and all further data processing and analyses were conducted using R version 4.4.0 (R Core Team 2024). Data visualization was achieved

using the R packages `ggplot2` version 3.5.1 (Wickham 2016), `ggalluvial` version 0.12.5 (Brunson and Read 2023), and `patchwork` version 1.2.0 (Pedersen 2024).

To describe the relationships between age and length for each species, von Bertalanffy growth curves were generated for Arctic Char ($n = 61$) and Dolly Varden ($n = 155$) that had both age and length data available. Growth curves were generated using the R package `FSA` version 0.10.0 (Ogle et al. 2025).

5.3.5 Acoustic telemetry

Acoustic tags (V16T, Innovasea, Halifax, Nova Scotia) were surgically implanted into 207 adult, anadromous char that were captured in Coronation Gulf and the Coppermine River from 2018 to 2023. Detailed capture and surgical methods are described in Smith et al. (2022). Fork length was measured to the nearest mm. Fork lengths at time of tagging were 560–725 mm for Arctic Char (median = 630.5 mm) and 539–889 mm for Dolly Varden (median = 711.5 mm). It should be noted that measurements taken at the time of tagging were excluded from analyses of length (see above), because fish were only retained with tag mass:fish body mass < 0.02 to avoid undue tag burden (Winter 1996). A portion of the adipose fin was removed and either frozen at -20°C , dried, or stored in reagent alcohol for subsequent genotyping (see Section 5.3.3 – Species identification – above).

An array of VR2Tx, VR2W, and VR2AR (Innovasea, Halifax, NS) acoustic telemetry receivers was deployed to detect tag transmissions in Coronation Gulf ($n = 22\text{--}47$) and the Coppermine River ($n = 7\text{--}9$; Figure 5.1B). A detailed list of deployments can be found in Table C1 in Appendix C. Detailed deployment methods are described in Smith et al. (2022) and processing methods in Smith et al. (2024; Chapter 3). The R package `mort` version 0.0.1 (Smith et al. 2025; Chapter 2) was used to identify detections from potential mortalities or shed tags, as described in Chapter 4.

5.3.6 Overwintering location

Detection data from acoustic telemetry were used to describe frequency and patterns of overwintering locations for both Arctic Char and Dolly Varden. Fish detected at the acoustic telemetry receiver above the falls (Figure 5.1) that had been previously detected in the Coppermine River below the falls in that same year were classified as overwintering above the falls. Detection efficiency (i.e., the probability that a tagged fish would be detected as it passed by a given receiver) above the falls was assumed to be complete; comparing fish detected by two receivers deployed in duplicate above the falls in 2019 indicated that all fish ($n = 55$) were detected by both receivers. Fish detected during the ice-covered

period by at least one receiver in the Coppermine River below the falls were classified as overwintering below the falls. No fish were detected at the receiver above the falls in October of any study year (i.e., no fish ascended the falls after September), so fish detected below the falls in October but before freeze-up were also assumed to be overwintering below the falls in that year. Fish were classified as skipping migration if they were detected above the falls in a previous year, not detected (either below the falls or in the marine environment) in the intermediate year, and detected (either below the falls or in the marine environment) in the following year. Fish last detected in the marine environment in a given year (i.e., not detected in the Coppermine River prior to freeze-up) and first detected in the marine environment in the following year were classified as overwintering in an alternate river system.

5.3.7 Patterns of return migration

To determine if intent to overwinter below the falls could be identified from movement patterns during return migrations to fresh water, we used acoustic telemetry to assess metrics related to directedness of travel (Table 5.1). Fish were included if genotyping data were available and if overwintering location was known in a given year (see Section 5.3.6 – Overwintering location – above). Fish were only included in the year they were tagged if the duration from time of tagging to return to fresh water was greater than two weeks.

5.3.7.1 Time of return to fresh water

Return to fresh water was identified as the first detection of an individual at one of the two receivers located at the river mouth, after which the individual was only detected within the river or the river plume (Figure 5.1). Detection efficiency of receivers at the river mouth was assumed to be complete; all fish ($n = 130$) that were detected in the marine environment and subsequently detected in the river were detected by one of the two receivers located at the river mouth. We inferred that any detections within the river plume subsequent to detection at the river mouth indicated staging (see below) before upstream movement. If an individual was detected at a single river mouth receiver for a single residence event (period of detection < 4 hours) and then moved into the marine environment outside the river plume, the event was assumed to be a temporary step during marine migration and was not considered return to fresh water. Two individuals returned to the Coppermine River, moved ~ 14 km upstream of the river mouth, moved back downstream to the marine environment, and later returned to overwinter below the falls. From the substantial upstream movement after the first return to fresh water, we

inferred that these individuals intended to return at the first return; metrics (Table 5.1; see detailed descriptions below) were calculated in relation to the first observed return for these two individuals.

Table 5.1: Summary of metrics used to describe patterns of return migration.

Metric	Indicates	Environment	Description
Upstream distance	Extent of upstream migration	River	In-water distance between river mouth and furthest upstream location
Duration	Speed of return migration	Marine	Time between leaving furthest marine location and returning to fresh water (at the river mouth); standardized by distance
		River	Time between leaving the river mouth and arriving at furthest upstream location; standardized by distance
Linearity	Directedness of return migration	Marine	Ratio of minimum possible distance from furthest location to the river mouth to minimum in-water distance an individual was observed to travel
		River	Ratio of minimum possible distance from river mouth to furthest upstream location to minimum in-water distance an individual was observed to travel
Staging	Delay in return migration	River plume (before return)	Time spent within the river plume before returning to freshwater
		River mouth	Time spent at the river mouth or within the river plume after returning to freshwater

5.3.7.2 Upstream distance

Minimum in-water distances were calculated between each river receiver (below the falls) and the two receivers located at the mouth of the Coppermine River (Figure 5.1). Distances were calculated using 16-cell neighbourhoods with the R package `gdistance` version 1.6.4 (van Etten 2017) and a raster with approximately 10 m x 10 m cells that was generated from shapefiles of waterbodies from the CanVec hydrographic series (Natural Resources Canada 2015). Upstream distance was calculated as the distance from the river mouth receiver where a fish was detected at the time of return (hereafter, “return receiver”) to the most upstream receiver (below the falls) where the fish was detected in the same year. Detection efficiencies of river receivers were relatively high; identifying if fish were detected at a given receiver as they passed upstream or downstream indicated that the proportion of fish detected by each river receiver ranged from 0.88 (the third receiver upstream of the river mouth) to 1 (the most upstream receiver below the falls; Figure 5.1).

5.3.7.3 Duration

Separate metrics were calculated for duration of return migration in the marine environment and in fresh water (Table 5.1). For marine movements, minimum in-water distances between each receiver in the study area to the two receivers located at the mouth of the Coppermine River were calculated in the same way as upstream distances (see above). Distances were compared between each marine location where a given fish was observed and the return receiver. The furthest marine receiver was designated the starting location for return migration. The duration of return migration was calculated as the time (hours) between when a fish was last detected at the furthest marine receiver and the time of return (see above). To account for differences in distances traveled, duration was standardized by the in-water distance between furthest marine location and the return receiver. For movements in fresh water, duration of return migration was calculated as the time (hours) between when a fish was last detected at a river mouth receiver and when it was first detected at the most upstream receiver where the fish was observed. Duration was standardized by the in-water distance between the return receiver at the river mouth and the most upstream receiver.

5.3.7.4 Linearity

Separate metrics were calculated for linearity in the marine environment and in the freshwater environment (Table 5.1). In the marine environment, movements from the furthest marine location where a fish was observed until the time of return (see above) were identified. The minimum possible in-water distance between the furthest marine location and the return receiver were calculated as above. The minimum observed in-water distance was calculated as the sum of distances between receivers for all observed marine movements. Minimum observed in-water distances were calculated using the R package `gdistance` as above. For movements that occurred when other receivers were active and located along the shortest path (but the fish was not detected by those receivers), minimum in-water distances were calculated with the additional constraint that paths avoided a 500 m (the approximate detection radius of a marine receiver, determined using mobile range testing) buffer around these receivers. Observed distances could be inflated by apparent movement if a fish was positioned where it could be detected by multiple receivers [near] simultaneously. To avoid artificially inflating observed distances, detections at neighbouring receivers that occurred within 180 seconds (the maximum interval between tag transmissions) of each other were assigned to the same event. The centroid of neighbouring receivers was calculated using the `st_centroid` function in the R package

sf version 1.0-16 (Pebesma 2018) and distances were calculated to/from the centroid. Linearity of return migration in the marine environment was calculated as the ratio of the minimum possible distance to the minimum observed distance. Although deviations from linearity may have been difficult to detect near the margins of the array (where receiver coverage was typically more limited), deviations from linearity were likely more detectable as fish moved nearer to the Coppermine River (where receiver coverage was more concentrated; Figure 5.1B). In the freshwater environment, movements were identified between the last detection of a fish at a river mouth receiver and the first detection at the most upstream receiver. Minimum possible in-water distances, minimum observed in-water distances, and linearity were calculated in the same way as they were for the marine environment.

5.3.7.5 Staging

Separate metrics were calculated for staging within the river plume (before the identified time of return) and staging at the river mouth (after the identified time of return; Table 5.1). Staging within the river plume was calculated as the time (days) between the first detection of a fish within the river plume and the time of return (at the river mouth; see Section 5.3.7.1 – Time of return to fresh water – above), provided there were no interim detections in the marine environment outside the river plume. Staging at the river mouth was calculated as the time (days) between the time of return and the last detection at a river mouth receiver before a fish was observed moving upstream.

5.3.7.6 Classification

Linear discriminant analysis (LDA) was applied to movement metrics (Table 5.1) to investigate patterns of return migration and determine if Dolly Varden that overwintered below the falls intended to overwinter below the falls or if they failed to ascend the falls. We assumed that patterns of return migration of Arctic Char reflected intent to overwinter below the falls because Arctic Char have never been detected above the falls. We assumed that patterns of return migration of Dolly Varden that migrated above the falls reflected intent to overwinter above the falls because we thought it unlikely that fish would successfully ascend a large obstacle by chance, and we have never detected an individual descending the falls after ascending the falls in the same year. We used LDA to classify Arctic Char (below falls) and Dolly Varden (above falls only) based on the metrics that were calculated to describe return migration (upstream distance, duration (marine and freshwater), linearity (marine and freshwater), and staging (marine and freshwater); Table 5.1). We then applied the fitted model to Dolly Varden that overwintered below the falls, to assess whether their patterns of return migration were

more likely to be classified as Arctic Char (evidence for intent to overwinter below the falls) or Dolly Varden that overwintered above the falls (evidence for intent, but failure to ascend the falls).

For individuals that were observed in multiple years, only one observation (year) was retained to ensure that the LDA assumption of independence was met. Observations that were selected for removal improved balance among group sizes (Dolly Varden were preferentially retained in a year that they overwintered below the falls) and among years (e.g., observations from 2022 and 2023 were preferentially retained). The reduced dataset was divided into a training dataset that included Arctic Char (all overwintered below the falls) and Dolly Varden that overwintered above the falls, and a test dataset that included Dolly Varden that overwintered below the falls. Metrics (Table 5.1) were inspected and transformed to reduce skewness and improve normality: a logarithmic transformation was applied to staging (both river mouth and river plume) and duration (both marine and freshwater) metrics, and an arcsin-square root transformation was applied to proportional (both marine and freshwater linearity) metrics. To allow an assessment of the relative contributions of each metric, all metrics were scaled (to standard deviation = 1) and centred (to mean = 0). The maximum collinearity among scaled variables was 0.44. Homogeneity of within-group covariance matrices was assessed using the `betadisper` function in the R package `vegan` version 2.6-10 (Oksanen et al. 2025). The assumption of homogeneity was met when upstream distance was removed, so this metric was removed and qualitatively compared among groups. Following Legendre and Legendre (2012) and Borcard et al. (2018), group means were compared with a one-way MANOVA using the `Wilks.test` function in the R package `rrcov` version 1.7-6 (Todorov and Filzmoser 2009) before conducting LDA using the `lda` function in the R package `MASS` version 7.3-60.2 (Venables and Ripley 2002). To assess performance of the classification, a confusion matrix was generated using leave-one-out cross validation. To apply the model to Dolly Varden that overwintered below the falls, metrics in the test dataset were scaled by the mean and standard deviation values in the training set. Posterior probabilities of classes were determined using the `predict.lda` function with “predictive” method (Venables and Ripley 2002). Fish were assigned to the class with posterior probability > 0.5.

Discriminant axes are determined by maximizing between-group differences. If Dolly Varden that overwintered below the falls formed a distinct group (in terms of metrics of return migration), rather than aligning with or being intermediate between the other two groups, the distinct grouping may not be apparent along a discriminant axis that was generated using only data from Arctic Char and Dolly Varden that overwintered above the falls. To assess whether Dolly Varden that overwintered below the

falls formed a distinct group, a second LDA was conducted that included data from all three groups: Arctic Char, Dolly Varden that overwintered above the falls, and Dolly Varden that overwintered below the falls. The analysis followed the same steps as the LDA with two groups.

5.3.8 Ethical statement

Fish captures, handling, and tagging for acoustic telemetry were conducted under Animal Utilization Project Protocols (AUPP) 18–07, 30071, and 44099, which were approved by the University of Waterloo Animal Care Committee. Samples from community programs were collected under AUPP 40576, approved by the University of Waterloo Animal Care Committee. All fieldwork was conducted under Nunavut Impact Review Board screening (File no. 18YN023), Kitikmeot Inuit Association Certificate of Exemption to access Inuit Owned Lands (Certificate no. KTX118N005), and Fisheries and Oceans Canada Licenses to Fish for Scientific Purposes (S-18/19-1025-NU, S-19/20-1023-NU, S-21/22-1034-NU, S-22/23-1050-NU, S-22/23-1008-NU, and S-23/24-1056-NU).

5.4 Results

5.4.1 Physical samples

Arctic Char typically had smaller fork lengths at a given age than Dolly Varden (Figure 5.2). The theoretical maximum fork length of Dolly Varden ($n = 155$), estimated from a von Bertalanffy model, was 902 mm (95% confidence interval 824–1058 mm). Similar growth parameters could not be estimated for Arctic Char, likely due to smaller sample size ($n = 61$) and few observations of older fish.

We observed a pronounced shift in the proportional representation of the two species (Arctic Char and Dolly Varden) captured between ice-free and ice-covered periods. Of 783 fish that were captured during ice-free periods and successfully genotyped, 12.5% ($n = 98$) were Arctic Char and 87.5% ($n = 685$) were Dolly Varden. Of 102 fish that were captured during ice-covered periods in the lower reaches of the Coppermine River (i.e., below the falls), 64% ($n = 55$) were Arctic Char and 36% ($n = 31$) were Dolly Varden.

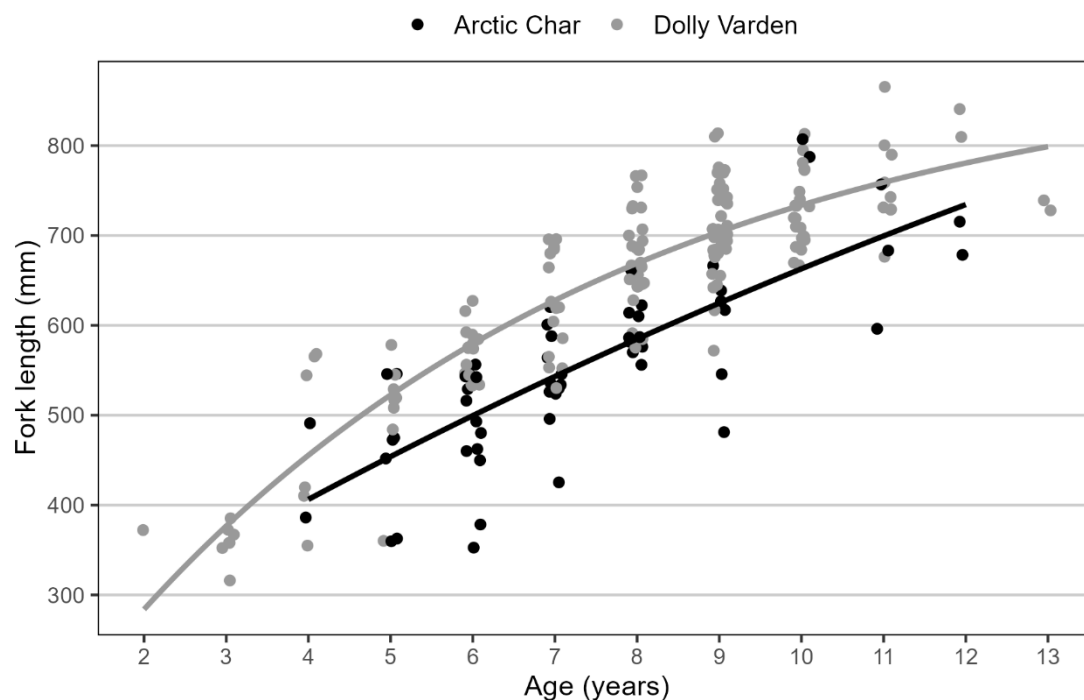


Figure 5.2: Ages and fork lengths of Arctic Char (black, $n = 61$) and Dolly Varden (grey, $n = 166$). Lines represent von Bertalanffy growth curves generated for each species. Note that ages are jittered (width = 0.1) around the x axis.

Younger Dolly Varden were more likely to overwinter below the falls in the Coppermine River. The median age of Dolly Varden captured in the river during ice-covered periods was 6 years (range 2–11, $n = 29$), whereas the median age of Dolly Varden captured in the larger study area (Figure 5.1B) during ice-free periods was 9 years (range 2–14, $n = 428$; Figure 5.3). Results of a Monte Carlo analysis indicated that the median age of Dolly Varden captured during ice-covered periods was significantly younger than the median age of Dolly Varden captured during ice-free periods (10 000 permutations, $p < 0.0001$). Younger Arctic Char were not more likely to overwinter below the falls in the Coppermine River. The median age of Arctic Char captured in the river during ice-covered periods was 7 years (range 5–12, $n = 49$), whereas the median age of Arctic Char captured in the study area during ice-free periods was 8 years (range 4–14, $n = 52$; Figure 5.3). Monte Carlo analysis indicated the median age of Arctic Char during ice-covered periods was not significantly younger than the median age during ice-free periods (10 000 permutations, $p = 0.463$).

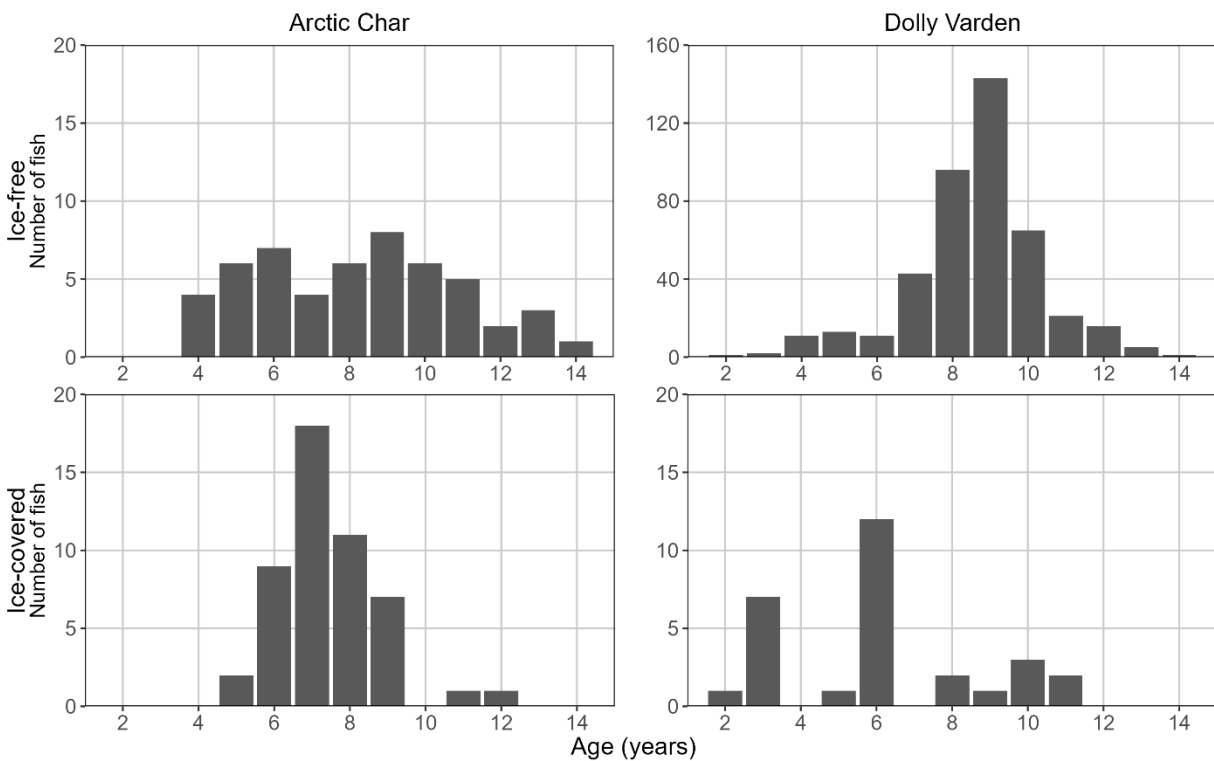


Figure 5.3: Age-frequency distributions by species of fish captured during ice-free periods and ice-covered periods. Fish captured during ice-free periods were captured throughout the study area and were assumed to be representative of all fish that migrated to the ocean. Fish captured during ice-covered periods were captured below the falls in the Coppermine River.

Comparisons of fork lengths between fish captured during ice-covered and ice-free periods were similar to comparisons of ages. The median fork length of Dolly Varden captured during ice-covered periods was smaller (546 mm; range 316–795 mm, $n = 24$) than the median fork length of Dolly Varden captured during ice-free periods (692 mm; range 355–909 mm, $n = 230$; Figure C1 in Appendix C). Results of a Monte Carlo analysis indicated that the median fork length of Dolly Varden during ice-covered periods was significantly shorter than the median fork length during ice-free periods (10 000 permutations, $p < 0.0001$). Similar to the results observed for age, median fork lengths of Arctic Char captured during ice-covered periods were not smaller than median fork lengths of Arctic Char captured during ice-free periods (Monte Carlo analysis; 10 000 permutations, $p = 0.774$). The median fork length of Arctic Char captured during ice-covered periods was 551 mm (range 353–690 mm, $n = 38$) and the median fork

length of Arctic Char captured during ice-free periods was 541.5 mm (range = 378–807 mm, n = 40; Figure C1 in Appendix C).

We did not observe evidence of under-ice foraging or spawning activity in 95 fish that were captured below the falls and under the ice in the Coppermine River in 2021. All stomachs of these fish were empty, except for one that contained two grains of coarse sand < 2 mm in diameter. Of the 50 fish that were genotyped as Arctic Char, 30 were females, 19 were males and 1 individual was of unknown sex (i.e., immature; sex could not be determined by visual examination of gonads). Of the 29 fish that were genotyped as Dolly Varden, 12 were females, 15 were males, and 2 individuals were of unknown sex. One male Arctic Char exhibited spawning colouration (darkening on dorsal side, orange-red on ventral side) and had a large gonadosomatic index (0.0030; weight of gonads divided by weight of fish) relative to other males with available measurements of weight (0.0002–0.0016). One female Dolly Varden appeared to be reabsorbing eggs (eggs of varying size and varying stages of atresis). We did not observe evidence that any other fish had prepared for spawning or had spawned in the season immediately preceding capture (e.g., spawning colours, prominent kype, and/or large flaccid/empty testes for males; atretic or mature eggs, and/or large flaccid/empty ovaries for females).

5.4.2 Overwintering location

Overwintering locations could be inferred from acoustic telemetry data for 24 Arctic Char and 101 Dolly Varden in at least one of the six years of the study (2018–2023). Overwintering location was inferred for some individuals in multiple years, yielding 38 Arctic Char*year and 186 Dolly Varden*year observations. We observed high variability in overwintering location among years (within individuals), among individuals, and between species (Figure 5.4). Arctic Char were never observed migrating above the falls in the Coppermine River. Four Arctic Char (16.7% of individual Arctic Char) were inferred to have overwintered in an alternate river system in at least one year. Dolly Varden were observed overwintering both above and below the falls; 22 individuals (41.5% of 53 individual Dolly Varden that were observed in more than one year) were observed overwintering below the falls in at least one year and above the falls in at least one year. More Dolly Varden were typically observed overwintering above the falls (69–100% within a year) than were observed overwintering below the falls, with the exception of 2018, when fish were tagged relatively late in the year and many fish had likely already migrated above the falls. Seven Dolly Varden (6.9% of individual Dolly Varden) were inferred to have skipped migration and remained in the upper reaches of the Coppermine River (above the falls) during the

ice-free period in at least one year. Only one Dolly Varden (1%) was inferred to have overwintered in an alternate river system in one year.

5.4.3 Patterns of return migration

Fifty-nine fish met the criteria for inclusion in comparisons of patterns of return migration in at least one year (i.e., species was known from genotyping, overwintering location was known, and minimum duration > 2 weeks between time of tagging and return to fresh water), including eight Arctic Char and fifty-one Dolly Varden. After removal of observations from fish that met the criteria in more than one year, final sample sizes were eight Arctic Char that overwintered below the falls and forty-one Dolly Varden that overwintered above the falls in the training dataset, and ten Dolly Varden that overwintered below the falls in the test dataset (see Table C2 in Appendix C for complete table of sample sizes by species, year, and overwintering location).

Patterns of return migration (characterized by duration, staging, and linearity; Table 5.1), differed significantly between Arctic Char that overwintered below the falls and Dolly Varden that overwintered above the falls (one-way MANOVA, Wilks' $\lambda = 0.3346$, $\chi^2 = 42.657$, $df = 6$, $p < 0.0001$).

Leave-one-out cross validation indicated that an LDA correctly classified 75% of Arctic Char (all overwintered below the falls) and 95% of Dolly Varden that overwintered above the falls. When the LDA was applied to Dolly Varden that overwintered below the falls, posterior probabilities of classes assigned four individuals (40%) to the class with Arctic Char and six individuals (60%) to the class with Dolly Varden that overwintered below the falls. There was relatively high confidence in the classifications; the lowest posterior probability for fish assigned to the class with Arctic Char was 0.88 and the lowest posterior probability for fish assigned to the class with Dolly Varden that overwintered above the falls was 0.97. Predicted values spanned the full range of the discriminant axis for Dolly Varden that

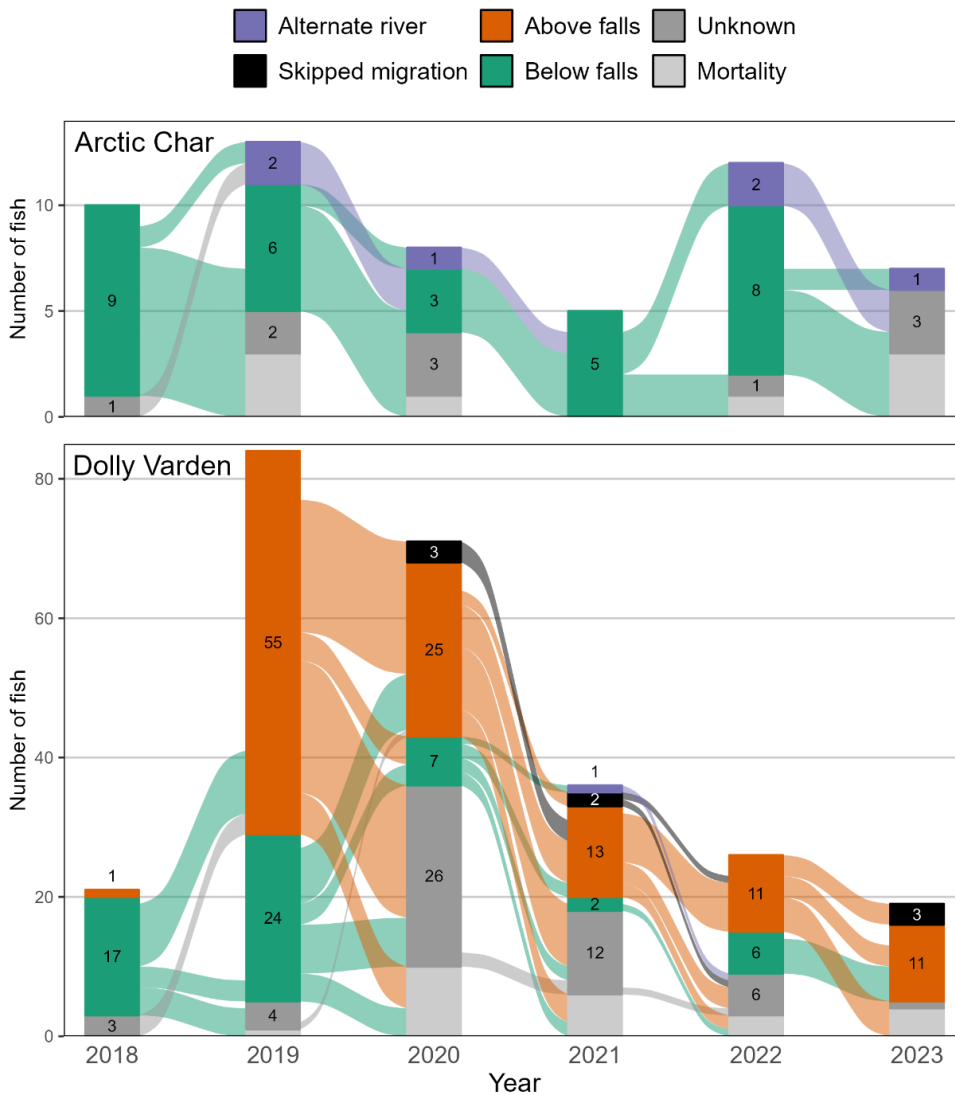


Figure 5.4: Overwintering locations inferred from acoustic telemetry data for Arctic Char and Dolly Varden. On the x-axis, “Year” indicates the starting year of each ice-covered period (e.g., 2018 indicates the ice-covered period from October 2018 to June 2019). Ribbons indicate patterns in overwintering location between years for individual fish (e.g., an orange ribbon from an orange bar to a green bar represents a fish that overwintered above the falls in one year and below the falls in the following year). Fish classified as “Skipped migration” overwintered above the falls but did not migrate to the ocean during the ice-free period. Fish classified as “Alternate river” were detected during the ice-free period in the marine environment, were not detected in or near the Coppermine River before river freeze-up, and were detected in the marine environment in the next ice-free period. Fish classified as “Unknown” in a given year were detected during the ice-free season of that year but overwintering location could not be

(Figure 5.4 continued): inferred from telemetry data. Fish classified as “Mortality” were confirmed (e.g., through tag returns) or inferred (e.g., lack of movement identified in R package `mort`) to have died or to have expelled their tag in that year.

overwintered below the falls (Figure 5.5). Leave-one-out cross validation indicated that an LDA with three classes (Arctic Char, Dolly Varden that overwintered above the falls, Dolly Varden that overwintered below the falls) did not correctly classify any Dolly Varden that overwintered below the falls, which indicated these fish did not form a distinct group based on patterns of return migration.

Qualitative comparison of the coefficients in the classification function of the LDA with two classes indicated that duration of upstream movement (coefficient = -1.54) had the largest influence on the discriminant axis, followed by staging at the river mouth (coefficient = -0.31). Arctic Char, which overwintered below the falls, typically moved upstream slower and staged at the river mouth longer before moving upstream than Dolly Varden that overwintered above the falls (Figure 5.6). The coefficients of all other metrics were ≤ 0.26 (absolute values; Table C3 in Appendix C), which suggests there were no pronounced differences between classes for return movements in the marine environment (duration and linearity) or staging in the river plume. Upstream distance was not included in the LDA to meet the assumption of homogeneity of covariance matrices. Arctic Char that overwintered below the falls did not travel as far upstream towards the falls (median = 10.2 km, range = 6.9–14.1 km) as Dolly Varden that overwintered above the falls (median = 16.0 km, range = 12.4–16.0 km); Dolly Varden that overwintered below the falls were observed at intermediate values of upstream distance (median = 14.2 km, range = 7.9–16.0 km).

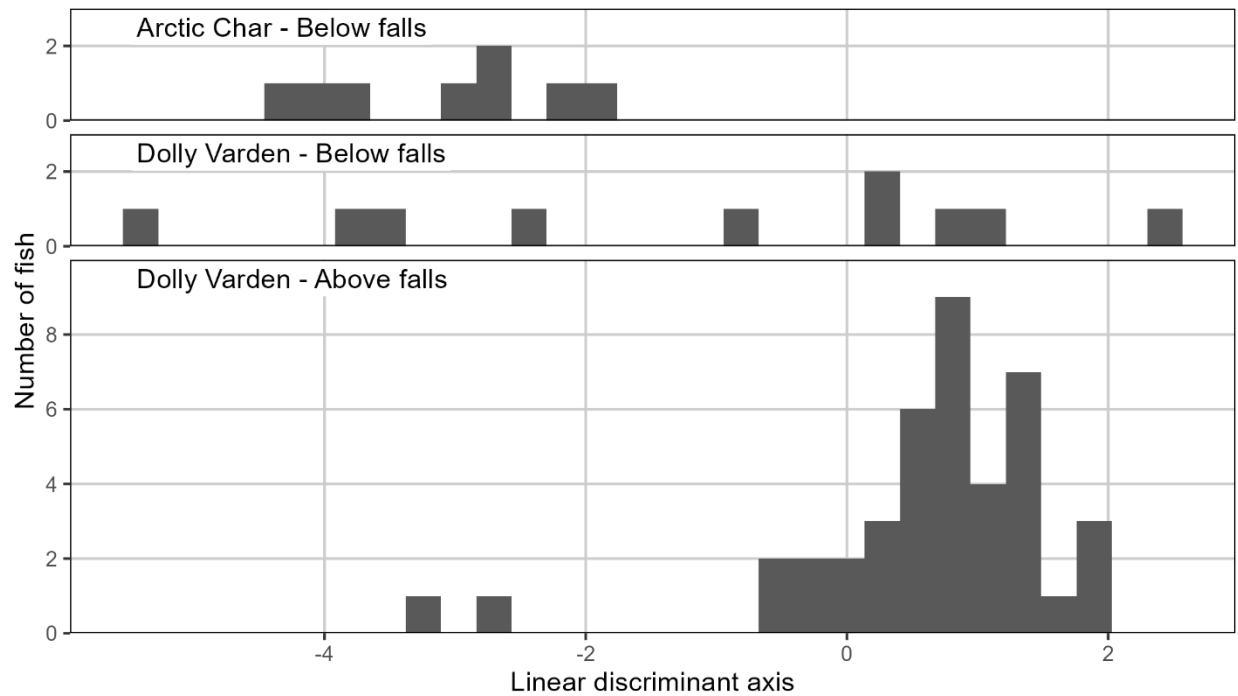


Figure 5.5: Results from linear discriminant analysis (LDA) that was conducted using two classes (Arctic Char, Dolly Varden that overwintered above the falls) and six metrics of return migration: duration of return movement (marine and freshwater), staging (river mouth and river plume), and linearity of movement (marine and freshwater). Note there is only one discriminant axis because the LDA was conducted with two classes. Values presented for Dolly Varden that overwintered below the falls were calculated using parameter estimates from the LDA.

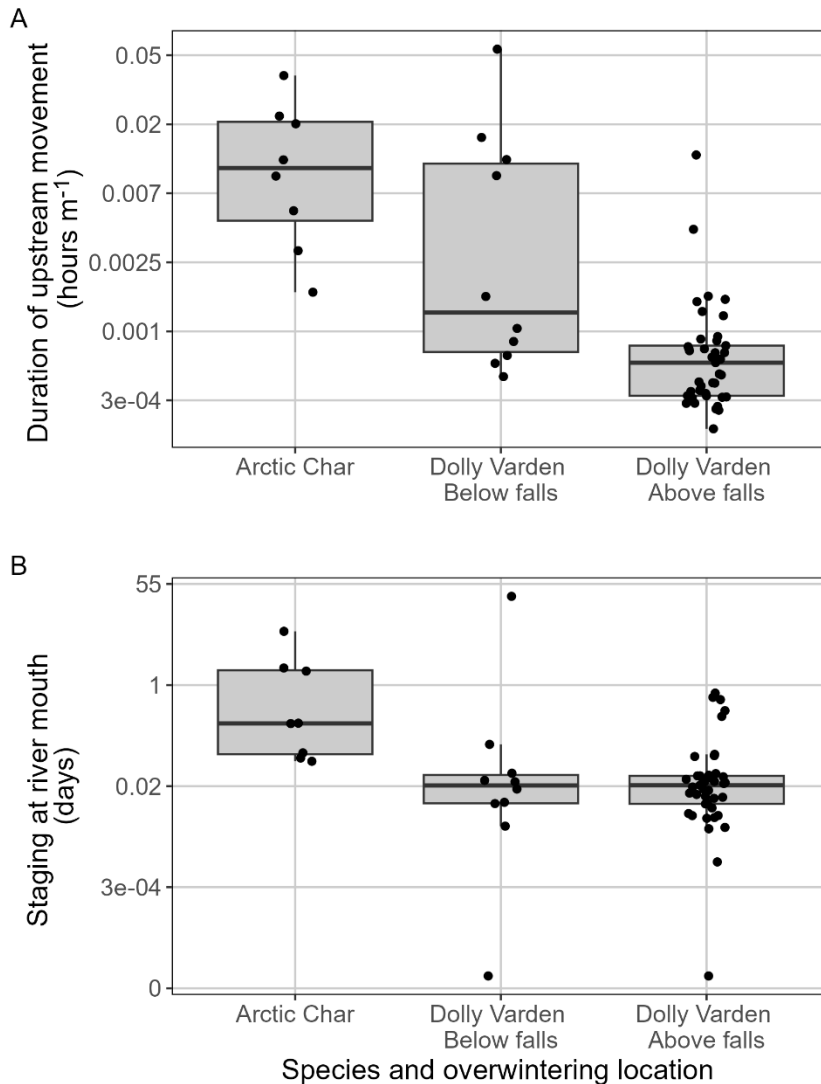


Figure 5.6: Duration of upstream movement (A; standardized by upstream distance) and staging at river mouth (B) for Arctic Char, Dolly Varden that overwintered below the falls, and Dolly Varden that overwintered above the falls. Note that both y-axes are presented on logarithmic scales. Points indicate observed values; outliers have been removed from boxplots to avoid duplication of data in the figure.

5.5 Discussion

5.5.1 Physical samples

5.5.1.1 Age and length

Dolly Varden that overwintered below the falls were significantly younger and smaller (fork length) than what we inferred to be representative of the Dolly Varden population in general – that is, Dolly Varden

captured during ice-free periods. This finding is not related to size selectivity of gear. All samples with known capture method were captured by gillnetting; sampling by gillnet is well-known to be size-selective and often results in size and age structure data that are unimodal (Hamley 1975). The mesh size of the gillnet used for sampling during ice-covered periods was the largest (127 mm or 5 inches) used in the study area (114–127 mm or 4.5–5 inches stretched mesh), and would have preferentially captured larger fish. The relatively high proportion of smaller and younger fish that we observed in samples captured during ice-covered periods would likely be even more pronounced if less size-biased sampling methods were used, or if all ice-free captures had used gillnets of the same (i.e., largest) mesh size. Our observations are also consistent with historic records from the Coppermine River that reported a modal age of 8 years for char (unknown species) captured during August 1981, whereas the modal age of char captured in October–November 1982 was only 5 years (Gillman and Kristofferson 1984).

Smaller fish may be less likely to migrate above the falls due to physiological or physical constraints or as an indirect effect of migration timing. The positive association between swimming speeds and fish length is well-established (Bainbridge 1958), but jumping performance remains understudied (Kraskura et al. 2024). Authors of a laboratory study of the jumping performance of Brook Trout (*Salvelinus fontinalis*) reported that longer fish were able to jump higher (Kondratieff and Myrick 2006), which would confer a benefit in ascending obstacles such as waterfalls. Conversely, Newton et al. (2018) found that larger Atlantic Salmon (*Salmo salar*) were less likely to successfully ascend a weir on the first attempt, possibly due to less thrust when the caudal fins of large fish were exposed in shallow water. Differences in migration timing among size classes may also affect ability to ascend the falls due to environmental conditions at the time of return. Jensen et al. (2020) observed that Arctic Char that were first-time migrants returned to fresh water later than veteran migrants in a Norwegian river system. Similarly, several authors have observed negative relationships between size of Arctic Char and return timing (i.e., smaller fish return to fresh water later; Johnson 1980; Dempson and Green 1985; Dempson and Kristofferson 1987; Berg and Jonsson 1989; Gulseth and Nilssen 2000; Svenning and Gullestad 2002). A negative relationship between fish size and timing of return to fresh water has also been observed for Dolly Varden in Kamchatka, Russia (Tiller 2013), but contradictory observations have been reported in northwest Alaska (DeCicco 1997). Although acoustic telemetry did not capture movements of smaller fish (fork lengths of fish tagged in this study were ≥ 539 mm), fish that overwintered below the falls in the Coppermine River returned to fresh water later than fish that overwintered above the

falls (Smith et al. 2024; Chapter 4). Additional research is necessary to ascertain whether smaller fish are less likely to successfully ascend the falls due to physiological/physical constraints, if environmental conditions are less favourable for ascent if/when smaller fish return later in the ice-free season, or if smaller and/or younger fish intend to overwinter below the falls.

Arctic Char captured below the falls during ice-covered periods were not significantly younger or smaller (fork length) than Arctic Char captured in the larger study area during ice-free periods. Although we were unable to identify the locations of alternate rivers where Arctic Char overwintered, some fish with floy tags that were deployed at Nulahugyuk Creek (68.724° N, 114.961° W, ~ 100 km north of the primary study area) have been captured in the Coppermine River (A. Dumond and E. Hitkolok, pers. obs.). Due to low water levels that prevent access later in the ice-free season, Arctic Char that overwinter in upstream lakes of Nulahugyuk Creek return to fresh water substantially earlier than fish that overwinter in other river systems of Coronation Gulf (Gilbert et al. 2016), and these fish are therefore proportionally less likely to be captured by harvesters within the study area. It follows that Arctic Char that are captured during ice-free periods would be more likely to overwinter in the Coppermine River, which would result in similar distributions of both age and size between ice-free and ice-covered periods.

5.5.1.2 Opportunities for marine foraging

We found no evidence of recent foraging, either in freshwater or marine environments, from stomach contents of 95 char that were captured under the ice in the Coppermine River in November and December 2021. Local fishers have harvested char through the ice in the marine environment near the Coppermine River (A. Dumond and E. Hitkolok, pers. obs.), and tagged char have been detected in the same area during ice-covered periods (Smith et al. 2022). It is unknown, however, if these individuals were foraging. Anadromous Arctic Char and Dolly Varden have previously been reported to reduce or cease feeding after returning to fresh water (Moore and Moore 1974; Craig 1977; McCart 1980; Boivin and Power 1990; Rikardsen et al. 2003), and water temperature in the Coppermine River is 0° C during ice-covered periods (Smith et al. 2022), which is colder than the lower thermal limit for feeding in Arctic Char (0.2° C; Elliott and Elliott 2010). Under-ice foraging is thus likely uncommon, but a larger sample size of fish collected at multiple times during ice-covered periods would be required to more thoroughly assess the potential occurrence and extent of under-ice foraging. Although we did not identify under-ice foraging early in the ice-covered season, overwintering below the falls allows access to the marine

environment prior to break-up of river ice (Smith et al. 2022). Arctic Char have been observed accessing the marine environment under sea ice elsewhere (Bégout Anras et al. 1999; Hammer et al. 2021), perhaps to take advantage of potential feeding opportunities from early pulses of productivity (Søreide et al. 2010). Early access to marine feeding habitats may also be beneficial for individual Arctic Char that are migrating to alternate river systems with low water levels, such as Nulahugyuk Creek (Gilbert et al. 2016).

5.5.1.3 Spawning status

We observed limited evidence of spawning activity below the falls in the Coppermine River. The age of maturity varies among anadromous populations for both Arctic Char (e.g., for females, 5 near Iqaluit, NU: Grainger 1953; 12 near Cambridge Bay, NU: McGowan 1990) and Dolly Varden (e.g., for females, 7 near Prudhoe Bay, AK: Craig and Haldorson 1980; 4 in the Babbage River, YT: Sandstrom et al. 1997). Although the historic species composition in the Coppermine River is unknown, the minimum age of maturity was four for males (350–400 mm size class) and five for females (400–450 mm size class) in 1981–1982, and most individuals of both sexes were sexually mature at age eight or nine (Gillman and Kristofferson 1984). This is consistent with the ages of Arctic Char that returned to Nulahugyuk Creek, likely to spawn (8–9 years old; Gilbert et al. 2016). The larger and/or older individuals captured through the ice in this study were thus likely sexually mature, but only one female Dolly Varden had ripened (and not spawned) and only one male Arctic Char was observed in spawning colours. Spawning locations, and therefore timing, are unknown within the Coppermine River system. Spawning typically occurs in September–October for both Arctic Char (Johnson 1980; Reist 2018) and Dolly Varden (Armstrong and Morrow 1980). It is possible that additional individuals, particularly males, had spawned or prepared for spawning, and evidence was no longer visible in the gonads at the time of capture approximately two months later. Local harvesters rarely catch char in spawning colours below the falls, and fry are not typically observed (A. Dumond and E. Hitkolok, pers. obs.). We believe that spawning below the falls occurs rarely, if at all, and that fish overwintering below the falls were largely immature or had skipped spawning, but further research is necessary.

Skipped spawning, or resting, has been observed for both Arctic Char (Johnson 1980) and Dolly Varden (Armstrong and Morrow 1980). Skipped spawning is thought to be a common occurrence, particularly in northern populations. For female fish of relatively long-lived and iteroparous species, skipped spawning is typically characterized as an adaptive trait, where reproductive output is sacrificed in years with low

availability of energy reserves in exchange for greater chance of survival, growth, and an associated increase in future reproductive output (Rideout et al. 2005). Skipped spawning is less well-documented for males than for females for most species of fish (Rideout and Tomkiewicz 2011), but Gallagher et al. (2018b) observed that male Dolly Varden from the Rat River, Northwest Territories, were more likely to skip spawning than females. Although energy allocation to gonads is typically greater for female fish than for males, male fish may invest substantial energy in development of secondary sexual characters (e.g., kype, colouration) and in competition (Rideout and Tomkiewicz 2011). Results from these studies suggest that large fish of both sexes from both species that we observed overwintering below the falls had skipped spawning.

5.5.2 Overwintering location

The high variability in overwintering location that we observed has previously been described in this system (Smith et al. 2022), but this is the first time that species (Arctic Char or Dolly Varden) has been identified (all fish were previously assumed to be Arctic Char). We observed from acoustic telemetry data that both Arctic Char and Dolly Varden overwintered in the fluvial environment below the falls in the Coppermine River, but only Dolly Varden overwintered above the falls. The pronounced shift in species composition that we observed from physical samples collected in the larger study area during ice-free periods (predominantly Dolly Varden) and physical samples collected below the falls during ice-covered periods (predominantly Arctic Char) supports our inference from acoustic telemetry data that Arctic Char overwinter below the falls more frequently than Dolly Varden. Arctic Char also overwintered in alternate river systems more frequently than Dolly Varden. Arctic Char rarely spawn in fluvial environments (Arostegui and Quinn 2019) and overwintering in non-natal systems in non-spawning years has been observed in other Arctic populations of Arctic Char in Canada (e.g., Moore et al. 2013; Spares et al. 2015; Gilbert et al. 2016). Arctic Char may thus migrate to other river systems in spawning years and overwinter in the lower reaches of the Coppermine River in non-spawning years, although further research is necessary to investigate this possibility. We did observe one male Arctic Char in spawning colours. Environmental conditions (e.g., low water levels) may have prevented this individual from reaching its intended spawning grounds in an alternate river system and caused it to overwinter in the lower reaches of the Coppermine River, which are accessible year-round. Future identification of spawning and rearing habitats is a priority, and would help explain the incidence of overwintering in alternate systems.

Spawning and rearing habitats are unknown for Dolly Varden as well as for Arctic Char, but the low incidence of overwintering in alternate rivers (a single observation) suggests that Dolly Varden spawn in the Coppermine River system. The young age, small size, and absence of confirmed spawning activity in Dolly Varden captured below the falls during ice-covered periods suggests that Dolly Varden may migrate above the falls in spawning years and overwinter below the falls in (some) non-spawning years. While requiring further research, this assertion is consistent with the observation that non-spawning, adult Dolly Varden aggregate and likely overwinter in a separate section of an Alaskan river system than spawning adults (Furniss 1975). More tagged Dolly Varden overwintered above the falls in a given year than overwintered below the falls. It is thus likely that some non-spawners also overwinter above the falls, but spawning frequency of Dolly Varden in the Coppermine River is unknown. We also observed some instances of skipped migration in Dolly Varden. Skipped migrations have been described in Dolly Varden from the Rat River, Northwest Territories, and skipped migrations in this system have been associated with skipped spawning; a subset of fish spawn in alternate years and migrate to the ocean in years when they do not spawn, but stay in fresh water in years when they spawn (Gallagher et al. 2018b). The relatively low incidence of skipped migrations that we observed suggests that not all spawning Dolly Varden in the Coppermine River forego migrating to the ocean. Identifying spawning locations, spawning frequency, and the number of populations of Dolly Varden that inhabit the Coppermine River is necessary to explain the occurrence and frequency of both skipped migrations and overwintering below the falls.

5.5.3 Patterns of return migration

Arctic Char that overwintered below the falls and Dolly Varden that overwintered above the falls exhibited distinct patterns in return migrations to fresh water. Movements in the marine environment did not contribute to differentiating between the two groups. Although increasing receiver coverage in the marine environment may reveal greater differences in return movements to fresh water, our finding is consistent with observations that directed, rapid movements in the marine environment characterize the return migration of Arctic Char to fresh water (Morris and Green 2012; Spares et al. 2015).

Compared to Dolly Varden that overwintered above the falls, Arctic Char staged longer at the river mouth before moving upstream, and then moved upstream more slowly. This finding is consistent with our previous research that suggested Arctic Char moved more passively into fresh water than Dolly Varden that overwintered above the falls (Chapter 4). As described above, it is likely that Arctic Char spawn and rear in alternate river systems, and it is possible that this affects movements during return

migrations to fresh water via effects on imprinting. Atlantic Salmon reared in hatcheries typically exhibit more erratic movements when returning to fresh water than wild individuals, which often results in greater duration of in-river movement (Thorstad et al. 2008). Similarly, Atlantic Salmon reared in hatcheries have been observed to make more reverse movements (from fresh water to the marine environment) during return migration than wild individuals, which may be due to reduced imprinting (Nilsen et al. 2023). If Arctic Char that overwintered in the Coppermine River had reared in different systems, a similar lack of imprinting could explain the differences in return migration that we observed between Arctic Char and Dolly Varden that overwintered above the falls.

Dolly Varden that overwintered above the falls had shorter/no staging at the river mouth compared to Arctic Char, and this may have implications for the cost of migration. Dolly Varden that overwintered above the falls returned to the Coppermine River when river temperatures were warm and potentially stressful (Chapter 4). Acclimation can improve swimming performance of Arctic Char in warm water temperatures (Gilbert et al. 2022), and likely also for closely related Dolly Varden. The minimal staging that we observed prior to upstream movement would likely be insufficient for effective acclimation and associated reduction in heat stress and improvements in swimming performance. Additional research on the thermal tolerance of northern form Dolly Varden and acclimation are necessary to assess the impacts of staging on migration success in this system.

Dolly Varden that overwintered below the falls exhibited the full range of patterns of return migration that we observed. The lack of consistent or distinct patterns of return migration displayed by Dolly Varden that overwintered below the falls contrasts with the distinct patterns observed for Dolly Varden that overwintered above the falls and for Arctic Char that overwintered below the falls, and suggests that there may be multiple mechanisms that determine overwintering location of Dolly Varden. Some individuals that exhibited return movements similar to Arctic Char may have intended to overwinter below the falls, perhaps due to spawning status or body condition. As described above, it is likely that overwintering location of larger Dolly Varden is not solely related to spawning status; individuals that overwintered below the falls but exhibited return movements similar to Dolly Varden that overwintered above the falls may have failed to ascend the falls. Non-spawning Dolly Varden arrive at the upper reaches of the Firth River, Yukon, one month after spawning Dolly Varden (Glova and McCart 1974), but it is unclear if there is a difference in timing of return to fresh water between non-spawners and spawners in this system. Similarly, Dolly Varden in the Canning River, Alaska, spent longer in the marine environment if they had spawned in the previous year than those that had skipped spawning in the

previous year (Brown et al. 2019). These observations are consistent with our previous observation that fish returned to fresh water later in years that they overwintered below the falls in the Coppermine River (Smith et al. 2024; Chapter 3). These individuals may experience unfavourable conditions for ascending the falls and/or have less time to successfully ascend the falls. As discussed above, only large individuals were tagged. Studying the movements of younger, smaller fish to identify if patterns of return migration change with age, size, and/or experience of Dolly Varden will be important in future discernment of drivers of overwintering below the falls.

5.6 Conclusion

Arctic Char were not detected migrating above Kugluk or Bloody Falls; all individuals overwintered below the falls in the Coppermine River. Arctic Char likely overwintered in other (unknown) river systems in spawning years and overwintered in the easily accessible lower reaches of the Coppermine River in non-spawning years, but further research is necessary. Overwintering below the falls allows early access to the marine environment for potential feeding and travel to other systems. Arctic Char exhibited patterns of return migration consistent with intent to overwinter below the falls, including longer staging at the river mouth before upstream movement, shorter distances traveled upstream, and slower (standardized by distance) movements upstream than exhibited by Dolly Varden that overwintered above the falls.

Younger and smaller Dolly Varden overwintered below the falls. Adult Dolly Varden also overwintered below the falls in years they likely skipped spawning, although further research is required and it is probable that some also overwintered above the falls in non-spawning years. Some large, adult Dolly Varden exhibited patterns of return migration similar to Arctic Char, and may have intended to overwinter below the falls. Conversely, others exhibited patterns similar to Dolly Varden that overwintered above the falls, and may have attempted but failed to ascend the falls.

The sympatric occurrence of anadromous Dolly Varden and anadromous Arctic Char in fresh water is extremely rare. Understanding migration patterns and drivers of overwintering location is crucial to further understanding the ecology of the two species, including variability in tactics and associated implications for survival and fitness. Harvesting char through the ice in the Coppermine River is a common practice that has numerous nutritional, economic, and cultural benefits for residents of Kugluktuk, Nunavut. Future efforts aimed at identifying spawning and rearing locations of Arctic Char, which we observed comprised the majority of char overwintering below the falls, will be critical in

ensuring the future sustainability of this important food source. Tagging smaller individuals of both species to assess movement patterns would fill a key knowledge gap regarding the drivers of overwintering location and help determine whether drivers change with fish age, size, and/or experience. Additional information on age-at-maturity and spawning frequency of Dolly Varden will be important to further inform the management of the local fishery, as well as studying spawning status and body condition over time and in relation to overwintering location and migration patterns.

Chapter 6

General Discussion

Anadromous Arctic Char and Dolly Varden are highly valued by Inuit fishers in the community of Kugluktuk, Nunavut. Both species are facultatively anadromous and anadromous individuals exhibit considerable diversity in migration tactics (e.g., Johnson 1989; Gilbert et al. 2016; Gallagher et al. 2018b). The Coppermine River and Coronation Gulf near Kugluktuk present a unique opportunity to study anadromous Arctic Char and Dolly Varden that occur in sympatry both in freshwater overwintering locations and in marine environments. Research in this thesis addressed community questions and gaps in both scientific and Inuit knowledge regarding life history and migration tactics of Arctic Char and Dolly Varden that use the Coppermine River. Key findings are synthesized below and summarized in Figure 6.1.

In Chapter 2, I described and demonstrated the application of the R package `mort`, which was developed with the goal of reducing bias and improving reproducibility in studies that use acoustic telemetry. This tool identifies potential mortalities or expelled tags from acoustic telemetry datasets and was subsequently applied to the datasets that were analyzed in Chapter 3, Chapter 4, and Chapter 5. As additional detection records were downloaded over the course of this thesis (four seasons of data in Chapter 3 to six seasons of data in Chapter 5), new detection histories and movement patterns were observed over time. The functions in `mort` were consistently able to identify detections from tags that were stationary or moving passively (e.g., likely to be from downstream drift rather than active movements), which were removed from the datasets before further analyses were conducted.

Genotyping data were not available or considered feasible at the time of writing and publishing Chapter 3. Network analysis and local spatial statistics indicated that char preferred coastal locations to locations offshore or near islands (Chapter 3), which is consistent with the suggestion that Arctic Char prefer coastal locations in another system in the central Arctic in Canada (Moore et al. 2016). Subsequent genotyping (Chapter 5) indicated that the majority of char tagged and tracked in Chapter 3 were Dolly Varden, which suggests that Dolly Varden may also have a preference for coastal locations. Dolly Varden have previously been observed frequenting offshore locations (Courtney et al. 2018; Gallagher et al. 2021), but preference was unknown.

Recent genotyping also indicated that no tagged Arctic Char migrated above Kugluk or Bloody Falls (hereafter, “the falls”); fish that migrated above the falls were all Dolly Varden. There was a link between overwintering location and patterns of movement in the marine environment. Although not all fish that migrated above the falls made intensive marine movements and movement patterns were not consistent or repeatable among years (i.e., within individual), all fish that exhibited intensive movements in the marine environment migrated above the falls upon return to fresh water (Chapter 3). Intensive movements were suggested to be a tactic to conserve energy (relative to long distance movements) in the marine environment. Dolly Varden are intermittent spawners (Armstrong and Morrow 1980; Gallagher et al. 2018b); individuals may thus have exhibited intensive movement patterns in spawning years (with spawning suggested to occur above the falls), but further information on spawning frequency is required in this system.

The length and difficulty of the migratory pathway in fresh water was associated with timing of return to fresh water; Dolly Varden that overwintered above the falls returned to fresh water earlier than Dolly Varden that overwintered below the falls (Chapter 3, with genotyping from Chapter 5). A similar relationship could not be identified for Arctic Char, because Arctic Char were only observed overwintering below the falls (i.e., a single migratory pathway in fresh water). The timing of return to fresh water was influenced by environment for both species (Chapter 4). The primary driver of freshwater return was sea surface temperature; all char returned to fresh water as sea surface temperatures increased. Sea surface temperature was a better predictor of return timing than day of year or photoperiod, which suggested that timing was a plastic response to environmental conditions. The threshold for return differed among groups; compared to Dolly Varden that overwintered above the falls, Arctic Char and Dolly Varden that overwintered below the falls returned when sea surface temperature was warmer (i.e., later in the season). Water temperatures in the Coppermine River were remarkably warm when Dolly Varden that overwintered above the falls returned to fresh water (Chapter 4), although thermal tolerances of Dolly Varden are largely unknown. Continued and early warming of river temperatures due to climate change may result in potential decoupling between the cue to return (sea surface temperature) and suitable environmental conditions in the river.

Environmental changes may have differential impacts on Arctic Char and Dolly Varden, due to differences in spawning locations between species. Char captured during the ice-free season, largely in the marine environment, were primarily Dolly Varden, whereas char captured during the ice-covered season in the Coppermine River were primarily Arctic Char (Chapter 5). Arctic Char likely migrated to

alternate (unknown) river systems in spawning years and overwintered in the easily accessible lower reaches of the Coppermine River in non-spawning years. Similarly, Dolly Varden likely migrated above the falls in spawning years and overwintered below the falls in (some) non-spawning years; younger and smaller Dolly Varden were more likely to overwinter below the falls and there was no conclusive evidence of spawning activity below the falls (Chapter 5). Spawning locations and frequency remain unknown for both Arctic Char and Dolly Varden that use the Coppermine River.

Although both species made rapid, directed movements towards fresh water while in the marine environment, Arctic Char exhibited movements after returning to fresh water that were consistent with intent to overwinter below the falls; Arctic Char staged longer at the river mouth and moved upstream more slowly than Dolly Varden that overwintered above the falls (Chapter 5). These movements were also consistent with the observation that char of both species that overwintered below the falls moved into the river passively (i.e., with rising tides; Chapter 4). Conversely, Dolly Varden that overwintered above the falls exhibited more directed movements; although tide may have assisted Dolly Varden in ascending the falls, return to fresh water was not influenced by tides and the interval between returning to fresh water and ascending the falls was brief (Chapter 4). Movements of Dolly Varden that overwintered above the falls thus reflected intent to overwinter above the falls. Environmental influences on return migration for Dolly Varden that overwintered below the falls were similar to Arctic Char (Chapter 4), but movement patterns during return migration were inconsistent (i.e., some movements were similar to Arctic Char and some were similar to Dolly Varden that overwintered above the falls; Chapter 5). Some Dolly Varden may thus intend to overwinter below the falls, whereas others may fail to ascend the falls.

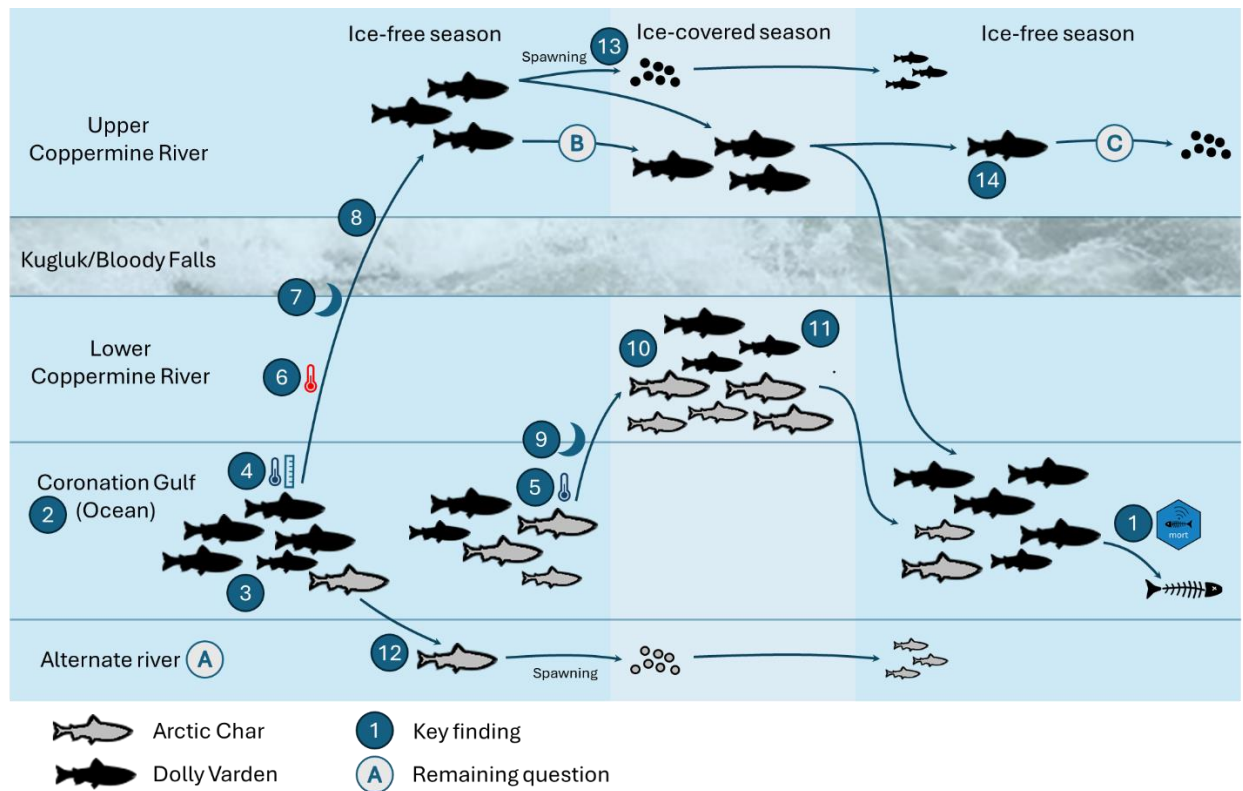


Figure 6.1: Graphical summary of key findings and remaining questions. Key findings or contributions from this thesis include: 1) development of the R package `mort` to identify potential mortalities and expelled tags in acoustic telemetry studies; 2) char preferentially used coastal habitats in the marine environment; 3) most char captured during the ice-free season were Dolly Varden; 4) Dolly Varden that overwintered above the falls returned to fresh water earlier, in response to sea surface temperature and a longer and more challenging migratory pathway; 5) Arctic Char and Dolly Varden that overwintered below the falls returned to fresh water in response to sea surface temperature, but at a higher (i.e., later in the year) temperature threshold than Dolly Varden that overwintered above the falls; 6) Dolly Varden that overwintered above the falls returned to fresh water when river temperatures were warm and potentially stressful; 7) Dolly Varden ascended the falls at rising or high tide; 8) only Dolly Varden (i.e., no Arctic Char) ascended the falls; 9) Arctic Char and Dolly Varden that overwintered below the falls returned to fresh water passively with rising or high tide, and Arctic Char staged longer and moved upstream slower than Dolly Varden that migrated above the falls; 10) most char that overwintered below the falls were Arctic Char; 11) younger, smaller, immature, and/or non-spawning Dolly Varden were more likely to overwinter below the falls; 12) Arctic Char likely spawn in alternate river systems (i.e., not the Coppermine River); 13) Dolly Varden likely spawn above the falls; and, 14) some Dolly

(Figure 6.1 continued): Varden skipped marine migrations in some years. Remaining questions include: A) alternate rivers (likely spawning locations) used by Arctic Char; B) spawning status of Dolly Varden that migrate above the falls; and, C) relationship between spawning status and skipped migration in some Dolly Varden.

6.1 Implications for fisheries management

The char fishery near Kugluktuk is managed by the community through the Kugluktuk Hunters and Trappers Organization. Although community members have voiced concerns regarding low numbers of harvested char and observed changes in migration patterns, no conservation concern has currently been identified. In years that some fishers reported low catches, others reported normal or high catches (numerous community members, pers. comm.). Freshwater systems in the Arctic are extremely vulnerable to climate change and face numerous interconnected impacts (Heino et al. 2020; Saros et al. 2023). If a conservation concern is identified in the future for Arctic Char and/or Dolly Varden in the Coppermine River and Coronation Gulf, several challenges and opportunities for fisheries management have been revealed from the research presented in this thesis.

Similarities in habitat use and migration timing either between species (Arctic Char and Dolly Varden) or between overwintering groups of Dolly Varden (above falls or below falls) present challenges for fisheries management. Arctic Char and Dolly Varden, regardless of overwintering location, preferentially used coastal habitats and were observed at similar locations in the marine environment (Chapter 3). Both Arctic Char and Dolly Varden were observed overwintering below the falls, and the timing of return to fresh water and the environmental influences on return timing were similar for individuals of both species that overwintered below the falls (Chapter 4). Dolly Varden that overwintered above the falls returned to fresh water earlier than fish that overwintered above the falls, but return timing depended on sea surface temperature and was variable among years (Chapter 4). Any management actions would thus likely need to incorporate annual environmental conditions. Targeting or avoiding harvests of a species or overwintering group will be challenging if there is future evidence (e.g., based on identification of spawning locations or frequency) that active management or conservation measures are necessary.

Arctic Char likely spawn in alternate river systems (i.e., rivers other than the Coppermine) and overwinter in the lower reaches of the Coppermine River in non-spawning years (Chapter 5). The winter fishery is important for many community members from Kugluktuk, who set nets under the ice in the

Coppermine River below the falls. Arctic Char are likely disproportionately captured in the winter fishery; the majority of char that overwinter below the falls are Arctic Char (Chapter 5). Arctic Char may also be more susceptible to harvesting pressures than Dolly Varden due to prolonged periods in areas of high harvest activity during return migration to fresh water; Arctic Char were observed to stage longer at the river mouth and move upstream more slowly than Dolly Varden that overwintered above the falls (Chapter 5). Spawning locations of Arctic Char are currently unidentified; environmental pressures in critical freshwater habitats (i.e., spawning habitats, or migratory pathways towards spawning habitats) and potential cumulative effects from multiple stressors are thus unknown and may impact the sustainability of the local char fishery. If a conservation concern is identified for Arctic Char in the future, possible management measures could include focusing harvests in the marine environment (most char captured in the marine environment were Dolly Varden; Chapter 5) or early in the ice-free season at the falls or in the river (Dolly Varden that migrated above the falls returned to fresh water earlier than other char, and no Arctic Char migrated above the falls; Chapter 4).

Dolly Varden that overwintered above the falls were observed returning to fresh water when river temperatures were warm, due to potential decoupling between migration cues (sea surface temperature) and suitable environmental conditions in the freshwater migration corridor (Chapter 4). The temperatures experienced by some Dolly Varden exceeded stressful and even lethal temperatures for Arctic Char, but thermal tolerances of Dolly Varden are unknown. Dolly Varden that overwintered above the falls exhibited minimal staging at the river mouth and moved upstream quickly after returning to fresh water (Chapter 5), and thus likely did not have an acclimation period before migrating upstream. Another potential stressor for Dolly Varden that overwinter above the falls is a reduced period of marine foraging; Dolly Varden that overwintered above the falls returned to fresh water earlier than char that overwintered below the falls (Chapter 3), and had less time to acquire resources for growth, reproduction, and/or survival. Snagging (capture by hooking the body) is a common fishing practice that occurs at the falls and can lead to injury of fish and is concerning to some community members (Amanda Dumond and Eric Hitkolok, pers. comm.). All char that were observed migrating above the falls were Dolly Varden, and all spawning Dolly Varden likely migrated above the falls (Chapter 5). Spawning Dolly Varden are thus likely to be disproportionately affected by warm river temperatures, changes in marine prey, and snagging. If a conservation concern is identified for Dolly Varden in the Coppermine River in the future, possible management measures could include focusing

harvests later in the season (after most Dolly Varden have migrated above the falls) or at locations other than the falls.

6.2 Future directions

The research presented in this thesis has provided key findings about migration patterns and tactics of char that use the Coppermine River, but several crucial questions remain (Figure 6.1). The primary objective that led to development and implementation of this research program was identification of spawning locations. Although it is likely that Arctic Char spawn in alternate river systems and Dolly Varden spawn in the upper reaches of the Coppermine River watershed (Chapter 5), spawning locations remain unknown for both species. The majority of tagged char were Dolly Varden; identifying overwintering locations of Arctic Char in alternate rivers using acoustic telemetry will require focusing tagging efforts at times and locations (e.g., late in the ice-free period, below the falls) that maximize probability of capturing Arctic Char, as well as potentially expanding receiver coverage to include a larger spatial area. Chemical tracers (e.g., strontium isotopes) in the freshwater rearing portion of Arctic Char otoliths could also be used to refine a list of candidate systems. A pilot radio tagging project has recently identified some overwintering locations of Dolly Varden in the main stem of the Coppermine River above the falls (DePasquale 2025), but it is unknown if these are also spawning locations, or if Dolly Varden move into other locations along the main stem or tributaries to spawn. Continued radio tracking is recommended to identify overwintering locations and consistency in overwintering locations among years. For both species, identification of suggested spawning locations should be confirmed by observation of spawning activity or redds (e.g., video footage from remote operated vehicle) and/or capture of fry.

Spawning frequency and age of maturity are unknown for both Arctic Char and Dolly Varden that use the Coppermine River. Information on age and/or size of maturity will be beneficial to fisheries managers in understanding the potential effects of size-selective fishing methods (e.g., gillnetting) on recruitment. Age of maturity can be identified by inspection of gonads (reproductive status) and otoliths (age). Typically, only the heads of char have been obtained from past community sampling initiatives; future sampling programs could collect both heads and internal organs from char harvested by subsistence fishers. Similarly, samples could be obtained from Dolly Varden harvested at the falls to identify spawning status and data could then be incorporated with migration patterns identified from acoustic telemetry data to infer spawning frequency. Identifying the spawning status of Dolly Varden

that migrate above the falls and determining if spawning status is related to movement patterns in the marine environment (e.g., intensive movements, Chapter 3) or timing of return migration (Chapter 4) will be essential in understanding potential stressors experienced by spawning individuals.

Spawning frequency in another population of Dolly Varden in Arctic Canada is associated with migration frequency, likely due to high energetic demands of reproduction (Gallagher et al. 2018b). The skipped migrations exhibited by some Dolly Varden that overwintered above the falls (Chapter 5) may similarly be associated with spawning and energy stores. Alternatively, a two-step migration may be required to access some spawning grounds (similar to Arctic Char in Nauyuk Lake, Nunavut; Johnson 1989).

Identifying spawning locations of Dolly Varden above the falls (see above) is necessary to identify potential environmental conditions (e.g., low water levels) that may restrict access to spawning locations. If skipped migrations are associated with two-step migrations to spawning locations and/or environmental conditions, past migration histories can be reconstructed using chemical tracers (e.g., strontium) in otoliths from historic and contemporary samples to infer if skipping migrations is a new response (e.g., to recent low water levels) or a historic adaptation.

Assessment of physical samples indicated that younger and smaller Dolly Varden were more likely to overwinter below the falls (Chapter 5). Tagged Dolly Varden were all large (fork lengths ≥ 539 mm), to minimize tag burden; it is unknown if any smaller individuals attempted or were successful in ascending the falls. Smaller and likely immature Dolly Varden could be tagged with smaller acoustic tags, which would allow determination of whether any smaller individuals ascend the falls and if migration patterns change with ontogeny. Results could provide insight into the movement patterns observed during return migration of larger Dolly Varden that overwintered below the falls (Chapter 5).

As mentioned above, Dolly Varden that overwintered above the falls returned to fresh water when river temperatures were warm and potentially stressful (Chapter 4) and movement patterns indicated there were minimal opportunities for individuals to acclimate to warm temperatures before migrating upstream (Chapter 5). Identifying the thermal tolerances and responses to acclimation through field-based studies (e.g., as conducted for Arctic Char; Gilbert et al. 2020, 2022) would elucidate whether Dolly Varden have a higher thermal tolerance than Arctic Char or if warm river temperatures may have adverse effects on migrating Dolly Varden. Continued monitoring of environmental conditions (sea surface temperature, river temperature) and timing of return migration to fresh water would allow

testing of predictions from the model generated in Chapter 4, and identify if migration cues (sea surface temperature) become further decoupled from suitable river conditions.

Finally, although recent advances in genotyping (Liu et al. 2023) have allowed the description of species composition in the marine environment during the ice-free season and in fresh water (below the falls) in the ice-covered season (Chapter 5), historic species composition of Arctic Char and Dolly Varden in the Coppermine River remains unknown. Dolly Varden may have previously inhabited the Coppermine River and been mis-identified as Arctic Char, or Dolly Varden may have more recently expanded into the Coppermine River system and displaced Arctic Char. Identifying historic species composition through genotyping of archived tissue samples, in concert with current and evolving knowledge of migration patterns and environmental influences, could provide important insight into potential competition between Arctic Char and Dolly Varden and interactions with ongoing impacts of environmental change.

6.3 Concluding remarks

The research presented in this thesis describes the life history and migration tactics of anadromous Arctic Char and Dolly Varden that use the Coppermine River, the only freshwater system that is known to support anadromous life history types of both species. Although anadromous individuals of both species occur in sympatry in the accessible lower reaches of the Coppermine River during ice-covered periods, spawning habitats are believed to be distinct; Dolly Varden likely spawn in the upper reaches of the Coppermine River system and Arctic Char likely spawn in alternate river systems (Chapter 5). The two species may thus be reproductively isolated, which has been observed in systems where anadromous Dolly Varden occur with resident Arctic Char (DeLacy and Morton 1943; Craig 1977; Taylor et al. 2008; May-McNally et al. 2015; Dennert et al. 2016). Environmental cues for migration timing differed between species and overwintering locations, and differences in experienced thermal conditions during return migration in fresh water (Chapter 4) may reflect differences in thermal tolerances between the two species. This information, along with future work to identify spawning locations and historic species composition of chars in the Coppermine River, will provide insight into potential interspecific competition and further knowledge of both current and future distributions of the two species in this and other regions.

The Arctic is experiencing rapid and unprecedented climate change (Rantanen et al. 2022). Arctic Char and Dolly Varden are both highly plastic species, as demonstrated by the diversity in migration patterns observed both among years and among individuals (Chapter 3, Chapter 4, and Chapter 5). Diversity in

migration tactics (e.g., multiple overwintering locations, annual or skipped migrations) may promote resilience in each of the two species, but a shift in tactics in response to changing environmental conditions will likely have consequences for individual fitness and may affect populations of each species differently. As iteroparous species, Arctic Char and Dolly Varden must balance reproductive effort with survival (and associated future reproductive effort). Anadromy is associated with increased body size and fecundity, relative to residency (Jonsson and Jonsson 1993), but environmental changes that affect survival would influence the relative benefits of anadromy (e.g., Reist et al. 2006). For instance, the potential mismatch or decoupling that we observed between the cue for return migration and thermal conditions in fresh water for Dolly Varden that overwintered above the falls (Chapter 4) may have implications for survival of anadromous individuals if river (i.e., the migration corridor) temperatures continue to warm. Similarly, if access to spawning locations or other critical habitats is hindered by low water levels, a reduction in survival and/or reproductive success of anadromous individuals may be observed. Within a conditional life history strategy, a change in the relative benefits of anadromy may select for a shift in thresholds at the decision point(s) that determine occurrence and/or frequency of anadromy. Both anadromous Dolly Varden and Arctic Char rely on the marine environment for foraging and cease or greatly reduce feeding in fresh water (Moore and Moore 1974; Boivin and Power 1990; Rikardsen et al. 2003; Stewart et al. 2009). A change in prevalence and/or frequency of migration would thus have cascading effects on freshwater ecosystems.

Results from current and future studies on how migration and other life history tactics respond to changes in environmental conditions are needed to broaden and deepen our understanding of life history and evolution in Salmonidae and other taxa. Research on members of the family Salmonidae has contributed greatly to our understanding of evolutionary processes (e.g., sympatric divergence, philopatry, sexual selection; Stearns and Hendry 2004) and life history theory (e.g., conditional life histories, status-dependent selection; Gross 1996). Both Arctic Char and Dolly Varden occupy and display adaptations to a diverse array of challenging Arctic environments. The remarkable phenotypic diversity and plasticity displayed by the two species, in conjunction with the rapid environmental changes that are already being experienced throughout their distributional ranges, means that responses to change and associated selection processes may be observed on short time scales relative to other long-lived and iteroparous species. Studying changes in migration and other life history tactics of Arctic Char and Dolly Varden may thus provide additional insights into evolutionary processes and life

history tradeoffs, and the Coppermine River provides a unique opportunity to study migration of the two species in sympatry.

Knowledge gained from this work regarding the life history and migration tactics of Arctic Char and Dolly Varden that use the Coppermine River informs future studies of these two species in other regions, and furthers our understanding of how the life history and population viability of each species may respond to climate change. The results also have practical and immediate importance. Char are harvested in or near the Coppermine River throughout the year by Inuit fishers from Kugluktuk, Nunavut. An abundant, local source of nutritious food such as char is of critical importance in a territory where over 75% of Inuit individuals experience food insecurity (Statistics Canada 2024), and where store-bought items are expensive and transported by air or once a year by barge. Harvesting and consuming country foods is essential for social and cultural well-being, and contributes to the vitality and maintenance of Indigenous languages and skills (Van Oostdam et al. 2005; Carter et al. 2025). Ongoing monitoring of life history and migration tactics of char that use the Coppermine River is critically important, as both freshwater and marine environments continue to experience effects of rapid climate change. Addressing remaining knowledge gaps, in particular locations and frequency of spawning, and how migration patterns relate to spawning status, will be essential to inform fisheries management and promote sustainability of these invaluable subsistence food fishes.

References

- Agostinelli, C., and Lund, U. 2023. R package “circular”: Circular Statistics. Available from CRAN.R-project.org/package=circular.
- Alerstam, T., Hedenström, A., and Åkesson, S. 2003. Long-distance migration: Evolution and determinants. *Oikos* **103**(2): 247–260. doi:10.1034/j.1600-0706.2003.12559.x.
- Anderson, D.R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer Science and Business Media, New York, NY.
- Anderson, J.H., Faulds, P.L., Atlas, W.I., and Quinn, T.P. 2013. Reproductive success of captively bred and naturally spawned Chinook Salmon colonizing newly accessible habitat. *Evol Appl* **6**(2): 165–179. doi:10.1111/j.1752-4571.2012.00271.x.
- Andrews, C.W., and Lear, E. 1956. The biology of Arctic Char (*Salvelinus alpinus* L.) in Northern Labrador. *J Fish Res Bd Can* **13**(6): 843–860. doi:10.1139/f56-047.
- Armstrong, R.H. 1974. Migration of anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. *J Fish Res Bd Can* **31**(4): 435–444. doi:10.1139/f74-071.
- Armstrong, R.H., and Morrow, J.E. 1980. The Dolly Varden Charr, *Salvelinus malma*. In Charrs: Salmonid Fishes of the Genus *Salvelinus*. Edited by E.K. Balon. Dr. W. Junk bv Publishers, The Hague, The Netherlands. pp. 99–140.
- Arostegui, M.C., and Quinn, T.P. 2019. Reliance on lakes by salmon, trout and charr (*Oncorhynchus*, *Salmo* and *Salvelinus*): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish Fish* **20**(4): 775–794. doi:10.1111/faf.12377.
- Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J Exp Biol* **35**(1): 109–133.
- Baisez, A., Bach, J., Leon, C., Parouty, T., Terrade, R., Hoffmann, M., and Laffaille, P. 2011. Migration delays and mortality of adult Atlantic Salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endang Species Res* **15**(3): 265–270. doi:10.3354/esr00384.
- Banks, J.W. 1969. A review of the literature on the upstream migration of adult salmonids. *J Fish Biol* **1**(2): 85–136. doi:10.1111/j.1095-8649.1969.tb03847.x.

- Barneche, D.R., Robertson, D.R., White, C.R., and Marshall, D.J. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* **360**(6389): 642–645. doi:10.1126/science.aao6868.
- Barton, K. 2019. MuMIn: Multi-Model Inference. Available from <https://cran.r-project.org/package=MuMIn>.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**(1): 1–48.
- Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press, New York, NY.
- Beamish, F.W.H. 1980. Biology of the North American anadromous Sea Lamprey, *Petromyzon marinus*. *Can J Fish Aquat Sci* **37**: 1924–1943.
- Beddow, T.A., Deary, C., and McKinley, R.S. 1998. Migratory and Reproductive Activity of Radio-Tagged Arctic Char (*Salvelinus alpinus* L.) in Northern Labrador. *In* *Advances in Invertebrates and Fish Telemetry*. Edited by J.-P. Lagardère, M.-L.B. Anras, and G. Claireaux. Springer Netherlands, Dordrecht. pp. 249–262. doi:10.1007/978-94-011-5090-3_29.
- Bégout Anras, M.L., Gyselman, E.C., Jorgenson, J.K., Kristofferson, A.H., and Anras, L. 1999. Habitat preferences and residence time for the freshwater to ocean transition stage in Arctic Charr. *J Mar Biol Assoc UK* **79**(1): 153–160. doi:10.1017/S0025315498000174.
- Bell, D.A., Kovach, R.P., Vulstek, S.C., Joyce, J.E., and Tallmon, D.A. 2017. Climate-induced trends in predator–prey synchrony differ across life-history stages of an anadromous salmonid. *Can J Fish Aquat Sci* **74**(9): 1431–1438. doi:10.1139/cjfas-2016-0309.
- Bentley, K.T., Schindler, D.E., Cline, T.J., Armstrong, J.B., Macias, D., Ciepiela, L.R., and Hilborn, R. 2014. Predator avoidance during reproduction: Diel movements by spawning Sockeye Salmon between stream and lake habitats. *J Anim Ecol* **83**(6): 1478–1489. doi:10.1111/1365-2656.12223.
- Berg, O.K., and Berg, M. 1989. Sea growth and time of migration of anadromous Arctic Char (*Salvelinus alpinus*) from the Vardnes River, in Northern Norway. *Can J Fish Aquat Sci* **46**(6): 955–960. doi:10.1139/f89-123.

- Berg, O.K., and Berg, M. 1993. Duration of sea and freshwater residence of Arctic Char (*Salvelinus alpinus*), from the Vardnes River in northern Norway. *Aquaculture* **110**(2): 129–140. doi:10.1016/0044-8486(93)90267-3.
- Berg, O.K., and Jonsson, B. 1989. Migratory Patterns of Anadromous Atlantic Salmon, Brown Trout and Arctic Charr from the Vardnes River in Northern Norway. *In* Proceedings of the Salmonid Migration and Distribution Symposium, June 23-25, 1987. *Edited by* E. Brannon and B. Jonsson. School of Fisheries, University of Washington, Seattle, WA. pp. 106–115.
- Bett, N.N., and Hinch, S.G. 2016. Olfactory navigation during spawning migrations: A review and introduction of the Hierarchical Navigation Hypothesis. *Biol Rev* **91**(3): 728–759. doi:10.1111/brv.12191.
- Biggs, C., and Nemeth, R. 2016. Spatial and temporal movement patterns of two snapper species at a multi-species spawning aggregation. *Mar Ecol Prog Ser* **558**: 129–142. doi:10.3354/meps11846.
- Bivand, R.S., and Wong, D.W.S. 2018. Comparing implementations of global and local indicators of spatial association. *TEST* **27**(3): 716–748. doi:10.1007/s11749-018-0599-x.
- Blackman, B.G. 2002. Radio telemetry studies of Arctic Grayling migrations to overwinter, spawning and summer feeding areas in the Parsnip River watershed. Peace/Williston Fish and Wildlife Compensation Program, Prince George, BC.
- Bohaboy, E.C., Guttridge, T.L., Hammerschlag, N., Van Zinnicq Bergmann, M.P.M., and Patterson, W.F. 2020. Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. *ICES J Mar Sci* **77**(1): 83–96. doi:10.1093/icesjms/fsz202.
- Boivin, T.G., and Power, G. 1990. Winter condition and proximate composition of anadromous Arctic Charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. *Can J Zool* **68**(11): 2284–2289. doi:10.1139/z90-319.
- Bommersbach, C.K., Grenier, G., Gendron, H., Harris, L.N., Janjua, M.Y., Mandrak, N.E., and Tallman, R.F. 2024. Climate change and Arctic Charr (*Salvelinus alpinus*) in North America: Modelling possible changes in range with different climate scenarios and interspecific interactions. *Ichthyol Res*. doi:10.1007/s10228-024-00987-9.

- Bond, M.H., Miller, J.A., and Quinn, T.P. 2015. Beyond dichotomous life histories in partially migrating populations: Cessation of anadromy in a long-lived fish. *Ecology* **96**(7): 1899–1910. doi:10.1890/14-1551.1.
- Bond, M.H., and Quinn, T.P. 2013. Patterns and influences on Dolly Varden migratory timing in the Chignik Lakes, Alaska, and comparison of populations throughout the northeastern Pacific and Arctic oceans. *Can J Fish Aquat Sci* **70**(5): 655–665. doi:10.1139/cjfas-2012-0416.
- Borcard, D., Gillet, F., and Legendre, P. 2018. Numerical Ecology With R. Second edition. Springer International Publishing, Cham, Switzerland.
- Bouchard, C., Geoffroy, M., LeBlanc, M., and Fortier, L. 2018. Larval and adult fish assemblages along the Northwest Passage: The shallow Kitikmeot and the ice-covered Parry Channel as potential barriers to dispersal. *Arct Sci* **4**(4): 781–793. doi:10.1139/as-2018-0003.
- Brock, G., Pihur, V., Datta, S., and Datta, S. 2008. cValid: An R package for cluster validation. *J Stat Softw* **25**(4): 1–22.
- Brooks, M., E., Kristensen, K., Benthem, K., J., van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., and Bolker, B., M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* **9**(2): 378. doi:10.32614/RJ-2017-066.
- Brown, R.J., Courtney, M.B., and Seitz, A.C. 2019. New insights into the biology of anadromous Dolly Varden in the Canning River, Arctic National Wildlife Refuge, Alaska. *Trans Am Fish Soc* **148**(1): 73–87. doi:10.1002/tafs.10122.
- Brown, R.J., Loewen, M.B., and Tanner, T.L. 2014. Overwintering locations, migrations, and fidelity of radio-tagged Dolly Varden in the Hulahula River, Arctic National Wildlife Refuge, 2007–09. *Arctic* **67**(2): 149. doi:10.14430/arctic4379.
- Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., and Lowerre-Barbieri, S.K. 2011. A standardized terminology for describing reproductive development in fishes. *Mar Coast Fish* **3**(1): 52–70. doi:10.1080/19425120.2011.555724.
- Brunson, J., and Read, Q. 2023. ggalluvial: Alluvial Plots in “ggplot2.” Available from <http://corybrunson.github.io/ggalluvial/>.

- Byers, T., Reist, J.D., and Sawatzky, C.D. 2019. Compilation and synopsis of literature on the Traditional Knowledge of Indigenous Peoples in the Northwest Territories concerning Dolly Varden. Fisheries and Oceans Canada.
- Bystriansky, J.S., Frick, N.T., Richards, J.G., Schulte, P.M., and Ballantyne, J.S. 2007. Wild Arctic Char (*Salvelinus alpinus*) upregulate gill Na⁺,K⁺-ATPase during freshwater migration. *Physiol Biochem Zool* **80**(3): 270–282. doi:10.1086/512982.
- Cameron, A., and van den Brand, T. 2022. geomtextpath: Curved Text in “ggplot2.” Available from <https://cran.r-project.org/package=geomtextpath>.
- Campbell, H.A., Watts, M.E., Dwyer, R.G., and Franklin, C.E. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. *Mar Freshwater Res* **63**(9): 815. doi:10.1071/MF12194.
- Canadian Hydrographic Service. 2022a. Non-navigational Bathymetric Data. Available from <https://data.chs-shc.ca> [accessed 17 April 2023].
- Canadian Hydrographic Service. 2022b. Tides, currents, and water levels. Available from <https://tides.gc.ca/en/> [accessed 28 November 2023].
- Canadian Ice Service. 2021. Climatic Ice Atlas 1991-2020. Available from <http://iceweb1.cis.ec.gc.ca/30Atlas/> [accessed 13 February 2023].
- Capizzano, C.W., Mandelman, J.W., Hoffman, W.S., Dean, M.J., Zemeckis, D.R., Benoît, H.P., Kneebone, J., Jones, E., Stettner, M.J., Buchan, N.J., Langan, J.A., and Sulikowski, J.A. 2016. Estimating and mitigating the discard mortality of Atlantic Cod (*Gadus morhua*) in the Gulf of Maine recreational rod-and-reel fishery. *ICES J Mar Sci* **73**(9): 2342–2355. doi:10.1093/icesjms/fsw058.
- Carothers, C., Black, J., Langdon, S.J., Donkersloot, R., Ringer, D., Coleman, J., Gavenus, E.R., Justin, W., Williams, M., Christiansen, F., Samuelson, J., Stevens, C., Woods, B., Clark, S.J., Clay, P.M., Mack, L., Raymond-Yakoubian, J., Sanders, A.A., Stevens, B.L., and Whiting, A. 2021. Indigenous peoples and salmon stewardship: A critical relationship. *Ecol Soc* **26**(1): 16. doi:10.5751/ES-11972-260116.
- Carter, N.A., Van Luijk, N., Dawson, J., Parker, C., Grey, K., Provencher, J., Emiktaut, C., Simonee, N., Song, G., and Wesche, S. 2025. *Niqivut* (our food)—dimensions of Inuit country food harvesting and

- significance in Arctic Canada: Bountiful, seasonal, “soul food.” *Arct Sci* **11**: 1–15. doi:10.1139/as-2024-0007.
- Chamberlain, S. 2024. rerddap: General Purpose Client for “ERDDAP” Servers. Available from <https://cran.r-project.org/package=rerddap>.
- Chapman, B.B., Brönmark, C., Nilsson, J., and Hansson, L. 2011. The ecology and evolution of partial migration. *Oikos* **120**(12): 1764–1775. doi:10.1111/j.1600-0706.2011.20131.x.
- Charnov, E.L., and Schaffer, W.M. 1973. Life-history consequences of natural selection: Cole’s result revisited. *Am Nat* **107**(958): 791–793. doi:10.1086/282877.
- Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Fisheries and Oceans Canada, Ottawa, ON.
- Coad, B.W. 2018. Family Osmeridae: Smelts, Éperlans. *In* Marine Fishes of Arctic Canada. *Edited by* B.W. Coad and J.D. Reist. University of Toronto Press, Toronto, ON. pp. 240–247.
- Coad, B.W., and Reist, J.D. 2018. Marine Fishes of Arctic Canada. University of Toronto Press, Toronto, ON.
- Colborne, S.F., Sheppard, L.W., O’Donnell, D.R., Reuman, D.C., Walter, J.A., Singer, G.P., Kelly, J.T., Thomas, M.J., and Rypel, A.L. 2022. Intraspecific variation in migration timing of Green Sturgeon in the Sacramento River system. *Ecosphere* **13**(6): e4139. doi:10.1002/ecs2.4139.
- Cole, L.C. 1954. The population consequences of life history phenomena. *Q Rev Biol* **29**(2): 103–137.
- Cott, P.A., Chavarie, L., Paszkowski, C.A., Swanson, H.K., and Tonn, W.M. 2023. Status and Management of Fisheries Resources in Canada’s Northern Territories. *In* Freshwater Fisheries in Canada: Historical and Contemporary Perspectives on the Resources and Their Management. *Edited by* C.T. Hasler, J.G. Imhof, N.E. Mandrak, and S.J. Cooke. American Fisheries Society, Bethesda, Maryland. pp. 177–203.
- Coulombe-Pontbriand, M., Reid, R., and Jackson, F. 1998. Coppermine River: Overview of the hydrology and water quality. Water Resources Division, Indian and Northern Affairs Canada, Yellowknife, NWT.

- Courtney, M.B., Scanlon, B., Brown, R.J., Rikardsen, A.H., Gallagher, C.P., and Seitz, A.C. 2018. Offshore ocean dispersal of adult Dolly Varden *Salvelinus malma* in the Beaufort Sea. *Polar Biol* **41**(4): 817–825. doi:10.1007/s00300-017-2246-5.
- Craig, P.C. 1977. Ecological Studies of Anadromous and Resident Populations of Arctic Char in the Canning River Drainage and Adjacent Coastal Waters of the Beaufort Sea, Alaska. *In* Fisheries Investigations Along the North Slope and Beaufort Sea Coast in Alaska with Emphasis on Arctic Char. *Edited by* P.J. McCart. Arctic Gas Biological Report. pp. 1–116.
- Craig, P.C., and Haldorson, L. 1980. Fish. *In* Environmental Assessment of the Alaskan Continental Shelf: Final Reports of Principal Investigators. Volume 7: Biological Studies. National Oceanic and Atmospheric Administration. pp. 384–687.
- Crane, P., Viavant, T., and Wenburg, J. 2005. Overwintering Patterns of Dolly Varden, *Salvelinus malma*, in the Sagavanirktok River in the Alaskan North Slope Inferred Using Mixed-Stock Analysis. U.S. Fish and Wildlife Service.
- Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., and Cooke, S.J. 2017. Acoustic telemetry and fisheries management. *Ecol Appl* **27**(4): 1031–1049. doi:10.1002/eap.1533.
- Csárdi, G., and Nepusz, T. 2006. The igraph software package for complex networks. Available from igraph.org.
- Currey, L.M., Heupel, M.R., Simpfendorfer, C.A., and Williams, A.J. 2014. Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. *Mar Biol* **161**(9): 2155–2166. doi:10.1007/s00227-014-2497-4.
- Curtis, J.M., Johnson, M.W., Diamond, S.L., and Stunz, G.W. 2015. Quantifying delayed mortality from barotrauma impairment in discarded Red Snapper using acoustic telemetry. *Mar Coast Fish* **7**(1): 434–449. doi:10.1080/19425120.2015.1074968.
- Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Löf, A., and Ragnarsson, B. 2004. The timing of spawning migration: Implications of environmental variation, life history, and sex. *Can J Zool* **82**(12): 1864–1870. doi:10.1139/z04-184.
- Dale, M.R.T. 2017. Applying Graph Theory in Ecological Research. Cambridge University Press, New York, NY.

- Dale, M.R.T., and Fortin, M.-J. 2014. Spatial Analysis: A Guide for Ecologists. Second edition. Cambridge University Press, Cambridge, United Kingdom.
- Davidson, J.G., Rikardsen, A.H., Thorstad, E.B., Halttunen, E., Mitamura, H., Præbel, K., Skarðhamar, J., and Næsje, T.F. 2013. Homing behaviour of Atlantic Salmon (*Salmo salar*) during final phase of marine migration and river entry. *Can J Fish Aquat Sci* **70**(5): 794–802. doi:10.1139/cjfas-2012-0352.
- DeCicco, A. 1997. Movements of postsmolt anadromous Dolly Varden in northwestern Alaska. *Am Fish S* **19**: 175–183.
- DeLacy, A.C., and Morton, W.M. 1943. Taxonomy and habits of the charrs, *Salvelinus malma* and *Salvelinus alpinus*, of the Karluk drainage system. *Trans Am Fish Soc* **72**(1): 79–91. doi:10.1577/1548-8659(1942)72[79:TAHOTC]2.0.CO;2.
- Dempson, J.B., and Green, J.M. 1985. Life history of anadromous Arctic Charr, *Salvelinus alpinus*, in the Fraser River, northern Labrador. *Can J Zool* **63**(2): 315–324. doi:10.1139/z85-048.
- Dempson, J.B., and Kristofferson, A.H. 1987. Spatial and Temporal Aspects of the Ocean Migration of Anadromous Arctic Char. *In* Common Strategies of Anadromous and Catadromous Fishes. *Edited by* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper. American Fisheries Society Symposium 1, Bethesda, Maryland. pp. 340–357.
- Dennert, A.M., May-McNally, S.L., Bond, M.H., Quinn, T.P., and Taylor, E.B. 2016. Trophic biology and migratory patterns of sympatric Dolly Varden (*Salvelinus malma*) and Arctic Char (*Salvelinus alpinus*). *Can J Zool* **94**(8): 529–539. doi:10.1139/cjz-2016-0004.
- DePasquale, S.W. 2025. Marine and freshwater habitats used by sympatric anadromous Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*S. malma malma*) in the central Canadian Arctic. Wilfrid Laurier University, Waterloo, ON. Available from <https://scholars.wlu.ca/etd/2780>.
- Dhellemmes, F., Aspillaga, E., and Monk, C.T. 2023. ATiltR: A solution for managing and filtering detections from passive acoustic telemetry data. *MethodsX* **10**: 102222. doi:10.1016/j.mex.2023.102222.
- Dickerson, B.R., Brinck, K.W., Willson, M.F., Bentzen, P., and Quinn, T.P. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology* **86**(2): 347–352. doi:10.1890/03-625.

- Dieperink, C., Bak, B.D., Pedersen, L. -F., Pedersen, M.I., and Pedersen, S. 2002. Predation on Atlantic Salmon and Sea Trout during their first days as postsmolts. *J Fish Biol* **61**(3): 848–852. doi:10.1111/j.1095-8649.2002.tb00917.x.
- Dingle, H., and Drake, V.A. 2007. What is migration? *BioScience* **57**(2): 113–121. doi:10.1641/B570206.
- Donaldson, M.R., Hinch, S.G., Suski, C.D., Fisk, A.T., Heupel, M.R., and Cooke, S.J. 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Front Ecol Environ* **12**(10): 565–573. doi:10.1890/130283.
- Dubos, V., May, P., Gillis, C.-A., St-Hilaire, A., and Bergeron, N. 2023. Nunavik anadromous Arctic Char life histories, behaviour, and habitat use informed by both Inuit knowledge and western science: A year in Ungava Bay. *Arct Sci*: as-2022-0019. doi:10.1139/as-2022-0019.
- Dunnington, D. 2022. ggspatial: Spatial Data Framework for ggplot2. Available from <https://cran.r-project.org/package=ggspatial>.
- Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic Charr (*Salvelinus alpinus*). *Copeia* **1986**(4): 945–955. doi:10.2307/1445291.
- Elliott, J.M., and Elliott, J.A. 2010. Temperature requirements of Atlantic Salmon *Salmo salar*, Brown Trout *Salmo trutta* and Arctic Charr *Salvelinus alpinus*: Predicting the effects of climate change. *J Fish Biol* **77**(8): 1793–1817. doi:10.1111/j.1095-8649.2010.02762.x.
- Ellis, T., Buckel, J., and Hightower, J. 2017. Winter severity influences Spotted Seatrout mortality in a southeast US estuarine system. *Mar Ecol Prog Ser* **564**: 145–161. doi:10.3354/meps11985.
- English, G., Wilson, B.M., Lawrence, M.J., Black, M., Hawkes, J.P., Hardie, D.C., Daniels, J.M., Carr, J.W., Rycroft, C., Crossin, G.T., Whoriskey, F.G., Den Heyer, C.E., Bordeleau, X., McKindsey, C.W., and Trudel, M. 2024. Determining early marine survival and predation by endothermic predators on acoustically tagged Atlantic Salmon (*Salmo salar*) post-smolts. *Can J Fish Aquat Sci* **81**(4): 387–402. doi:10.1139/cjfas-2023-0206.
- Environment and Climate Change Canada. 2024. Coppermine River above Copper Creek (10PC004). Available from https://wateroffice.ec.gc.ca/report/real_time_e.html?stn=10PC004 [accessed 25 January 2024].

- Erkinaro, J., Økland, F., Moen, K., Niemelä, E., and Rahiala, M. 1999. Return migration of Atlantic Salmon in the River Tana: The role of environmental factors. *J Fish Biol* **55**: 506–516.
- Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F., and Lowe, C.G. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fish Res* **108**(2–3): 364–371. doi:10.1016/j.fishres.2011.01.011.
- van Etten, J. 2017. R Package gdistance: Distances and routes on geographical grids. *J Stat Softw* **76**(13). doi:10.18637/jss.v076.i13.
- Figge, F. 2004. Bio-folio: Applying portfolio theory to biodiversity. *Biodivers Conserv* **13**(4): 827–849. doi:10.1023/B:BIOC.0000011729.93889.34.
- Finstad, A.G., and Hein, C.L. 2012. Migrate or stay: Terrestrial primary productivity and climate drive anadromy in Arctic Char. *Glob Change Biol* **18**(8): 2487–2497. doi:10.1111/j.1365-2486.2012.02717.x.
- Finstad, B., Nilssen, K.J., and Arnesen, A.M. 1989. Seasonal changes in sea-water tolerance of Arctic Charr (*Salvelinus alpinus*). *J Comp Physiol B* **159**(4): 371–378.
- Fitak, R.R., and Johnsen, S. 2017. Bringing the analysis of animal orientation data full circle: Model-based approaches with maximum likelihood. *J Exp Biol*: jeb.167056. doi:10.1242/jeb.167056.
- Flávio, H., and Baktoft, H. 2021. actel: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. *Methods Ecol Evol* **12**(1): 196–203. doi:10.1111/2041-210X.13503.
- Flávio, H., Kennedy, R., Ensing, D., Jepsen, N., and Aarestrup, K. 2020. Marine mortality in the river? Atlantic Salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fisheries Manag Ecol* **27**(1): 92–101. doi:10.1111/fme.12405.
- Fletcher, R., and Fortin, M.-J. 2018. *Spatial Ecology and Conservation Modeling: Applications in R*. Springer International Publishing.
- Fox, J., and Weisberg, S. 2019. *An R Companion to Applied Regression*. Third edition. Sage, Thousand Oaks, California, US. Available from <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

- Freeman, L.C., Borgatti, S.P., and White, D.R. 1991. Centrality in valued graphs: A measure of betweenness based on network flow. *Soc Networks* **13**(2): 141–154. doi:10.1016/0378-8733(91)90017-N.
- Furniss, R.A. 1975. Inventory and Cataloging of the Arctic Area Waters. Alaska Department of Fish and Game.
- Gallagher, C.P., Bajno, R., Reist, J.D., and Howland, K.L. 2020. Genetic mixed-stock analyses, catch-effort, and biological characteristics of Dolly Varden (*Salvelinus malma malma*) from the Rat River collected from subsistence harvest monitoring programs: 2009-2014. Fisheries and Oceans Canada, Ottawa, ON.
- Gallagher, C.P., Courtney, M.B., Seitz, A.C., Lea, E.V., and Howland, K.L. 2021. Ocean-entry timing and marine habitat-use of Canadian Dolly Varden: Dispersal among conservation, hydrocarbon exploration, and shipping areas in the Beaufort Sea. *Estuar Coast Shelf Sci* **262**: 107609. doi:10.1016/j.ecss.2021.107609.
- Gallagher, C.P., Howland, K.L., Bajno, R., Sandstrom, S.J., and Reist, J.D. 2018a. Population abundance, biological characteristics, and contribution to coastal mixed-stock fisheries of Dolly Varden (*Salvelinus malma malma*) from the Babbage River: 2010-2014. Fisheries and Oceans Canada, Ottawa, ON.
- Gallagher, C.P., Howland, K.L., Sandstrom, S.J., and Halden, N.M. 2018b. Migration tactics affect spawning frequency in an iteroparous salmonid (*Salvelinus malma*) from the Arctic. *PLOS ONE* **13**(12): e0210202. doi:10.1371/journal.pone.0210202.
- Gallagher, C.P., Morrison, C.M., Lea, E.V., Halden, N.M., and Howland, K.L. 2019. Growth and reproductive characteristics of rarely observed resident female Dolly Varden (*Salvelinus malma malma*) in North America. *Hydrobiologia* **840**(1): 189–205. doi:10.1007/s10750-019-3927-6.
- Gerlier, M., and Roche, P. 1998. A radio telemetry study of the migration of Atlantic Salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. In *Advances in Invertebrates and Fish Telemetry. Edited by J.-P. Lagardère, M.-L.B. Anras, and G. Claireaux*. Springer Netherlands, Dordrecht. pp. 283–293. doi:10.1007/978-94-011-5090-3_32.
- Getis, A., and Ord, J.K. 1992. The analysis of spatial association by use of distance statistics. *Geogr Anal* **24**(3): 189–206. doi:10.1111/j.1538-4632.1992.tb00261.x.

- Gienapp, P., and Bregnballe, T. 2012. Fitness consequences of timing of migration and breeding in cormorants. *PLOS ONE* **7**(9): e46165. doi:10.1371/journal.pone.0046165.
- Gilbert, M.J.H., Donadt, C.R., Swanson, H.K., and Tierney, K.B. 2016. Low annual fidelity and early upstream migration of anadromous Arctic Char in a variable environment. *Trans Am Fish Soc* **145**(5): 931–942. doi:10.1080/00028487.2016.1173095.
- Gilbert, M.J.H., and Farrell, A.P. 2021. The thermal acclimation potential of maximum heart rate and cardiac heat tolerance in Arctic Char (*Salvelinus alpinus*), a northern cold-water specialist. *J Therm Biol* **95**: 102816. doi:10.1016/j.jtherbio.2020.102816.
- Gilbert, M.J.H., Harris, L.N., Malley, B.K., Schimnowski, A., Moore, J.-S., and Farrell, A.P. 2020. The thermal limits of cardiorespiratory performance in anadromous Arctic Char (*Salvelinus alpinus*): A field-based investigation using a remote mobile laboratory. *Conserv Physiol* **8**(1): coaa036. doi:10.1093/conphys/coaa036.
- Gilbert, M.J.H., Middleton, E.K., Kanayok, K., Harris, L.N., Moore, J.-S., Farrell, A.P., and Speers-Roesch, B. 2022. Rapid cardiac thermal acclimation in wild anadromous Arctic Char (*Salvelinus alpinus*). *J Exp Biol* **225**(17): jeb244055. doi:10.1242/jeb.244055.
- Gillman, D.V., and Kristofferson, A.H. 1984. Biological Data on Arctic Charr, *Salvelinus alpinus* (L.), from the Coppermine River, Northwest Territories, 1981–82. Fisheries and Oceans Canada, Winnipeg, MB.
- Glova, G., and McCart, P. 1974. Life History of Arctic Char (*Salvelinus alpinus*), in the Firth River, Yukon Territory.
- Goetz, F.A., Beamer, E., Connor, E.J., Jeanes, E., Kinsel, C., Chamberlin, J.W., Morello, C., and Quinn, T.P. 2021. The timing of anadromous Bull Trout migrations in estuarine and marine waters of Puget Sound, Washington. *Environ Biol Fish* **104**(9): 1073–1088. doi:10.1007/s10641-021-01136-1.
- Gowans, A.R.D., Armstrong, J.D., and Priede, I.G. 1999. Movements of adult Atlantic Salmon in relation to a hydroelectric dam and fish ladder. *J Fish Biol* **54**: 713–726.
- Grainger, E.H. 1953. On the age, growth, migration, reproductive potential and feeding habits of the Arctic Char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. *J Fish Res Bd Can* **10**(6): 326–370. doi:10.1139/f53-023.

- Groot, C., and Margolis, L. 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, BC, Canada.
- Gross, M.R. 1987. Evolution of Diadromy in Fishes. *In* Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society Symposium 1, Bethesda, Maryland.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: Diversity within sexes. *Trends Ecol Evol* **11**(2): 92–98. doi:10.1016/0169-5347(96)81050-0.
- Gross, M.R., Coleman, R.M., and McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**(4845): 1291–1293. doi:10.1126/science.239.4845.1291.
- Gross, M.R., and Repka, J. 1998. Stability with inheritance in the conditional strategy. *J Theor Biol* **192**(4): 445–453. doi:10.1006/jtbi.1998.0665.
- Guðjónsson, S. 1987. Migration of Anadromous Arctic Char (*Salvelinus alpinus* L.) in a Glacier River, River Blanda, North Iceland. *In* Proceedings of the Salmonid Migration and Distribution Symposium. Edited by E.L. Brannon and B. Jonsson. Trondheim. pp. 116–123.
- Gulseth, O.A., and Nilssen, K.J. 2000. The brief period of spring migration, short marine residence, and high return rate of a Northern Svalbard population of Arctic Char. *Trans Am Fish Soc* **129**: 782–796.
- Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods Ecol Evol* **8**(9): 1063–1071. doi:10.1111/2041-210X.12726.
- Hamley, J.M. 1975. Review of gillnet selectivity. *J Fish Res Bd Can* **32**(11): 1943–1969.
- Hammer, L., Hussey, N., Marcoux, M., Pettitt-Wade, H., Hedges, K., Tallman, R., and Furey, N. 2022. Arctic Char *Salvelinus alpinus* movement dynamics relative to ice breakup in a high Arctic embayment. *Mar Ecol Prog Ser* **682**: 221–236. doi:10.3354/meps13939.
- Hammer, L.J., Hussey, N.E., Marcoux, M., Pettitt-Wade, H., Hedges, K., Tallman, R., and Furey, N.B. 2021. Arctic Char enter the marine environment before annual ice breakup in the high Arctic. *Environ Biol Fish*. doi:10.1007/s10641-021-01099-3.
- Hardin, J.W., and Hilbe, J.M. 2018. Generalized Linear Models and Extensions. Fourth edition. Stata Press, College Station, Texas.

- Harris, L., Yurkowski, D., Gilbert, M., Else, B., Duke, P., Ahmed, M., Tallman, R., Fisk, A., and Moore, J. 2020. Depth and temperature preference of anadromous Arctic Char *Salvelinus alpinus* in the Kitikmeot Sea, a shallow and low-salinity area of the Canadian Arctic. *Mar Ecol Prog Ser* **634**: 175–197. doi:10.3354/meps13195.
- Harris, L.N., Bajno, R., Gallagher, C.P., Koizumi, I., Johnson, L.K., Howland, K.L., Taylor, E.B., and Reist, J.D. 2015. Life-history characteristics and landscape attributes as drivers of genetic variation, gene flow, and fine-scale population structure in northern Dolly Varden (*Salvelinus malma malma*) in Canada. *Can J Fish Aquat Sci* **72**(10): 1477–1493. doi:10.1139/cjfas-2015-0016.
- Harris, L.N., Moore, J.-S., Bajno, R., and Tallman, R.F. 2016. Genetic stock structure of anadromous Arctic Char in Canada’s Central Arctic: Potential implications for the management of Canada’s largest Arctic Char commercial fishery. *N Am J Fish Manage* **36**(6): 1473–1488. doi:10.1080/02755947.2016.1227399.
- Harris, L.N., Yurkowski, D.J., Malley, B.K., Jones, S.F., Else, B.G.T., Tallman, R.F., Fisk, A.T., and Moore, J. 2022. Acoustic telemetry reveals the complex nature of mixed-stock fishing in Canada’s largest Arctic Char commercial fishery. *N Am J Fish Manage* **42**(5): 1250–1268. doi:10.1002/nafm.10816.
- Hartig, F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. Available from <https://cran.r-project.org/package=DHARMa>.
- Harwood, L.A., and Babaluk, J.A. 2014. Spawning, overwintering and summer feeding habitats used by anadromous Arctic Char (*Salvelinus alpinus*) of the Hornaday River, Northwest Territories, Canada. *Arctic* **67**(4): 449–461. doi:10.14430/arctic4422.
- Hauser, D.D.W., Laidre, K.L., Stafford, K.M., Stern, H.L., Suydam, R.S., and Richard, P.R. 2017. Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Glob Change Biol* **23**(6): 2206–2217. doi:10.1111/gcb.13564.
- Heino, J., Culp, J.M., Erkinaro, J., Goedkoop, W., Lento, J., Rühland, K.M., and Smol, J.P. 2020. Abruptly and irreversibly changing Arctic freshwaters urgently require standardized monitoring. *J Appl Ecol* **57**(7): 1192–1198. doi:10.1111/1365-2664.13645.
- Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. Anadromy Versus Non-Anadromy in Salmonids. *In* *Evolution Illuminated: Salmon and their Relatives*. Edited by A.P. Hendry and S.C. Stearns. Oxford University Press. pp. 92–125.

- Hightower, J.E., and Harris, J.E. 2017. Estimating fish mortality rates using telemetry and multistate models. *Fisheries* **42**(4): 210–219. doi:10.1080/03632415.2017.1276347.
- Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and Patterson, D.A. 2012. Dead fish swimming: A review of research on the early migration and high premature mortality in adult Fraser River Sockeye Salmon *Oncorhynchus nerka*. *J Fish Biol* **81**(2): 576–599. doi:10.1111/j.1095-8649.2012.03360.x.
- Hocutt, C.H., Seibold, S.E., Harrell, R.M., Jesien, R.V., and Bason, W.H. 1990. Behavioral observations of Striped Bass (*Morone saxatilis*) on the spawning grounds of the Choptank and Nanticoke Rivers, Maryland, USA. *J Appl Ichthyol* **6**(4): 211–222. doi:10.1111/j.1439-0426.1990.tb00581.x.
- Hodgson, S., and Quinn, T.P. 2002. The timing of adult Sockeye Salmon migration into fresh water: Adaptations by populations to prevailing thermal regimes. *Can J Zool* **80**(3): 542–555. doi:10.1139/z02-030.
- Hodgson, S., Quinn, T.P., Hilborn, R., Francis, R.C., and Rogers, D.E. 2006. Marine and freshwater climatic factors affecting interannual variation in the timing of return migration to fresh water of Sockeye Salmon (*Oncorhynchus nerka*). *Fish Oceanogr* **15**(1): 1–24. doi:10.1111/j.1365-2419.2005.00354.x.
- Holbrook, C.M., Hayden, T.A., Binder, T.R., and Pye, J. 2022. glatos: A package for the Great Lakes Acoustic Telemetry Observation System. Available from <https://github.com/ocean-tracking-network/glatos>.
- Holdo, R.M., Holt, R.D., Sinclair, A.R.E., Godley, B.J., and Thirgood, S. 2011. Migration impacts on communities and ecosystems: Empirical evidence and theoretical insights. *In* *Animal Migration: A Synthesis*. Edited by E.J. Milner-Gulland, J.M. Fryxell, and A.R.E. Sinclair. Oxford University Press, New York, NY. pp. 131–143.
- Hollins, J., Pettitt-Wade, H., Gallagher, C.P., Lea, E.V., Loseto, L.L., and Hussey, N.E. 2022. Distinct freshwater migratory pathways in Arctic Char (*Salvelinus alpinus*) coincide with separate patterns of marine spatial habitat-use across a large coastal landscape. *Can J Fish Aquat Sci* **79**(9): 1447–1464. doi:10.1139/cjfas-2021-0291.

- Huang, B., Liu, C., Banzon, V., Freeman, E., Graham, G., Hankins, B., Smith, T., and Zhang, H.-M. 2021. Improvements of the daily optimum interpolation sea surface temperature (DOISST) version 2.1. *J Climate* **34**(8): 2923–2939. doi:10.1175/JCLI-D-20-0166.1.
- Hughes, N.F., and Reynolds, J.B. 1994. Why do Arctic Grayling (*Thymallus arcticus*) get bigger as you go upstream? *Can J Fish Aquat Sci* **51**(10): 2154–2163. doi:10.1139/f94-216.
- Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E., and Whoriskey, F.G. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science* **348**(6240): 1255642–1255642. doi:10.1126/science.1255642.
- Hutchings, J.A. 2021. *A Primer of Lifes Histories: Ecology, Evolution, and Application*. Oxford University Press, New York, NY.
- Inuit Circumpolar Council. 2012. Food Security across the Arctic: Background paper of the Steering Committee of the Circumpolar Inuit Health Strategy. Inuit Circumpolar Council.
- Jacoby, D.M.P., Brooks, E.J., Croft, D.P., and Sims, D.W. 2012. Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses: Network analyses of animal movement. *Methods Ecol Evol* **3**(3): 574–583. doi:10.1111/j.2041-210X.2012.00187.x.
- Jacoby, D.M.P., and Freeman, R. 2016. Emerging network-based tools in movement ecology. *Trends Ecol Evol* **31**(4): 301–314. doi:10.1016/j.tree.2016.01.011.
- Jensen, A.J., Diserud, O.H., Finstad, B., Fiske, P., and Rikardsen, A.H. 2015. Between-watershed movements of two anadromous salmonids in the Arctic. *Can J Fish Aquat Sci* **72**(6): 855–863. doi:10.1139/cjfas-2015-0015.
- Jensen, A.J., Finstad, B., and Fiske, P. 2019. The cost of anadromy: Marine and freshwater mortality rates in anadromous Arctic Char and Brown Trout in the Arctic region of Norway. *Can J Fish Aquat Sci* **76**(12): 2408–2417. doi:10.1139/cjfas-2018-0428.
- Jensen, A.J., Finstad, B., Fiske, P., Diserud, O.H., and Thorstad, E.B. 2020. Repeatable individual variation in migration timing in two anadromous salmonids and ecological consequences. *Ecol Evol* **10**(20): 11727–11738. doi:10.1002/ece3.6808.

- Jensen, A.J., Heggberget, T.G., and Johnsen, B.O. 1986. Upstream migration of adult Atlantic Salmon, *Salmo salar* L., in the River Vefsna, northern Norway. *J Fish Biol* **29**(4): 459–465. doi:10.1111/j.1095-8649.1986.tb04961.x.
- Johnson, L. 1980. The Arctic Charr, *Salvelinus alpinus*. In *Charrs: Salmonid Fishes of the Genus Salvelinus*. Edited by E.K. Balon. Dr. W. Junk bv Publishers, The Hague, The Netherlands. pp. 15–98.
- Johnson, L. 1989. The anadromous Arctic Charr (*Salvelinus alpinus*) of Nauyuk Lake, N.W.T., Canada. *Physiol Ecol Jpn Special Volume 1*: 201–227.
- Jonsson, B., and Jonsson, N. 1993. Partial migration: Niche shift versus sexual maturation in fishes. *Rev Fish Biol Fisher* **3**(4): 348–365. doi:10.1007/BF00043384.
- Jonsson, B., Jonsson, N., and Hansen, L.P. 2007. Factors affecting river entry of adult Atlantic Salmon in a small river. *J Fish Biol* **71**(4): 943–956. doi:10.1111/j.1095-8649.2007.01555.x.
- Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nord J Freshw Res* **66**: 20–35.
- Jonsson, N., and Jonsson, B. 2002. Migration of anadromous Brown Trout *Salmo trutta* in a Norwegian river. *Freshwater Biol* **47**(8): 1391–1401. doi:10.1046/j.1365-2427.2002.00873.x.
- Joo, R., Boone, M.E., Clay, T.A., Patrick, S.C., Clusella-Trullas, S., and Basille, M. 2020. Navigating through the R packages for movement. *J Anim Ecol* **89**(1): 248–267. doi:10.1111/1365-2656.13116.
- Jørgensen, E.H., Johansen, S.J.S., and Jobling, M. 1997. Seasonal patterns of growth, lipid deposition and lipid depletion in anadromous Arctic Charr. *J Fish Biol* **51**(2): 312–326. doi:10.1111/j.1095-8649.1997.tb01668.x.
- Jørgensen, E.H., and Johnsen, H.K. 2014. Rhythmic life of the Arctic Charr: Adaptations to life at the edge. *Mar Genom* **14**: 71–81. doi:10.1016/j.margen.2013.10.005.
- Juanes, F., Gephard, S., and Beland, K.F. 2004. Long-term changes in migration timing of adult Atlantic Salmon (*Salmo salar*) at the southern edge of the species distribution. *Can J Fish Aquat Sci* **61**(12): 2392–2400. doi:10.1139/f04-207.
- Kassambara, A., and Mundt, F. 2020. factoextra: Extract and visualize the results of multivariate data analyses. Available from CRAN.R-project.org/package=factoextra.

- Kennedy, R.J., Moffett, I., Allen, M.M., and Dawson, S.M. 2013. Upstream migratory behaviour of wild and ranched Atlantic Salmon *Salmo salar* at a natural obstacle in a coastal spate river. *J Fish Biol* **83**(3): 515–530. doi:10.1111/jfb.12189.
- Klemetsen, A. 2010. The charr problem revisited: Exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshw Rev* **3**(1): 49–74. doi:10.1608/FRJ-3.1.3.
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O’Connell, M.F., and Mortensen, E. 2003. Atlantic Salmon *Salmo salar* L., Brown Trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecol Freshw Fish* **12**(1): 1–59. doi:10.1034/j.1600-0633.2003.00010.x.
- Klinard, N.V., and Matley, J.K. 2020. Living until proven dead: Addressing mortality in acoustic telemetry research. *Rev Fish Biol Fisher* **30**(3): 485–499. doi:10.1007/s11160-020-09613-z.
- Knickle, D.C., and Rose, G.A. 2014a. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes. *Environ Biol Fish* **97**(4): 343–355. doi:10.1007/s10641-013-0156-0.
- Knickle, D.C., and Rose, G.A. 2014b. Examination of fine-scale spatial-temporal overlap and segregation between two closely related congeners *Gadus morhua* and *Gadus ogac* in coastal Newfoundland. *J Fish Biol* **85**(3): 713–735. doi:10.1111/jfb.12454.
- Koizumi, I., and Maekawa, K. 2003. Spawning migration of stream-dwelling Dolly Varden in spring-fed tributaries of the Shiisorapuchi River, Japan. *J Freshwater Ecol* **18**(2): 321–331. doi:10.1080/02705060.2003.9664499.
- Kondratieff, M.C., and Myrick, C.A. 2006. How high can Brook Trout jump? A laboratory evaluation of Brook Trout jumping performance. *Trans Am Fish Soc* **135**(2): 361–370. doi:10.1577/T04-210.1.
- Kovach, R.P., Ellison, S.C., Pyare, S., and Tallmon, D.A. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. *Glob Change Biol* **21**(5): 1821–1833. doi:10.1111/gcb.12829.
- Kovach, R.P., Joyce, J.E., Echave, J.D., Lindberg, M.S., and Tallmon, D.A. 2013. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLOS ONE* **8**(1): e53807. doi:10.1371/journal.pone.0053807.

- Kraskura, K., Patterson, D.A., and Eliason, E.J. 2024. A review of adult salmon maximum swim performance. *Can J Fish Aquat Sci* **81**(9): 1174–1216. doi:10.1139/cjfas-2023-0246.
- Kristinsson, K.Ó., Gudbergsson, G., and Gislason, G.M. 2015. Variable migration and delay in two stock components of an Atlantic Salmon population. *Environ Biol Fish* **98**(6): 1513–1523. doi:10.1007/s10641-015-0378-4.
- Kristoffersen, K. 1994. The influence of physical watercourse parameters on the degree of anadromy in different lake populations of Arctic Charr (*Salvelinus alpinus* (L.)) in northern Norway. *Ecol Freshw Fish* **3**(2): 80–91. doi:10.1111/j.1600-0633.1994.tb00109.x.
- Landler, L., Ruxton, G.D., and Malkemper, E.P. 2019. The Hermans–Rasson test as a powerful alternative to the Rayleigh test for circular statistics in biology. *BMC Ecol* **19**(1): 30. doi:10.1186/s12898-019-0246-8.
- Landler, L., Ruxton, G.D., and Malkemper, E.P. 2021. Advice on comparing two independent samples of circular data in biology. *Sci Rep* **11**(1): 20337. doi:10.1038/s41598-021-99299-5.
- Lea, E.V., Gallagher, C.P., Maier, K., and Ayles, B. 2021. Dolly Varden (*Salvelinus malma malma*) fisheries in the Inuvialuit Settlement Region and the Gwich'in Settlement Area 2009-2014: Harvest, monitoring and communications in an adaptive co-management setting. Fisheries and Oceans Canada, Ottawa, ON.
- Lea, J.S.E., Humphries, N.E., von Brandis, R.G., Clarke, C.R., and Sims, D.W. 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *P Roy Soc B-Biol Sci* **283**(1834): 20160717. doi:10.1098/rspb.2016.0717.
- Leblond, M., St-Laurent, M.-H., and Côté, S.D. 2016. Caribou, water, and ice – Fine-scale movements of a migratory Arctic ungulate in the context of climate change. *Mov Ecol* **4**(1): 14. doi:10.1186/s40462-016-0079-4.
- Legendre, P., and Legendre, L. 2012. Numerical Ecology. Third edition. Elsevier, Amsterdam.
- Lennox, R.J., Thorstad, E.B., Diserud, O.H., Økland, F., Cooke, S.J., Aasestad, I., and Forseth, T. 2018. Biotic and abiotic determinants of the ascent behaviour of adult Atlantic Salmon transiting passable waterfalls. *River Res Applic* **34**(8): 907–917. doi:10.1002/rra.3329.

- Lilly, J., Honkanen, H.H., Rodger, J.R., Del Villar, D., Boylan, P., Green, A., Pereiro, D., Wilkie, L., Kennedy, R., Barkley, A., Rosell, R., Maoiléidigh, N.Ó., O'Neill, R., Waters, C., Cotter, D., Bailey, D., Roche, W., McGill, R., Barry, J., Beck, S.V., Henderson, J., Parke, D., Whoriskey, F.G., Shields, B., Ramsden, P., Walton, S., Fletcher, M., Whelan, K., Bean, C.W., Elliott, S., Bowman, A., and Adams, C.E. 2024. Migration patterns and navigation cues of Atlantic Salmon post-smolts migrating from 12 rivers through the coastal zones around the Irish Sea. *J Fish Biol* **104**(1): 265–283. doi:10.1111/jfb.15591.
- Liu, A., Geraldes, A., and Taylor, E.B. 2023. Development and testing of diagnostic molecular markers to differentiate among three species of *Salvelinus*: Arctic Char, Dolly Varden, and Bull Trout. *Conserv Genet Resour* **15**(3): 83–96. doi:10.1007/s12686-023-01305-7.
- MacCrimmon, H.R., and Gordon, D.J. 1981. Salmonid spawning runs and estimated ova production in Normandale Creek of Lake Erie. *J Great Lakes Res* **7**(2): 155–161. doi:10.1016/S0380-1330(81)72041-0.
- Mainguy, J., Arsenault, A., Tran, L., Martyniuk, M.A.C., Paquet, C., Moore, J., and Power, M. 2023. Otolith-inferred patterns of marine migration frequency in Nunavik Arctic Charr. *J Fish Biol* **103**(5): 884–896. doi:10.1111/jfb.15491.
- Mardia, K.V., and Jupp, P.E. 2000. *Directional Statistics*. John Wiley & Sons, Ltd., Toronto, ON.
- Markevich, G., Esin, E., and Anisimova, L. 2018. Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden *Salvelinus malma* from the Lake Kronotskoe Basin. *Ecol Evol* **8**(5): 2554–2567. doi:10.1002/ece3.3806.
- Martins, E., O'Connor, B., Bottoms, J., Clevenger, I., Smith, D., Auger-Méthé, M., Power, M., Patterson, D., Shrimpton, M., and Cooke, S. 2022. Spatial Ecology of Arctic Grayling in the Parsnip Core Area. Fish and Wildlife Compensation Program – Peace Region, Prince George, BC.
- Mathisen, O.A., and Berg, M. 1968. Growth rates of the char *Salvelinus alpinus* (L.) in the Vardnes River, Troms, Northern Norway. *Rep Inst Freshw Res Drottningholm* **48**(246): 177–186.
- Matley, J.K., Klinard, N.V., Barbosa Martins, A.P., Aarestrup, K., Aspillaga, E., Cooke, S.J., Cowley, P.D., Heupel, M.R., Lowe, C.G., Lowerre-Barbieri, S.K., Mitamura, H., Moore, J.-S., Simpfendorfer, C.A., Stokesbury, M.J.W., Taylor, M.D., Thorstad, E.B., Vandergoot, C.S., and Fisk, A.T. 2022. Global

- trends in aquatic animal tracking with acoustic telemetry. *Trends Ecol Evol* **37**(1): 79–94. doi:10.1016/j.tree.2021.09.001.
- May-McNally, S.L., Quinn, T.P., and Taylor, E.B. 2015. Low levels of hybridization between sympatric Arctic Char (*Salvelinus alpinus*) and Dolly Varden Char (*Salvelinus malma*) highlights their genetic distinctiveness and ecological segregation. *Ecol Evol* **5**(15): 3031–3045. doi:10.1002/ece3.1583.
- Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., Andrew, M.E., Leyk, S., Pearse, I.S., and Schneider, D.C. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Sci Rep* **7**(1): 1902. doi:10.1038/s41598-017-02045-z.
- McCart, P.J. 1980. A Review of the Systematics and Ecology of Arctic Char, *Salvelinus alpinus*, in the Western Arctic. Department of Fisheries and Oceans, Winnipeg, MB.
- McClure, M.M., Carlson, S.M., Beechie, T.J., Pess, G.R., Jorgensen, J.C., Sogard, S.M., Sultan, S.E., Holzer, D.M., Travis, J., Sanderson, B.L., Power, M.E., and Carmichael, R.W. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evol Appl* **1**(2): 300–318. doi:10.1111/j.1752-4571.2008.00030.x.
- McGowan, D.K. 1990. Enumeration and biological data from the upstream migration of Arctic Charr, *Salvelinus alpinus* (L.), in the Cambridge Bay area, Northwest Territories, 1979-1983. Department of Fisheries and Oceans, Winnipeg, MB.
- McNicholl, D.G., Dunmall, K.M., Majewski, A.R., Niemi, A., Gallagher, C.P., Sawatzky, C., and Reist, J.D. 2020. Distribution of marine and anadromous fishes of Darnley Bay and the Anguniaqvia niqiqiyuam marine protected area, NT. Fisheries and Oceans Canada, Winnipeg, MB.
- McPhail, J.D. 2007. The Freshwater Fishes of British Columbia. University of Alberta Press, Edmonton, AB.
- Mochnac, N.J., Schroeder, B.S., Sawatzky, C.D., and Reist, J.D. 2010. Assessment of Northern Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792), Habitat in Canada. Fisheries and Oceans Canada, Winnipeg, MB.
- Moller, A.P., Rubolini, D., and Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *P Natl Acad Sci* **105**(42): 16195–16200. doi:10.1073/pnas.0803825105.

- Moore, J.-S., Harris, L.N., Kessel, S.T., Bernatchez, L., Tallman, R.F., and Fisk, A.T. 2016. Preference for nearshore and estuarine habitats in anadromous Arctic Char (*Salvelinus alpinus*) from the Canadian high Arctic (Victoria Island, Nunavut) revealed by acoustic telemetry. *Can J Fish Aquat Sci* **73**(9): 1434–1445. doi:10.1139/cjfas-2015-0436.
- Moore, J.-S., Harris, L.N., Le Luyer, J., Sutherland, B.J.G., Rougemont, Q., Tallman, R.F., Fisk, A.T., and Bernatchez, L. 2017. Genomics and telemetry suggest a role for migration harshness in determining overwintering habitat choice, but not gene flow, in anadromous Arctic Char. *Mol Ecol* **26**(24): 6784–6800. doi:10.1111/mec.14393.
- Moore, J.-S., Harris, L.N., Tallman, R.F., and Taylor, E.B. 2013. The interplay between dispersal and gene flow in anadromous Arctic Char (*Salvelinus alpinus*): Implications for potential for local adaptation. *Can J Fish Aquat Sci* **70**(9): 1327–1338. doi:10.1139/cjfas-2013-0138.
- Moore, J.W. 1975. Distribution, movements, and mortality of anadromous Arctic Char, *Salvelinus alpinus* L., in the Cumberland Sound area of Baffin Island. *J Fish Biol* **7**(3): 339–348. doi:10.1111/j.1095-8649.1975.tb04608.x.
- Moore, J.W., and Moore, I.A. 1974. Food and growth of Arctic Char, *Salvelinus alpinus* (L.), in the Cumberland Sound area of Baffin Island. *J Fish Biol* **6**(1): 79–92. doi:10.1111/j.1095-8649.1974.tb04525.x.
- Morfin, M., Simon, J., Morandeau, F., Baulier, L., Méhault, S., and Kopp, D. 2019. Using acoustic telemetry to estimate post-release survival of Undulate Ray *Raja undulata* (Rajidae) in northeast Atlantic. *Ocean Coast Manage* **178**: 104848. doi:10.1016/j.ocecoaman.2019.104848.
- Morin, B., Hudon, C., and Whoriskey, F. 1991. Seasonal distribution, abundance, and life-history traits of Greenland Cod, *Gadus ogac*, at Wemindji, eastern James Bay. *Can J Zool* **69**: 3061–3070.
- Morita, K. 2019. Earlier migration timing of salmonids: An adaptation to climate change or maladaptation to the fishery? *Can J Fish Aquat Sci* **76**(3): 475–479. doi:10.1139/cjfas-2018-0078.
- Morita, K., Tamate, T., Kuroki, M., and Nagasawa, T. 2014. Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *J Anim Ecol* **83**(6): 1268–1278. doi:10.1111/1365-2656.12240.
- Morris, C., and Green, J.M. 2012. Migrations and harvest rates of Arctic Charr (*Salvelinus alpinus*) in a marine protected area. *Aquat Conserv* **22**(6): 743–750. doi:10.1002/aqc.2263.

- Mottola, G., Kristensen, T., and Anttila, K. 2020. Compromised thermal tolerance of cardiovascular capacity in upstream migrating Arctic Char and Brown Trout—Are hot summers threatening migrating salmonids? *Conserv Physiol* **8**(1): coaa101. doi:10.1093/conphys/coaa101.
- Mulder, I.M., Morris, C.J., Dempson, J.B., Fleming, I.A., and Power, M. 2020. Marine temperature and depth use by anadromous Arctic Char correlates to body size and diel period. *Can J Fish Aquat Sci* **77**(5): 882–893. doi:10.1139/cjfas-2019-0097.
- Mundy, P.R., and Evenson, D.F. 2011. Environmental controls of phenology of high-latitude Chinook Salmon populations of the Yukon River, North America, with application to fishery management. *ICES J Mar Sci* **68**(6): 1155–1164. doi:10.1093/icesjms/fsr080.
- Murdoch, A., Mantyka-Pringle, C., and Sharma, S. 2020. Impacts of co-occurring environmental changes on Alaskan stream fishes. *Freshwater Biol* **65**(10): 1685–1701. doi:10.1111/fwb.13569.
- Myrvold, K.M., Mawle, G.W., Andersen, O., and Aas, Ø. 2019. The Social, Economic and Cultural values of wild Atlantic Salmon: A review of the literature for the period 2009-2019 and an assessment of changes in values. Norwegian Institute for Nature Research.
- Nakagawa, S., Johnson, P.C.D., and Schielzeth, H. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J R Soc Interface* **14**(134).
- National Research Council Canada. 2020. Sunrise/sunset calculator. Available from <https://nrc.canada.ca/en/research-development/products-services/software-applications/sun-calculator/>.
- Natural Resources Canada. 2015. Lakes, Rivers and Glaciers in Canada – CanVec Series – Hydrographic Features (canvec_50K_NU_Hydro). Natural Resources Canada. Available from <https://open.canada.ca/data/en/dataset/9d96e8c9-22fe-4ad2-b5e8-94a6991b744b>.
- Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O., and Jonsson, B. 2019. Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). *Fish Fish* **20**(6): 1051–1082. doi:10.1111/faf.12396.

- Newton, M., Dodd, J.A., Barry, J., Boylan, P., and Adams, C.E. 2018. The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. *Hydrobiologia* **806**(1): 251–264. doi:10.1007/s10750-017-3364-3.
- Nielsen, J.R., and Andersen, M. 2001. Feeding habits and density patterns of Greenland Cod, *Gadus ogac* (Richardson 1836), at West Greenland compared to those of the coexisting Atlantic Cod, *Gadus morhua* L. *J Northwest Atl Fish Sci* **29**: 1–22.
- Nilsen, C.I., Vollset, K.W., Velle, G., Barlaup, B.T., Normann, E.S., Stöger, E., and Lennox, R.J. 2023. Atlantic salmon of wild and hatchery origin have different migration patterns. *Can J Fish Aquat Sci* **80**(4): 690–699. doi:10.1139/cjfas-2022-0120.
- Nordeng, H. 1983. Solution to the “char problem” based on Arctic Char (*Salvelinus alpinus*) in Norway. *Can J Fish Aquat Sci* **40**(9): 1372–1387.
- Nugent, C.M., Leong, J.S., Christensen, K.A., Rondeau, E.B., Brachmann, M.K., Easton, A.A., Ouellet-Fagg, C.L., Crown, M.T.T., Davidson, W.S., Koop, B.F., Danzmann, R.G., and Ferguson, M.M. 2019. Design and characterization of an 87k SNP genotyping array for Arctic Charr (*Salvelinus alpinus*). *PLOS ONE* **14**(4): e0215008. doi:10.1371/journal.pone.0215008.
- Nunavut Land Claims Agreement Act, S.C. 1993, c. 29. 1993. Available from <https://laws-lois.justice.gc.ca/eng/acts/n-28.7/FullText.html>.
- Núñez, J., and Duponchelle, F. 2009. Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. *Fish Physiol Biochem* **35**(1): 167–180. doi:10.1007/s10695-008-9241-2.
- Ogle, D., Doll, J., Wheeler, P., and Dinno, A. 2025. FSA: Simple fisheries stock assessment methods. Available from <https://github.com/droglenc/FSA>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O’Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., and Borman, T. 2025. vegan: Community Ecology Package. Available from <https://cran.r-project.org/package=vegan>.

- Onarheim, I.H., Eldevik, T., Smedsrud, L.H., and Stroeve, J.C. 2018. Seasonal and regional manifestation of Arctic sea ice loss. *J Climate* **31**(12): 4917–4932. doi:10.1175/JCLI-D-17-0427.1.
- Ord, J.K., and Getis, A. 1995. Local spatial autocorrelation statistics: Distributional issues and an application. *Geogr Anal* **27**(4): 286–306. doi:10.1111/j.1538-4632.1995.tb00912.x.
- Partridge, L., and Sibly, R. 1991. Constraints in the evolution of life histories. *Philos T Roy Soc B* **332**(1262): 3–13.
- Pebesma, E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. *R J* **10**(1): 439–446. doi:10.32614/RJ-2018-009.
- Pebesma, E., and Graeler, B. 2023. gstat: Spatial and spatio-temporal geostatistical modelling, prediction and simulation. Available from <https://cran.r-project.org/package=gstat>.
- Pedersen, T.L. 2022. ggraph: An Implementation of Grammar of Graphics for Graphs and Networks. Available from <https://cran.r-project.org/package=ggraph>.
- Pedersen, T.L. 2024. patchwork: The Composer of Plots. Available from <https://cran.r-project.org/package=patchwork>.
- Persson, L., Raunsgard, A., Thorstad, E.B., Østborg, G., Urdal, K., Sægrov, H., Ugedal, O., Hindar, K., Karlsson, S., Fiske, P., and Bolstad, G.H. 2023. Iteroparity and its contribution to life-history variation in Atlantic Salmon. *Can J Fish Aquat Sci* **80**(3): 577–592. doi:10.1139/cjfas-2022-0126.
- Peters, L.M., Reinhardt, U.G., and Pegg, M.A. 2008. Factors influencing radio wave transmission and reception: Use of radiotelemetry in large river systems. *N Am J Fish Manage* **28**(1): 301–307. doi:10.1577/M06-146.1.
- Pihur, V., Datta, S., and Datta, S. 2020. RankAggreg: Weight rank aggregation. Available from <https://CRAN.R-project.org/package=RankAggreg>.
- Power, G., and Barton, D.R. 1987. Some effects of physiographic and biotic factors on the distribution of anadromous Arctic Char (*Salvelinus Alpinus*) in Ungava Bay, Canada. *Arctic* **40**(3): 198–203. doi:10.14430/arctic1767.
- Power, M., and Reist, J.D. 2018. *Salvelinus alpinus*. In *Marine Fishes of Arctic Canada*. Edited by B.W. Coad and J.D. Reist. University of Toronto Press, Toronto, ON. pp. 283–289.

- Priest, H., and Usher, P.J. 2004. The Nunavut Wildlife Harvest Study. Nunavut Wildlife Management Board, Nunavut, Canada.
- Prno, J. 2019. Traditional Knowledge Study on the Arctic Char Fishery in the Lower Coppermine River, Nunavut. Angoniatit Niovikvia Ltd. (a subsidiary of the Kugluktuk Hunters and Trappers Organization).
- Prno, J., Bradshaw, B., Wandel, J., Pearce, T., Smit, B., and Tozer, L. 2011. Community vulnerability to climate change in the context of other exposure-sensitivities in Kugluktuk, Nunavut. *Polar Res* **30**(1): 7363. doi:10.3402/polar.v30i0.7363.
- Prowse, T., Alfredsen, K., Beltaos, S., Bonsal, B., Duguay, C., Korhola, A., McNamara, J., Pienitz, R., Vincent, W.F., Vuglinsky, V., and Weyhenmeyer, G.A. 2011. Past and future changes in Arctic lake and river ice. *AMBIO* **40**(S1): 53–62. doi:10.1007/s13280-011-0216-7.
- Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American Shad and Sockeye Salmon. *Ecology* **77**(4): 1151–1162. doi:10.2307/2265584.
- Quinn, T.P., McGinnity, P., and Reed, T.E. 2016. The paradox of “premature migration” by adult anadromous salmonid fishes: Patterns and hypotheses. *Can J Fish Aquat Sci* **73**(7): 1015–1030. doi:10.1139/cjfas-2015-0345.
- R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.
- Radtke, R., Svenning, M., Malone, D., Klementsén, A., Ruzicka, J., and Fey, D. 1996. Migrations in an extreme northern population of Arctic Charr *Salvelinus alpinus*: Insights from otolith microchemistry. *Mar Ecol Prog Ser* **136**: 13–23. doi:10.3354/meps136013.
- Rantanen, M., Karpechko, A.Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., and Laaksonen, A. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ* **3**(1): 168. doi:10.1038/s43247-022-00498-3.
- Rayleigh. 1880. On the resultant of a large number of vibrations of the same pitch and of arbitrary phase. *London Edinburgh Dublin Philos Mag & J Sci* **10**(60): 73–78.
- Reist, J.D. 2018. *Salvelinus malma*. In *Marine Fishes of Arctic Canada*. Edited by B.W. Coad and J.D. Reist. University of Toronto Press, Toronto, ON. pp. 292–297.

- Reist, J.D., and Sawatzky, C.D. 2010. Diversity and Distribution of Charrs, Genus *Salvelinus*, in Northwestern North America in the Context of Northern Dolly Varden (*Salvelinus malma malma* (Walbaum 1792)). Fisheries and Oceans Canada, Winnipeg, MB.
- Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., and Sawatzky, C.D. 2006. General effects of climate change on Arctic fishes and fish populations. *AMBIO* **35**(7): 370–380. doi:10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2.
- Reubens, J., Verhelst, P., Van Der Knaap, I., Deneudt, K., Moens, T., and Hernandez, F. 2019. Environmental factors influence the detection probability in acoustic telemetry in a marine environment: Results from a new setup. *Hydrobiologia* **845**(1): 81–94. doi:10.1007/s10750-017-3478-7.
- Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., and Schlax, M.G. 2007. Daily high-resolution-blended analyses for sea surface temperature. *J Climate* **20**(22): 5473–5496.
- Rideout, R.M., Rose, G.A., and Burton, M.P.M. 2005. Skipped spawning in female iteroparous fishes. *Fish* **6**(1): 50–72. doi:10.1111/j.1467-2679.2005.00174.x.
- Rideout, R.M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: More common than you might think. *Mar Coast Fish* **3**(1): 176–189. doi:10.1080/19425120.2011.556943.
- Rikardsen, A.H., Amundsen, P.-A., and Bodin, P.J. 2003. Growth and diet of anadromous Arctic Charr after their return to freshwater. *Ecol Freshw Fish* **12**(1): 74–80. doi:10.1034/j.1600-0633.2003.00001.x.
- Rivinoja, P., McKinnell, S., and Lundqvist, H. 2001. Hindrances to upstream migration of Atlantic Salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. *Regul River* **17**(2): 101–115. doi:10.1002/rrr.607.
- Rothermel, E.R., Balazik, M.T., Best, J.E., Breece, M.W., Fox, D.A., Gahagan, B.I., Haulsee, D.E., Higgs, A.L., O'Brien, M.H.P., Oliver, M.J., Park, I.A., and Secor, D.H. 2020. Comparative migration ecology of Striped Bass and Atlantic Sturgeon in the US Southern mid-Atlantic bight flyway. *PLOS ONE* **15**(6): e0234442. doi:10.1371/journal.pone.0234442.
- Roux, M.-J., Tallman, R.F., and Lewis, C.W. 2011. Small-scale Arctic Charr *Salvelinus alpinus* fisheries in Canada's Nunavut: Management challenges and options. *J Fish Biol* **79**(6): 1625–1647. doi:10.1111/j.1095-8649.2011.03092.x.

- Runde, B.J., Bacheler, N.M., Shertzer, K.W., Rudershausen, P.J., Sauls, B., and Buckel, J.A. 2021. Discard mortality of Red Snapper released with descender devices in the U.S. South Atlantic. *Mar Coast Fish* **13**(5): 478–495. doi:10.1002/mcf2.10175.
- Runde, B.J., Michelot, T., Bacheler, N.M., Shertzer, K.W., and Buckel, J.A. 2020. Assigning gates in telemetry studies using hidden Markov models: An application to deepwater groupers released with descender devices. *N Am J Fish Manage* **40**(6): 1417–1434. doi:10.1002/nafm.10504.
- Rustadbakken, A., L'Abée-Lund, J.H., Arnekleiv, J.V., and Kraabøl, M. 2004. Reproductive migration of Brown Trout in a small Norwegian river studied by telemetry. *J Fish Biol* **64**(1): 2–15. doi:10.1111/j.1095-8649.2004.00275.x.
- Sandstrom, S.J., Lemieux, P.J., and Reist, J.D. 1997. Enumeration and Biological Data from the Upstream Migration of Dolly Varden Charr (*Salvelinus malma*) (W.), from the Babbage River, Yukon North Slope, 1990 to 1992. Fisheries and Oceans Canada, Winnipeg, MB.
- Saros, J.E., Arp, C.D., Bouchard, F., Comte, J., Couture, R.-M., Dean, J.F., Lafrenière, M., MacIntyre, S., McGowan, S., Rautio, M., Prater, C., Tank, S.E., Walvoord, M., Wickland, K.P., Antoniadis, D., Ayala-Borda, P., Canario, J., Drake, T.W., Folhas, D., Hazuková, V., Kivilä, H., Klanten, Y., Lamoureux, S., Laurion, I., Pilla, R.M., Vonk, J.E., Zolkos, S., and Vincent, W.F. 2023. Sentinel responses of Arctic freshwater systems to climate: Linkages, evidence, and a roadmap for future research. *Arct Sci* **9**(2): 356–392. doi:10.1139/as-2022-0021.
- Sawatzky, C.D., and Reist, J.D. 2021. Life history types and stages of northern form Dolly Varden, *Salvelinus malma malma* (Walbaum, 1792). Fisheries and Oceans Canada, Winnipeg, MB.
- Scanlon, B.P. 2000. The Ecology of Arctic Char and Dolly Varden in the Becharof Lake Drainage, Alaska. Master's thesis, University of Alaska Fairbanks, Fairbanks, AK.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* **465**(7298): 609–612. doi:10.1038/nature09060.
- Scott, W.B., and Crossman, E.J. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada, Ottawa, ON.
- Sergeant, C.J., Armstrong, J.B., and Ward, E.J. 2015. Predator-prey migration phenologies remain synchronised in a warming catchment. *Freshwater Biol* **60**(4): 724–732. doi:10.1111/fwb.12524.

- Smith, R., Bottoms, J., del Villar-Guerra, D., Loewen, T., and Swanson, H. 2025. mort: An R package to conservatively identify mortalities and shed tags in passive telemetry arrays. *J Anim Ecol* **94**(6): 1120–1132. doi:10.1111/1365-2656.70045.
- Smith, R., Hitkolok, E., Loewen, T., Dumond, A., Kristensen, K., and Swanson, H. 2022. Overwintering ecology and movement of anadromous Arctic Char (*Salvelinus alpinus*) in a large, ice-covered river in the Canadian Arctic. *J Fish Biol* **100**(6): 1432–1446. doi:10.1111/jfb.15054.
- Smith, R., Hitkolok, E., Loewen, T., Dumond, A., and Swanson, H. 2024. Migration timing and marine space use of an anadromous Arctic fish (Arctic Char, *Salvelinus alpinus*) revealed by local spatial statistics and network analysis. *Mov Ecol* **12**(1): 12. doi:10.1186/s40462-024-00455-z.
- Smoothey, A.F., Lee, K.A., and Peddemors, V.M. 2019. Long-term patterns of abundance, residency and movements of bull sharks (*Carcharhinus leucas*) in Sydney Harbour, Australia. *Sci Rep* **9**(1): 18864. doi:10.1038/s41598-019-54365-x.
- Søreide, J.E., Leu, E., Berge, J., Graeve, M., and Falk-Petersen, S. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob Change Biol* **16**(11): 3154–3163. doi:10.1111/j.1365-2486.2010.02175.x.
- Spares, A.D., Stokesbury, M.J.W., Dadswell, M.J., O’Dor, R.K., and Dick, T.A. 2015. Residency and movement patterns of Arctic Charr *Salvelinus alpinus* relative to major estuaries. *J Fish Biol* **86**(6): 1754–1780. doi:10.1111/jfb.12683.
- Spares, A.D., Stokesbury, M.J.W., O’Dor, R.K., and Dick, T.A. 2012. Temperature, salinity and prey availability shape the marine migration of Arctic Char, *Salvelinus alpinus*, in a macrotidal estuary. *Mar Biol* **159**(8): 1633–1646. doi:10.1007/s00227-012-1949-y.
- Statistics Canada. 2016. Provinces/Territories, Cartographic Boundary File - 2016 Census (lpr_000b16a_e). Statistics Canada, Ottawa, ON. Available from <https://open.canada.ca/data/en/dataset/a883eb14-0c0e-45c4-b8c4-b54c4a819edb>.
- Statistics Canada. 2024. Table 41-10-0063-01 Food security status of First Nations people living off reserve, Métis and Inuit by age group. doi:<https://doi.org/10.25318/4110006301-eng>.
- Stearns, S.C., and Hendry, A.P. 2004. Introduction: The Salmonid Contribution to Key Issues in Evolution. *In* *Evolution Illuminated: Salmon and their Relatives*. Edited by A.P. Hendry and S.C. Stearns. Oxford University Press. pp. 3–19.

- Stehfest, K.M., Patterson, T.A., Barnett, A., and Semmens, J.M. 2015. Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. *Oikos* **124**(3): 307–318. doi:10.1111/oik.01429.
- Stewart, D.B., Mochnacz, N.J., Carmichael, T.J., Sawatzky, C.D., and Reist, J.D. 2009. Fish diets and food webs in the Northwest Territories: Dolly Varden (*Salvelinus malma*). Fisheries and Oceans Canada, Winnipeg, MB.
- Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2010. Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*). Fisheries and Oceans Canada, Winnipeg, MB.
- Summers, D.W. 1995. Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. *Fisheries Manag Ecol* **2**(2): 147–156. doi:10.1111/j.1365-2400.1995.tb00107.x.
- Svenning, M.-A., and Gullestad, N. 2002. Adaptations to stochastic environmental variations: The effects of seasonal temperatures on the migratory window of Svalbard Arctic Charr. *In Ecology, behaviour and conservation of the charrs, genus Salvelinus. Edited by P. Magnan, C. Audet, H. Glémet, M. Legault, M.A. Rodríguez, and E.B. Taylor.* Springer Netherlands, Dordrecht. pp. 165–174. doi:10.1007/978-94-017-1352-8_13.
- Tallman, R.F., Ferguson, S.H., Harris, L.N., Hedges, K.J., Howland, K.L., Hussey, N.E., Marcoux, M., Matthews, C.J.D., Martin, Z.A., and Moore, J.-S. 2019. Migration, Dispersal, and Gene Flow of Harvested Aquatic Species in the Canadian Arctic. *In Biological Research in Aquatic Science. Edited by Y. Bozkurt.* IntechOpen. doi:10.5772/intechopen.85902.
- Taylor, E.B. 2016. The Arctic Char (*Salvelinus alpinus*) “complex” in North America revisited. *Hydrobiologia* **783**(1): 283–293. doi:10.1007/s10750-015-2613-6.
- Taylor, E.B., Geraldès, A., and Shen, J. 2025. History of speciation inferred from genomic analysis of a species complex of north temperate fishes. *Evolution*.
- Taylor, E.B., Lowery, E., Lilliestrål, A., Elz, A., and Quinn, T.P. 2008. Genetic analysis of sympatric char populations in western Alaska: Arctic char (*Salvelinus alpinus*) and Dolly Varden *Salvelinus malma*) are not two sides of the same coin. *Journal of Evolutionary Biology* **21**(6): 1609–1625. doi:10.1111/j.1420-9101.2008.01603.x.

- Taylor, P.D., Crewe, T.L., Mackenzie, S.A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C.M., Guglielmo, C.G., Hamilton, D.J., Holberton, R.L., Loring, P.H., Mitchell, G.W., Norris, D.R., Paquet, J., Ronconi, R.A., Smetzer, J.R., Smith, P.A., Welch, L.J., and Woodworth, B.K. 2017. The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv Ecol* **12**(1): Article 8. doi:10.5751/ACE-00953-120108.
- Taylor, S.G. 2008. Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Glob Change Biol* **14**(2): 229–235. doi:10.1111/j.1365-2486.2007.01494.x.
- Thorstad, E.B., Økland, F., Aarestrup, K., and Heggberget, T.G. 2008. Factors affecting the within-river spawning migration of Atlantic Salmon, with emphasis on human impacts. *Rev Fish Biol Fisher* **18**(4): 345–371. doi:10.1007/s11160-007-9076-4.
- Tibblin, P., Forsman, A., Borger, T., and Larsson, P. 2016. Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. *J Anim Ecol* **85**(1): 136–145. doi:10.1111/1365-2656.12439.
- Tiller, I.V. 2013. Biology and fishery of the Dolly Varden Charr (*Salvelinus malma*) on the east coast of Kamchatka. *J Ichthyol* **53**(10): 875–883. doi:10.1134/S0032945213100135.
- Tillotson, M.D., Arostegui, M.C., Austin, C.S., Lincoln, A.E., Matsubu, W., McElroy, K.N., and Quinn, T.P. 2021. Challenges in the identification and interpretation of phenological shifts: Anthropogenic influences on adult migration timing in salmonids. *Rev Fish Sci Aquac* **29**(4): 769–790. doi:10.1080/23308249.2021.1874292.
- Todd, C.D., Friedland, K.D., MacLean, J.C., Whyte, B.D., Russell, I.C., Lonergan, M.E., and Morrissey, M.B. 2012. Phenological and phenotypic changes in Atlantic Salmon populations in response to a changing climate. *ICES J Mar Sci* **69**(9): 1686–1698. doi:10.1093/icesjms/fss151.
- Todorov, V., and Filzmoser, P. 2009. An object-oriented framework for robust multivariate analysis. *J Stat Softw* **32**(3). doi:10.18637/jss.v032.i03.
- Udyawer, V., Dwyer, R.G., Hoenner, X., Babcock, R.C., Brodie, S., Campbell, H.A., Harcourt, R.G., Huveneers, C., Jaïne, F.R.A., Simpfendorfer, C.A., Taylor, M.D., and Heupel, M.R. 2018. A standardised framework for analysing animal detections from automated tracking arrays. *Anim Biotelemetry* **6**(1): 17. doi:10.1186/s40317-018-0162-2.

- United States Census Bureau. 2017. Cartographic Boundary Files - Shapefile (cb_2017_us_state_20m).
United States Census Bureau. Available from <https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.2017.html>.
- United States Navy. 2023. Astronomical Applications API v4.0.1. [accessed 28 November 2023].
- Van Oostdam, J., Donaldson, S.G., Feeley, M., Arnold, D., Ayotte, P., Bondy, G., Chan, L., Dewailly, É., Furgal, C.M., Kuhnlein, H., Loring, E., Muckle, G., Myles, E., Receveur, O., Tracy, B., Gill, U., and Kalhok, S. 2005. Human health implications of environmental contaminants in Arctic Canada: A review. *Sci Total Environ* **351–352**: 165–246. doi:10.1016/j.scitotenv.2005.03.034.
- VanGerwen-Toyne, M., Lewis, C., Tallman, R., and Martin, Z. 2013. Information to support the assessment of Arctic Char (*Salvelinus alpinus*) in the Sylvia Grinnell River, Nunavut, 2009-2011. Fisheries and Oceans Canada, Ottawa, ON.
- Venables, W.N., and Ripley, B.D. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York.
- Villegas-Ríos, D., Alós, J., Palmer, M., Lowerre-Barbieri, S., Bañón, R., Alonso-Fernández, A., and Saborido-Rey, F. 2014. Life-history and activity shape catchability in a sedentary fish. *Mar Ecol Prog Ser* **515**: 239–250. doi:10.3354/meps11018.
- Waldman, J., Wilson, K.A., Mather, M., and Snyder, N.P. 2016. A resilience approach can improve anadromous fish restoration. *Fisheries* **41**(3): 116–126. doi:10.1080/03632415.2015.1134501.
- Wandsvik, A., and Jobling, M. 1982. Overwintering mortality of migratory Arctic Charr, *Salvelinus alpinus*, (L.) reared in salt water. *J Fish Biol* **20**(6): 701–706. doi:10.1111/j.1095-8649.1982.tb03980.x.
- Waters, C., Cotter, D., O'Neill, R., Drumm, A., Cooney, J., Bond, N., Rogan, G., and Maoiléidigh, N.Ó. 2024. The use of predator tags to explain reversal movement patterns in Atlantic Salmon smolts (*Salmo salar* L.). *J Fish Biol*: jfb.15658. doi:10.1111/jfb.15658.
- Watson, G.S. 1962. Goodness-of-fit tests on a circle. II. *Biometrika* **49**(1/2): 57–63.
- Webb, J., Verspoor, E., Aubin-Horth, N., Romakkaniemi, A., and Amiro, P. 2007. The Atlantic Salmon. *In* The Atlantic Salmon: Genetics, Conservation and Management. Edited by E.E. Verspoor, L. Stradmeyer, and J. Nielsen. Blackwell Publishing Ltd., Ames, Iowa. pp. 17–56.

- Wedel, J.H., Olding, B.J., and Palmer, M. 1988. An Overview Study of the Coppermine River Basin. Environment Canada, Yellowknife, NWT.
- Weinstein, S. 2023. Community-partnered research on subsistence char fisheries near Kugluktuk, Nunavut: Novel insights from traditional knowledge and western science. PhD dissertation, University of Waterloo, Waterloo, ON.
- Weinstein, S.Y., Gallagher, C.P., Hale, M.C., Loewen, T.N., Power, M., Reist, J.D., and Swanson, H.K. 2024. An updated review of the post-glacial history, ecology, and diversity of Arctic Char (*Salvelinus alpinus*) and Dolly Varden (*S. malma*). *Environ Biol Fish* **107**(1): 121–154. doi:10.1007/s10641-023-01492-0.
- Weinz, A.A., Matley, J.K., Klinard, N.V., Fisk, A.T., and Colborne, S.F. 2020. Identification of predation events in wild fish using novel acoustic transmitters. *Anim Biotelemetry* **8**(1): 28. doi:10.1186/s40317-020-00215-x.
- Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Available from <https://ggplot2.tidyverse.org>.
- Williams-Grove, L.J., and Szedlmayer, S.T. 2016. Mortality estimates for Red Snapper based on ultrasonic telemetry in the northern Gulf of Mexico. *N Am J Fish Manage* **36**(5): 1036–1044. doi:10.1080/02755947.2016.1184197.
- Williamson, M.J., Tebbs, E.J., Dawson, T.P., Curnick, D.J., Ferretti, F., Carlisle, A.B., Chapple, T.K., Schallert, R.J., Tickler, D.M., Harrison, X.A., Block, B.A., and Jacoby, D.M.P. 2021. Analysing detection gaps in acoustic telemetry data to infer differential movement patterns in fish. *Ecol Evol* **11**(6): 2717–2730. doi:10.1002/ece3.7226.
- Winter, E.R., Hindes, A.M., Lane, S., and Britton, J.R. 2021. Detection range and efficiency of acoustic telemetry receivers in a connected wetland system. *Hydrobiologia* **848**(8): 1825–1836. doi:10.1007/s10750-021-04556-3.
- Winter, J. 1996. Advances in Underwater Telemetry. *In* Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland. pp. 555–590.
- Yergey, M.E., Grothues, T.M., Able, K.W., Crawford, C., and DeCristofer, K. 2012. Evaluating discard mortality of Summer Flounder (*Paralichthys dentatus*) in the commercial trawl fishery:

- Developing acoustic telemetry techniques. *Fish Res* **115–116**: 72–81.
doi:10.1016/j.fishres.2011.11.009.
- Zuur, A.F., and Ieno, E.N. 2021. *The World of Zero-inflated Models*. Highland Statistics Ltd, Newburgh.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. *Methods Ecol Evol* **1**(1): 3–14. doi:10.1111/j.2041-210X.2009.00001.x.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science and Business Media, New York, NY.

Appendices

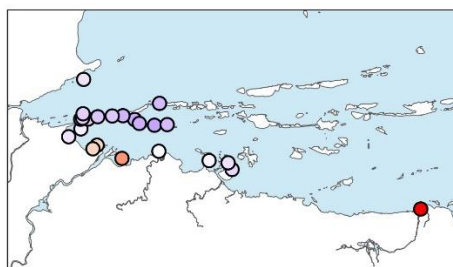
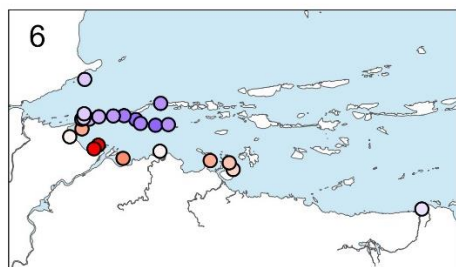
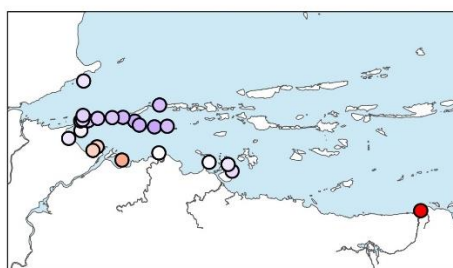
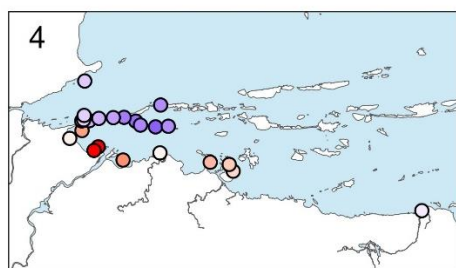
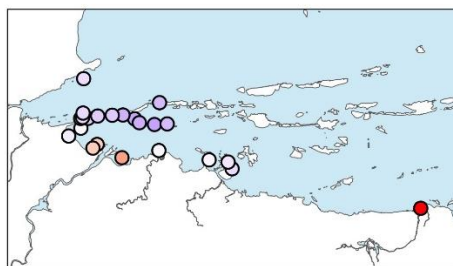
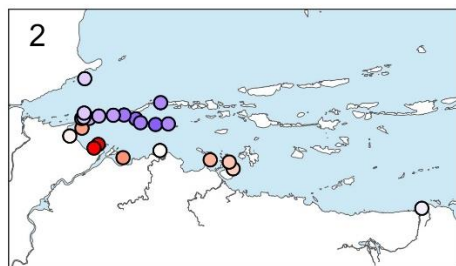
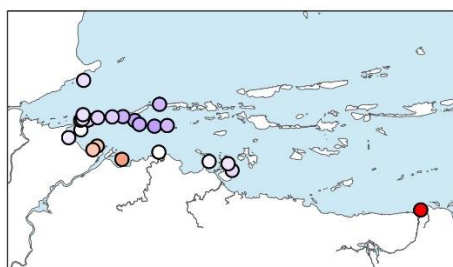
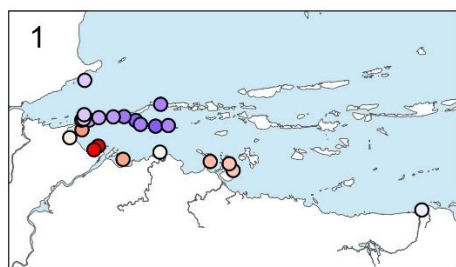
Appendix A

Supplementary information for Chapter 3

Local Getis G^* (hereafter, G^*) was used to identify hotspots (clusters of high activity) and coldspots (clusters of low activity) in terms of time, rather than movement. G^* values were calculated based on the duration of residence events at each receiver location. The threshold that was used to define residence events was 24 hours. The choice of threshold can influence both the number and duration of residence events. To assess whether the choice of residence threshold impacted the results and interpretation of G^* values, the analysis was conducted using a range of thresholds (1, 2, 4, 6, 12, 18, 22, 23, 24, 25, 26, 36, and 48 hours). The G^* values presented in the plots below indicate that findings were consistent among residence thresholds. The residence threshold used to generate each plot is identified in the upper left corner of each row of plots. Red points represent receivers identified as hotspots, blue points represent receivers identified as coldspots, and white points represent G^* values of 0, indicating no evidence of spatial association or hot/coldspots.

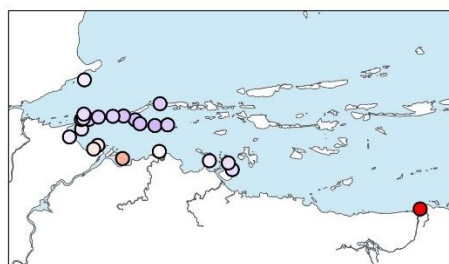
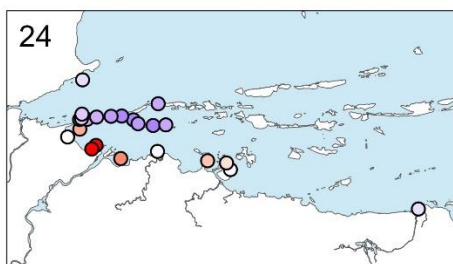
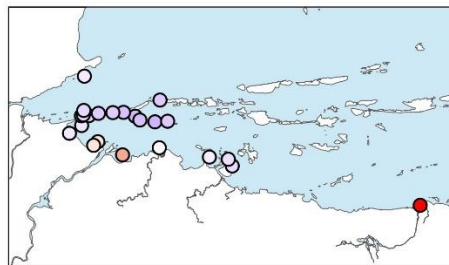
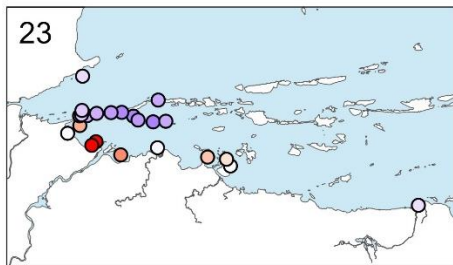
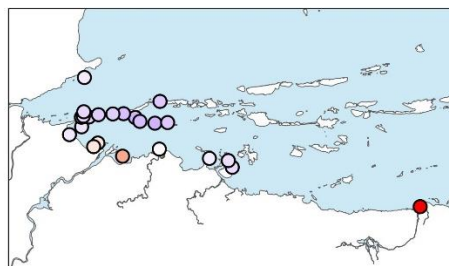
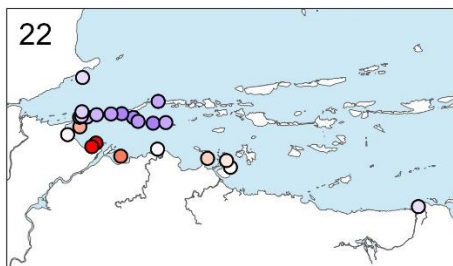
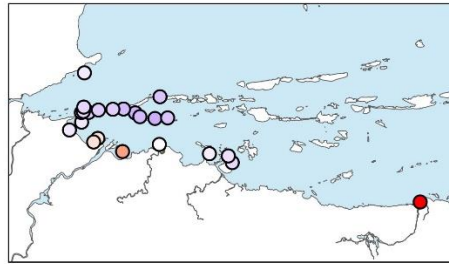
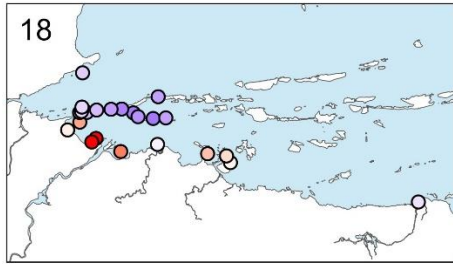
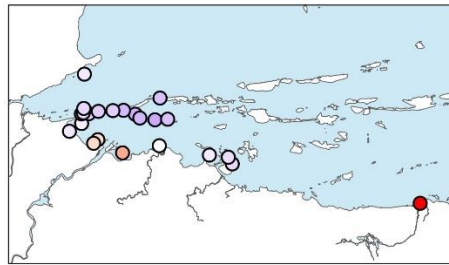
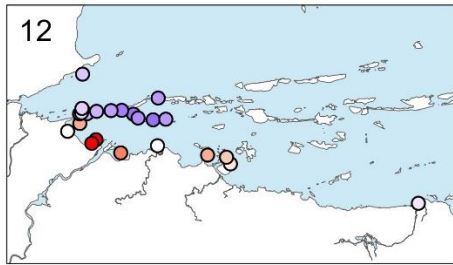
Above falls

Below falls



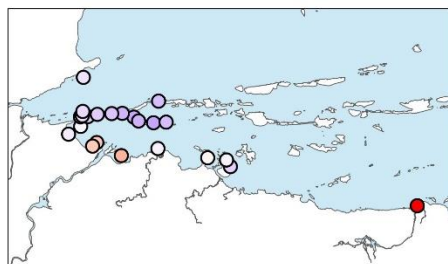
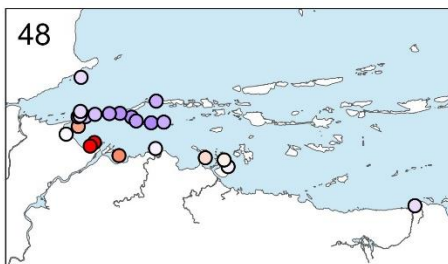
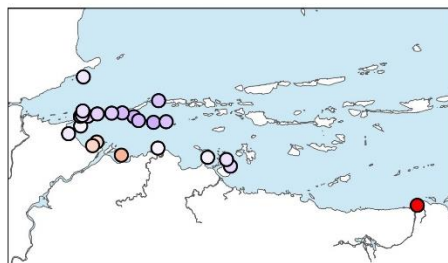
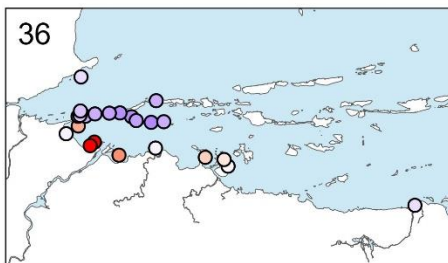
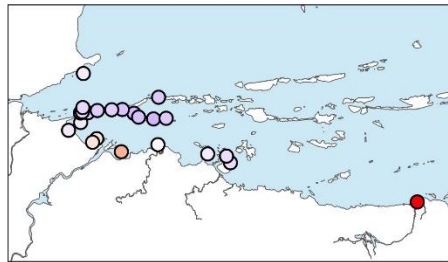
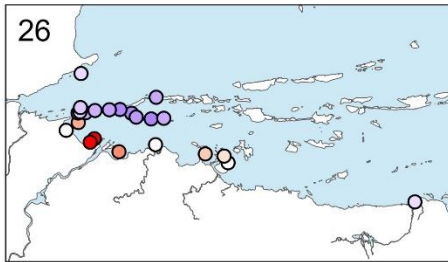
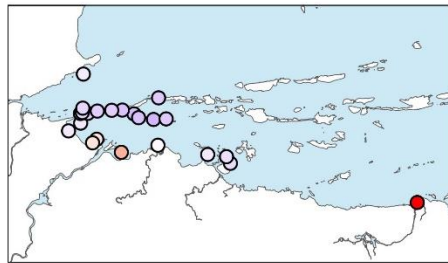
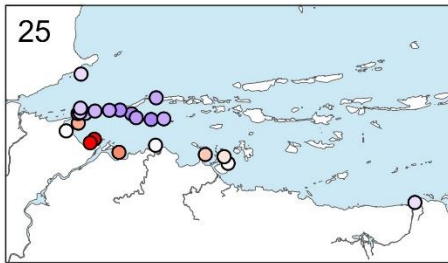
Above falls

Below falls



Above falls

Below falls



Appendix B

Supplementary information for Chapter 4

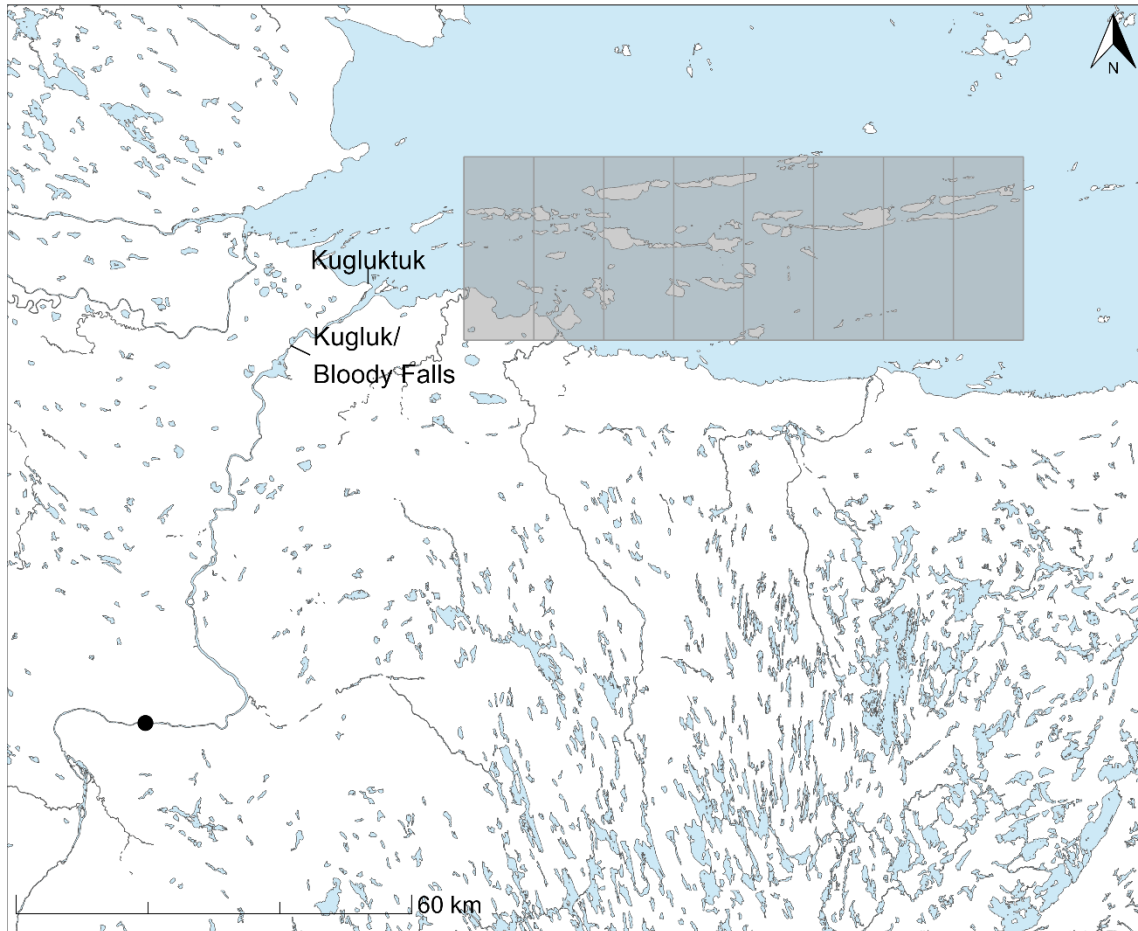


Figure B1: Map of locations where environmental variables were obtained from other sources. Black point indicates location of Environment and Climate Change Canada’s Hydrometric Station 10PC004, where the discharge values used in this study were calculated (Environment and Climate Change Canada 2024). Grey shaded boxes indicate grid cells where sea surface temperature data were extracted from the National Oceanic and Atmospheric Administration Daily Optimum Interpolation SST Version 2.1 high resolution dataset (Reynolds et al. 2007; Huang et al. 2021). Note that available grid cells did not extend farther west to include the mouth of the Coppermine River.

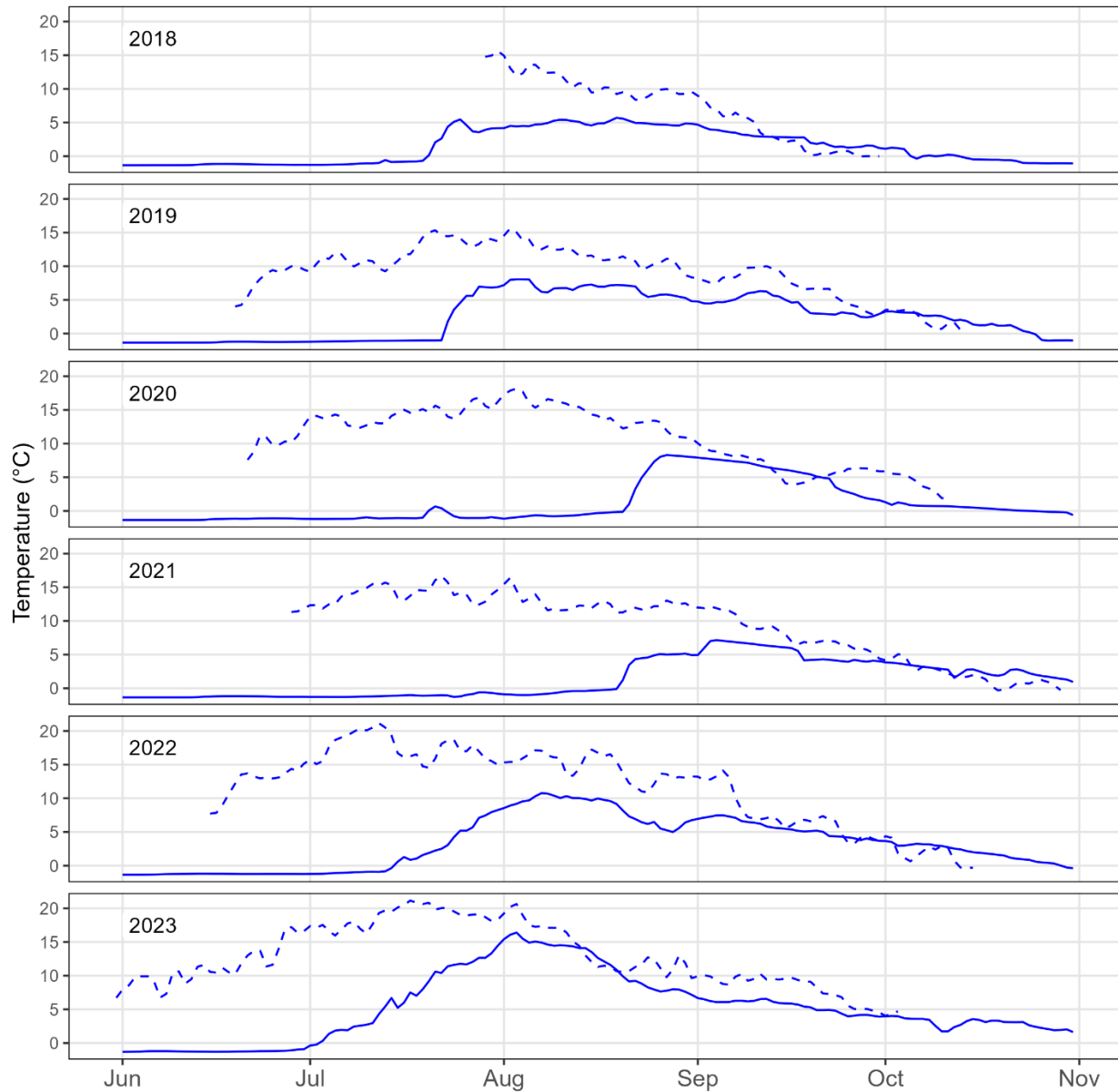


Figure B2: Sea surface temperature (solid lines) and river temperature (dashed lines) for each year of the study period. Daily sea surface temperature (SST) data were obtained from 01 June to 31 October from the National Oceanic and Atmospheric Administration Daily Optimum Interpolation SST Version 2.1 high resolution dataset (Reynolds et al. 2007; Huang et al. 2021). River temperature data were extracted from acoustic receiver logs and are presented from date of river break-up to date of river freeze-up each year, with three exceptions: 1) 2018 break-up (receiver was deployed part-way through ice-free season); 2) 2020 freeze-up and 2021 break-up (receiver was not deployed in winter 2020–2021 due to equipment shortages); and, 3) 2023 freeze-up (data used for this study were retrieved before freeze-up).

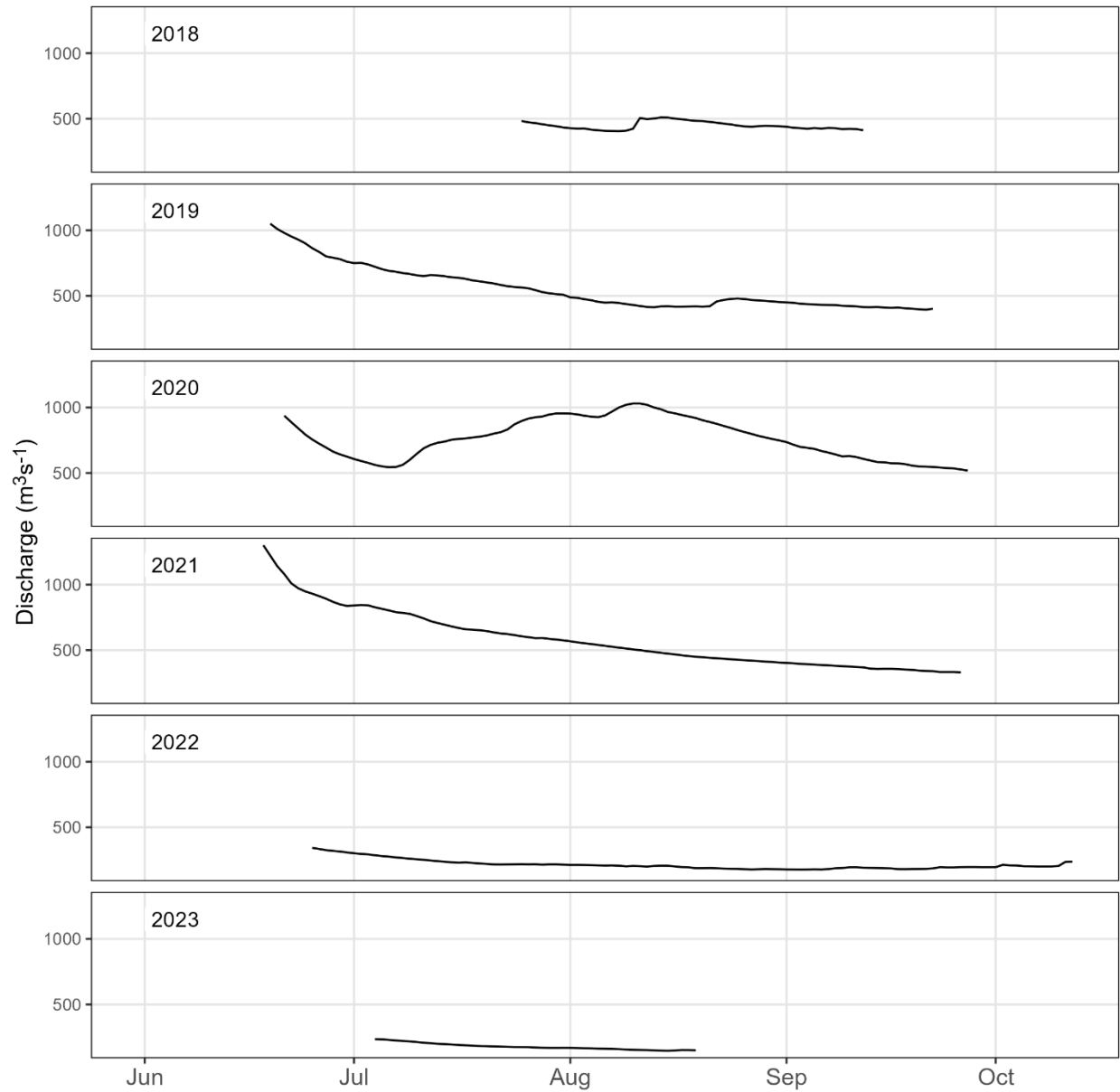


Figure B3: Discharge of Coppermine River for each year of the study period. Discharge data were obtained from Environment and Climate Change for hydrometric station 10PC004, located ~ 70 km upstream of Kugluk or Bloody Falls.

Table B1: Generalized linear mixed models (logit link) relating freshwater return to environmental variables. The null model includes only the random factor of fish ID. AICc scores were used to rank models. Models are presented in order of increasing AICc or decreasing rank. Model deviance (-2I) is -2log-likelihood. Coefficients apply to scaled and centred variables. Marginal R² only considers fixed factors and conditional R² considers both fixed and random factors.

Model	Coefficient estimates (± standard error)														
	AICc	ΔAICc	-2I	Discharge	Temperature	SST	Photoperiod/ Day of year	Species (Dolly Varden)	Overwintering location (Above falls)	*Overwintering location	*Species	Zero-inflation intercept	Marginal R ²	Conditional R ²	
Temperature*Overwintering location + SST (weekly) + Discharge + Photoperiod*Overwintering location + Species	1054.56	0.00	1032.49	0.60 (0.28)	-3.18 (1.50)	4.23 (1.18)	-5.62 (2.69)	9.22 (3.77)	6.56 (3.05)	Temperature: 3.86 (1.55) Photoperiod: 4.83 (2.70)	—	1.79 (0.12)	0.85	0.85	
Temperature*Overwintering location + SST (weekly) + Discharge + Photoperiod*Overwintering location + Photoperiod*Species	1055.31	0.75	1031.23	0.62 (0.30)	-3.33 (1.62)	5.13 (1.56)	-4.98 (2.64)	4.42 (5.19)	12.43 (6.59)	Temperature: 4.03 (1.67) Photoperiod: 11.70 (7.76)	-7.57 (7.41)	1.82 (0.11)	0.90	0.90	
Temperature*Overwintering location + SST (weekly) + Photoperiod*Overwintering location + Photoperiod*Species	1058.27	3.71	1036.20	—	-3.20 (1.60)	4.43 (1.57)	-4.25 (2.46)	3.95 (5.01)	11.26 (7.00)	Temperature: 4.08 (1.69) Photoperiod: 10.66 (8.82)	-7.74 (8.40)	1.82 (0.12)	0.89	0.89	
Temperature*Overwintering location + SST (weekly) + Photoperiod + Species	1060.49	5.93	1042.44	—	-2.31 (0.87)	3.85 (1.21)	-1.50 (0.37)	7.78 (3.05)	1.76 (1.09)	3.19 (0.98)	—	1.81 (0.11)	0.73	0.73	
SST (weekly) + Photoperiod*Overwintering location + Species	1064.19	9.63	1048.15	—	—	4.32 (1.26)	-11.24 (4.4)	7.04 (2.96)	12.33 (4.76)	9.91 (4.37)	—	—	0.90	0.90	
Temperature*Overwintering location + SST (weekly) + Discharge + Species	1066.22	0	1048.17	0.97 (0.27)	-2.04 (0.75)	5.55 (1.43)	—	7.26 (2.94)	1.39 (0.95)	2.74 (0.83)	—	1.82 (0.11)	0.73	0.73	
Temperature*Overwintering location + Discharge*Overwintering location + SST	1067.88	1.67	1047.83	1.60 (1.18)	-2.06 (0.75)	5.82 (1.58)	—	6.38 (3.50)	1.99 (1.54)	Temperature: 2.76 (0.83) Discharge: -0.64 (1.16)	—	1.83 (0.11)	0.73	0.73	
Temperature*Overwintering location + SST (weekly)*Overwintering location + Discharge +	1068.19	13.64	1048.14	0.97 (0.27)	-2.13 (0.90)	6.02 (3.11)	—	8.23 (6.42)	1.14 (1.71)	Temperature: 2.82 (0.97) SST: -0.56 (3.26)	—	1.82 (0.11)	0.75	0.75	
Temperature*Overwintering location + SST (weekly)*Overwintering location + Discharge*Overwintering location + Species	1068.97	14.41	1046.90	4.06 (4.06)	-3.45 (2.30)	11.74 (8.25)	—	12.63 (8.93)	2.17 (2.83)	Temperature: 4.15 (2.33) SST: -6.26 (8.30) Discharge: -3.12 (4.06)	—	1.85 (0.11)	0.86	0.86	
Temperature*Overwintering location + SST (weekly) + Species	1081.96	27.40	1065.92	—	-1.89 (0.72)	4.06 (1.40)	—	6.11 (3.00)	1.13 (0.88)	2.59 (0.79)	—	1.80 (0.12)	0.31	0.31	
Temperature*Overwintering location + SST (weekly)*Overwintering location + Species	1083.95	29.39	1065.90	—	-1.96 (0.87)	4.46 (3.12)	—	6.93 (6.36)	0.94 (1.60)	Temperature: 2.65 (0.92) SST: -0.46 (3.24)	—	1.80 (0.12)	0.31	0.32	
Temperature + SST (weekly)*Overwintering location + Species	1092.83	38.28	1076.80	—	0.63 (0.29)	22.16 (12.13)	—	20.20 (13.18)	-6.66 (4.96)	-17.48 (12.23)	—	1.94 (0.10)	0.94	0.94	
SST (weekly)*Overwintering location + SST (weekly)*Species	1093.93	39.37	1081.91	—	—	4.90 (1.59)	—	4.13 (2.20)	1.11 (0.80)	—	—	1.89 (0.12)	0.66	0.66	
SST (weekly)*Overwintering location + Species	1095.87	41.31	1081.84	—	—	5.35 (2.92)	—	4.64 (3.51)	0.74 (1.69)	-0.79 (3.20)	—	1.89 (0.12)	0.66	0.66	
SST (weekly) + Overwintering location + Species	1100.14	45.59	1088.12	—	—	4.29 (1.42)	—	—	2.27 (1.30)	0.49 (2.39)	—	1.92 (0.11)	0.62	0.62	
SST*Overwintering location + Species	1110.72	56.16	1096.69	—	—	11.09 (6.39)	—	5.64 (5.40)	-3.15 (3.09)	-9.07 (6.39)	—	1.92 (0.12)	0.79	0.79	
SST*Overwintering location + SST*Species	1112.18	57.62	1096.14	—	—	3.46 (1.45)	—	4.41 (2.66)	-2.70 (2.44)	-8.06 (5.29)	6.41 (5.44)	1.80 (0.17)	0.61	0.61	
Photoperiod*Overwintering location + Species	1128.48	73.92	1114.45	—	—	—	-2.72 (0.68)	1.14 (0.70)	2.04 (0.76)	1.13 (0.58)	—	-0.10 (0.88)	0.24	0.34	
Day of year*Overwintering location + Species	1128.92	74.37	1114.89	—	—	—	2.42 (0.55)	1.13 (0.68)	1.57 (0.64)	-0.72 (0.47)	—	-0.05 (0.76)	0.21	0.32	

Table B1 continued:

Model	Coefficient estimates ($\pm$ standard error)												Marginal R ²	Conditional R ²
	AICc	Δ AICc	-2l	Discharge	Temperature	SST	Photoperiod/ Day of year	Species (Dolly Varden)	Overwintering location (Above falls)	*Overwintering location	*Species	Zero-inflation intercept		
Photoperiod*Overwintering location + Photoperiod*Species	1130.10	75.55	1114.07	—	—	—	-2.54 (0.63)	0.43 (1.33)	2.42 (0.96)	1.45 (0.71)	-0.52 (0.84)	0.01 (0.51)	0.24	0.34
Day of year*Overwintering location + Day of year*Species	1130.18	75.63	1114.15	—	—	—	2.18 (0.51)	0.31 (1.14)	1.96 (0.79)	-1.07 (0.57)	0.60 (0.69)	0.02 (0.45)	0.21	0.32
Temperature*Overwintering location + Species	1240.14	185.58	1226.11	—	-2.02 (0.39)	—	—	1.00 (0.44)	0.52 (0.39)	2.05 (0.41)	—	1.06 (0.30)	0.11	0.11
Temperature*Overwintering location + Temperature*Species	1242.04	187.48	1226.00	—	-1.89 (0.53)	—	—	0.83 (0.68)	0.58 (0.44)	2.14 (0.51)	-0.23 (0.67)	1.03 (0.31)	0.11	0.11
Discharge*Overwintering location + Species	1250.51	195.96	1238.49	-1.19 (0.16)	—	—	—	0.70 (0.29)	-0.33 (0.26)	0.81 (0.19)	—	—	0.04	0.05
Discharge (weekly)*Overwintering location + Species	1251.01	196.45	1238.99	-1.12 (0.15)	—	—	—	0.67 (0.28)	-0.34 (0.25)	0.73 (0.18)	—	—	0.04	0.04
Discharge*Overwintering location + Discharge*Species	1252.17	197.62	1238.15	-1.30 (0.25)	—	—	—	0.87 (0.40)	-0.39 (0.27)	0.73 (0.23)	0.19 (0.32)	—	0.04	0.05
Discharge (weekly)*Overwintering location + Discharge (weekly)*Species	1252.67	198.11	1238.64	-1.22 (0.23)	—	—	—	0.83 (0.40)	-0.39 (0.27)	0.65 (0.22)	0.17 (0.30)	—	0.04	0.05
Temperature (weekly)*Overwintering location	1257.04	202.48	1247.02	—	-1.04 (0.16)	—	—	—	0.07 (0.30)	1.29 (0.20)	—	—	0.03	0.09
Temperature (weekly)*Overwintering location + Species	1258.42	203.87	1246.40	—	-1.05 (0.16)	—	—	0.32 (0.41)	-0.06 (0.34)	1.30 (0.20)	—	—	0.03	0.09
Temperature (weekly)*Overwintering location + Temperature (weekly)*Species	1260.38	205.83	1246.36	—	-1.01 (0.23)	—	—	0.25 (0.52)	-0.03 (0.36)	1.33 (0.25)	-0.07 (0.31)	—	0.03	0.08
SST (weekly rate)*Overwintering location	1273.07	218.52	1263.06	—	—	-0.50 (0.23)	—	—	-0.87 (0.27)	0.99 (0.24)	—	—	0.03	0.07
SST (weekly rate)*Overwintering location + Species	1275.08	220.52	1263.06	—	—	-0.50 (0.23)	—	0.00 (0.38)	-0.87 (0.31)	0.99 (0.24)	—	—	0.03	0.07
SST (weekly rate)*Overwintering location + SST (weekly rate)*Species	1276.37	221.82	1262.34	—	—	-0.71 (0.36)	—	0.15 (0.42)	-0.93 (0.31)	0.82 (0.29)	0.38 (0.45)	—	0.03	0.07
Temperature (weekly rate)*Overwintering location	1282.89	228.33	1272.88	—	-0.53 (0.14)	—	—	—	-0.49 (0.27)	0.08 (0.18)	—	—	0.02	0.07
Temperature (weekly rate)*Overwintering location + Species	1284.88	230.33	1272.86	—	-0.53 (0.14)	—	—	0.05 (0.39)	-0.50 (0.31)	0.08 (0.18)	—	—	0.02	0.07
Temperature (weekly rate)*Overwintering location + Temperature (weekly reate)*Species	1286.11	231.55	1272.08	—	-0.41 (0.19)	—	—	-0.15 (0.45)	0.04 (0.34)	0.21 (0.23)	-0.24 (0.28)	—	0.02	0.07
Discharge (daily rate)*Overwintering location	1313.26	258.70	1303.24	-0.15 (0.16)	—	—	—	0.83 (0.40)	-0.85 (0.26)	0.10 (0.20)	—	—	0.01	0.08
Discharge (weekly rate)*Overwintering location	1313.87	259.32	1303.86	0.01 (0.16)	—	—	—	—	-0.83 (0.26)	0.07 (0.20)	—	—	0.01	0.08
Discharge (daily rate)*Overwintering location + Species	1315.25	260.70	1303.23	-0.15 (0.16)	—	—	—	-0.05 (0.42)	-0.83 (0.32)	0.10 (0.20)	—	—	0.01	0.08
Discharge (daily rate)*Overwintering location + Discharge (daily rate)*Species	1315.62	261.06	1301.59	0.11 (0.24)	—	—	—	-0.05 (0.42)	-0.82 (0.32)	0.26 (0.24)	0.42 (0.32)	—	0.01	0.08
Discharge (weekly rate)*Overwintering location + Species	1315.85	261.29	1303.83	0.01 (0.16)	—	—	—	-0.08 (0.42)	-0.79 (0.32)	0.07 (0.20)	—	—	0.01	0.08
Discharge (weekly rate)*Overwintering location + Discharge (weekly rate)*Species	1317.28	262.72	1303.25	0.18 (0.27)	—	—	—	-0.04 (0.42)	-0.81 (0.32)	0.15 (0.22)	-0.25 (0.33)	—	0.01	0.08
Null	1318.56	264.00	1314.56	—	—	—	—	—	—	—	—	—	0.00	0.08

Appendix C

Supplementary Information for Chapter 5

Methods for extracting DNA by salt precipitation

The methods described here were compiled from multiple sources. The materials and order of the steps were consistent for each extraction, but ranges are provided (e.g., 11 000–14 000 RPM) when settings or durations varied among extractions.

- Added 600 µL of 100% isopropanol to 1.5 mL microcentrifuge tube (one for each sample) and froze at -20° C
- Cut ~ 25 mg piece of tissue and placed in 1.5 mL microcentrifuge tube
- Added 600 µL of Buffer ATL (Qiagen) and 20–80 µL of Proteinase K
- Vortexed to mix and incubated at 55° C until as much of the tissue was dissolved as possible (~ 24 hours); vortexed every hour when possible
- Removed samples from incubator and placed on ice
- Added 200 µL of 7.5 M ammonium acetate
- Vortexed for 20 seconds
- Centrifuged at 11 000–14 000 RPM for 8–30 minutes
- Transferred supernatant to previously prepared tube of cold 100% isopropanol
- Inverted tube gently ~ 50 times to mix
- Placed in freezer at -20° C for a minimum of one hour
- Removed tube from freezer and centrifuged at 10 000–14 000 RPM for 10–30 minutes
- Discarded supernatant and blotted tube on paper towel to remove remaining supernatant
- Added 600 µL of cold (4° C) 70% ethanol
- Inverted tube gently to mix
- Centrifuged at 10 000 RPM for 8 minutes
- Discarded supernatant and blotted tube on paper towel to remove remaining supernatant
- Covered tube with Kimwipe and left in fume hood overnight to allow remaining ethanol to evaporate
- Added 100 µL of Buffer AE (Qiagen)
- Rehydrated overnight at room temperature

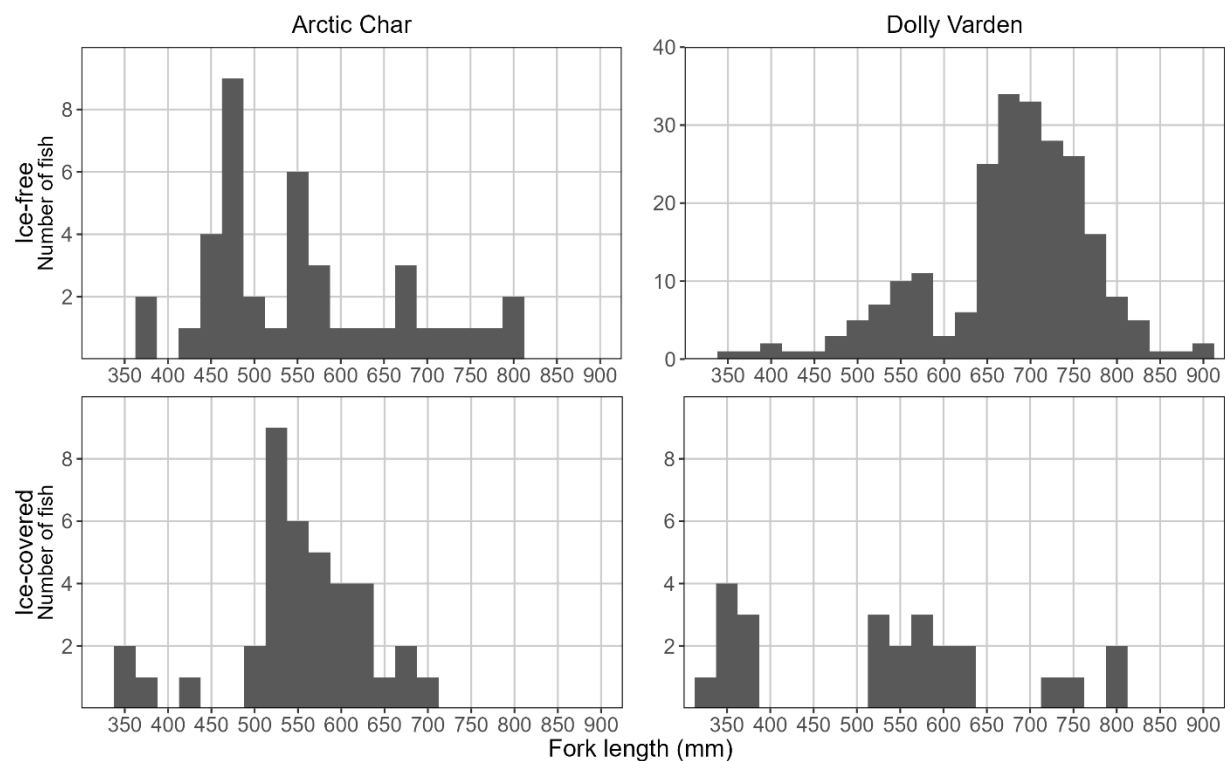


Figure C1: Distributions of fork length (mm) by species of fish captured during ice-free periods and ice-covered periods. Fish captured during ice-free periods were captured throughout the study area and were assumed to be representative of all fish that migrated to the ocean. Fish captured during ice-covered periods were captured below the falls in the Coppermine River.

Table C1: Locations and years of deployment for each acoustic receiver station.

Station	Longitude	Latitude	Years deployed
4MB-R-1	-115.27006	67.85629	2019, 2020, 2021, 2022, 2023
7MI-E-R-1	-114.76061	67.92680	2019, 2020, 2021, 2022, 2023
7MI-E-R-2	-114.60216	67.93903	2021, 2022, 2023
7MI-S-R-1	-114.90007	67.89266	2019, 2020, 2021, 2022, 2023
7MI-W-R-1	-114.96566	67.90073	2019, 2020, 2021, 2022, 2023
ASK-E-R-1A	-114.38439	67.75729	2018, 2019, 2021, 2022
ASK-E-R-1B	-114.38138	67.76173	2018, 2019, 2021, 2022
ASK-W-R-1	-114.43455	67.77609	2018, 2019, 2021, 2022
ASK-W-R-2	-114.48264	67.80590	2019, 2020, 2021, 2022, 2023
COD-E-R-1	-114.78908	67.88064	2019, 2020, 2021, 2022, 2023
COD-E-R-2	-114.71762	67.88195	2019, 2020, 2021, 2022, 2023
COD-E-R-3	-114.61826	67.88013	2021, 2022, 2023
COD-W-R-1	-114.87378	67.88442	2019, 2020, 2021, 2022, 2023
COP-L-R-0	-115.07463	67.82375	2018, 2019, 2020, 2021, 2022, 2023
COP-L-R-0B	-115.08849	67.80489	2019, 2020, 2021, 2022
COP-L-R-1	-115.15628	67.78768	2018, 2019, 2020, 2021, 2022, 2023
COP-L-R-2	-115.19177	67.78013	2018, 2019, 2020, 2021, 2022, 2023
COP-L-R-3	-115.21380	67.77589	2018, 2019, 2020, 2021, 2023
COP-L-R-4	-115.30361	67.76380	2018, 2019, 2020, 2021, 2022, 2023
COP-L-R-5	-115.33204	67.75601	2018, 2019, 2020, 2021, 2022, 2023
COP-L-R-6	-115.36504	67.74421	2020, 2021, 2022, 2023
COP-U-R-1	-115.38235	67.73383	2018, 2019, 2020, 2021, 2022, 2023
KDL-E-R-1	-115.06386	67.97935	2021, 2022, 2023
KDL-E-R-2	-114.93891	67.97967	2021, 2022, 2023
KDL-E-R-3	-114.81613	67.97596	2021, 2022, 2023
KDL-E-R-4	-114.69442	67.96861	2021, 2022, 2023
KIK-W-R-0	-114.35400	67.78711	2019, 2020, 2021, 2022, 2023
KIK-W-R-1	-114.37610	67.80128	2019, 2020, 2021, 2022, 2023
KIK-W-R-2	-114.50605	67.82686	2019, 2021, 2022, 2023
KUG-E-R-1	-113.27386	67.71543	2018, 2019, 2021, 2022, 2023
KUG-L-R-0	-113.29658	67.70361	2018, 2019, 2020, 2021, 2022, 2023
KUG-W-R-1	-113.32095	67.70080	2018, 2019, 2021, 2022, 2023
MRK-R-1	-115.02572	67.90021	2019, 2020, 2021, 2022, 2023
NAP-E-R-1	-114.63661	67.81611	2018, 2019, 2020, 2021, 2022, 2023
NAP-W-R-1	-114.76437	67.82568	2018, 2019, 2020, 2021, 2022, 2023
PT1-R-1	-115.20150	67.87289	2018, 2019, 2020, 2021, 2022, 2023
PT1-R-2	-115.16126	67.89364	2018, 2019, 2020, 2021, 2022, 2023
PT1-R-3	-115.10702	67.89859	2019, 2020, 2021, 2022, 2023
PT2-R-1	-115.20277	67.89336	2018, 2019, 2020, 2021, 2022, 2023
PT2-R-2	-115.19198	67.89556	2018, 2019, 2020, 2021, 2022, 2023

Table C1 continued:

Station	Longitude	Latitude	Years deployed
PT1-R-3	-115.10702	67.89859	2019, 2020, 2021, 2022, 2023
PT2-R-1	-115.20277	67.89336	2018, 2019, 2020, 2021, 2022, 2023
PT2-R-2	-115.19198	67.89556	2018, 2019, 2020, 2021, 2022, 2023
PT2-R-3	-115.18944	67.90483	2018, 2019, 2020, 2021, 2022, 2023
RAE-L-R-0	-115.53608	67.91893	2018, 2019, 2021, 2022
RAE-N-R-0	-115.50999	67.92113	2022, 2023
RAE-N-R-1	-115.48327	67.92677	2018, 2019, 2021, 2022
RAE-N-R-2	-115.18604	67.97748	2019, 2020, 2021, 2022, 2023
RIC-E-R-1	-115.43068	67.90552	2018, 2019, 2021, 2022, 2023
RIC-E-R-2	-115.37357	67.88950	2018, 2019, 2021, 2022
RIC-E-R-3	-115.31660	67.88483	2018, 2019, 2021, 2022
RIC-L-R-1	-115.52847	67.89441	2018, 2019, 2021, 2022
SND-E-R-1	-115.02675	67.83323	2019, 2021, 2022
SND-W-R-1	-115.11050	67.83847	2019, 2020, 2021, 2022, 2023
YCO-E-R-1A	-114.97195	67.80048	2018, 2019, 2021, 2022, 2023
YCO-E-R-1B	-114.97125	67.81057	2019, 2020, 2021, 2022, 2023
YCO-E-R-2	-114.93707	67.82537	2018, 2019, 2022, 2023
YCO-E-R-3	-114.85112	67.81895	2018, 2021, 2022, 2023
YCO-W-R-1	-115.13400	67.83081	2019, 2020, 2021, 2022, 2023
YCO-W-R-2	-115.21331	67.84895	2019, 2021, 2022, 2023

Table C2: Number of individuals by year from each group (Arctic Char, Dolly Varden that overwintered below the falls, and Dolly Varden that overwintered above the falls) that were included in linear discriminant analyses.

Year	Arctic Char Below falls	Dolly Varden Below falls	Dolly Varden Above falls
2018	1	-	-
2019	2	3	10
2020	2	6	14
2021	2	1	6
2022	1	-	7
2023	-	-	4

Table C3: Scalings (coefficients) from linear discriminant analysis of scaled and centred movement metrics of Arctic Char that overwintered below the falls and Dolly Varden that overwintered above the falls. Scalings are presented in descending order of absolute magnitude (i.e., from greatest importance to least importance). A logarithmic transformation was applied to staging (both river mouth and river plume) and duration (both marine and freshwater) metrics, and an arcsin-square root transformation was applied to proportional (both marine and freshwater linearity) metrics.

Variable	Scaling
Duration (river)	-1.5357
Staging (river mouth)	-0.3100
Linearity (river)	0.2565
Staging (river plume)	-0.0729
Linearity (marine)	0.051
Duration (marine)	-0.0061