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Offshore ocean dispersal of adult Dolly Varden Salvelinus malma in the Beaufort Sea

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Abstract

While it is known that Dolly Varden *Salvelinus malma* occupies offshore waters of the Bering and Chukchi seas in Alaska, the general scientific consensus is that this species typically occupies nearshore waters of the Beaufort Sea during its summer feeding season. Because of the importance of offshore waters for many upper trophic level vertebrates in this region, we tested if Dolly Varden occupies this area as well. Therefore, we attached pop-up satellite archival tags (PSATs) to Dolly Varden in the Beaufort Sea. Ten PSATs released from the fish and floated to the surface on pre-programmed dates throughout the summer, and transmitted archived depth and temperature data to satellites, while providing tag end locations. PSATs documented offshore dispersal of up to 69 km from the coast by Dolly Varden during the summer. Tagged fish were surface oriented with mean depths of individuals ranging from 0.1 to 2.2 m (total depth range 0–18.8 m), and experienced an ambient thermal environment of mostly 2–8 °C. The findings of this study highlight the importance of the offshore waters of the Beaufort Sea for Dolly Varden. Such knowledge aids in understanding potential impacts of human activities and environmental change in the Arctic.

Keywords Beaufort Sea · Dispersal · Dolly Varden · PSATs · Telemetry

Introduction

In Arctic Alaska, a rapidly changing climate and increased human activities such as transpolar shipping, and hydrocarbon exploration and extraction, have the potential to impact important marine food sources of indigenous residents (Reist et al. 2006; Dunham et al. 2008; Holland-Bartels and Pierce 2011). One frequently landed and important fish

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species captured in subsistence fisheries in Arctic Alaska, including Kaktovik (Fig. 1), is the Dolly Varden *Salvelinus malma* (Pedersen and Linn 2005; Magdanz et al. 2010). To understand potential impacts of climate change and human activities on animals such as Dolly Varden, as well as to design potential management strategies in response to these stressors, it is imperative to have a sound understanding of their biology and ecology.

The Dolly Varden is found throughout a wide range in northern North America (Armstrong and Morrow 1980). In North America, the northern form of Dolly Varden *S. m. malma* encompasses all populations west of the Mackenzie River to north of the Alaska Peninsula, whereas the southern form *S. m. lordi* is found from the south side of the Alaska Peninsula to Puget Sound (Armstrong and Morrow 1980). Northern form Dolly Varden (referred to hereafter) life history in the Arctic has been explored for decades and generalized patterns have emerged from these studies (Yoshihara 1973; Furniss 1975; Craig 1977; McCart 1980; DeCicco 1985, 1997). These fish can either be classified as resident or anadromous individuals. Residents never migrate to sea and remain in their natal river throughout their life, whereas Fig. 1 Tagging/release locations (triangles) and end locations (circles) of Dolly Varden *Salvelinus malma* tagged with pop-up satellite archival tags in 2015 (white) and 2016 (black). Tag identification numbers are noted for reference purposes



anadromous individuals spawn and rear in freshwater and feed in saltwater later in life (Armstrong and Morrow 1980). For anadromous individuals (the subject of this study), juveniles rear in freshwater for 2-5 years before beginning a pattern of annual migrations to marine waters in the spring to feed on epipelagic prey, mainly zooplankton and various fish species (Craig 1977; Armstrong and Morrow 1980; Craig and Haldorson 1981; West and Wiswar 1985). After the summer feeding season, they return to rivers to overwinter, typically in close proximity to groundwater springs (Armstrong and Morrow 1980; DeCicco 1997; Brown et al. 2014). Anadromous Dolly Varden usually undertake three to five ocean migrations before reaching maturity. Once becoming sexually mature, spawning occurs in the fall and it is thought that they usually spawn biennially (Furniss 1975; DeCicco 1989).

Although generalized life history patterns of northern Dolly Varden previously have been described (Armstrong and Morrow 1980; McCart 1980; DeCicco 1997), important details of their marine dispersal have not been thoroughly examined. This has resulted in untested assumptions regarding marine movements and habitat use, some of which currently are being challenged. For example, originally it was thought that anadromous Dolly Varden did occupy offshore areas of the ocean. However, northern form Dolly Varden tagged in northwestern Alaska were recovered in Russia as far as 1690 km away from their tagging site 14 months after being released, indicating that these tagged fish occupied offshore waters in the Bering and Chukchi seas (DeCicco 1992). Also, using 35 years of bycatch data from offshore salmon fisheries south of the Bering Strait, Morita et al. (2009) found that Dolly Varden (southern and northern form) were distributed throughout a wide range in the Pacific Ocean, including nearshore and offshore waters of the Japan Sea, Bering Sea, Okhotsk Sea, and the Gulf of Alaska. Most recently, Courtney et al. (2016a) documented occupation of offshore waters of the Chukchi Sea by northern form Dolly Varden during the summer feeding season and proposed that the outer continental shelf north of Russia may be an important feeding area for this species. The occupation of offshore areas is thought to be a result of high densities of zooplankton upon which this species is assumed to prey upon (Citta et al. 2015; Courtney et al. 2016a).

In contrast, few research programs have been conducted with the proper sampling gear in which to capture Dolly Varden in offshore waters of the Beaufort Sea, and thus the occupation of offshore waters is not understood for Dolly Varden in this region. In general, it is assumed that Dolly Varden optimize energetic and physiological processes by strictly occupying relatively warm, brackish nearshore waters of the Beaufort Sea (Craig and McCart 1976; Griffiths et al. 1977; Craig and Haldorson 1981; Craig 1984; Craig et al. 1985; Craig 1989; Underwood et al. 1996; Jarvela and Thorsteinson 1997, 1999). However, while little direct information exists, several studies have suggested offshore dispersal and long distance movements of Dolly Varden in the summer in the Beaufort Sea. Specifically, summer growth patterns of Dolly Varden smolts from the Sagavanirktok River showed slow growth in early summer, which contrasted with the growth patterns found in juvenile broad whitefish Coregonus nasus and Arctic cisco C. autumnalis (Fechhelm et al. 1997). This finding

suggests a delay in initiation of summer feeding as a result of Dolly Varden traveling to offshore areas to forage (Fechhelm et al. 1997). Additionally, limited research has documented catches of Dolly Varden in the Beaufort Sea up to 5 km (n = 34) from shore with purse seines (Thorsteinson et al. 1990) and 15 km from shore with fyke nets (n = 3;LGL 1990). Therefore, while knowledge about the marine distribution of Dolly Varden in the Beaufort Sea is limited, occupation of offshore waters elsewhere, in addition to several lines of emerging evidence, suggest that this species may occupy offshore waters throughout its range, including the Beaufort Sea. Here we report details of 10 pop-up satellite archival tags (PSATs) attached to Dolly Varden that made summer migrations to the Beaufort Sea, to examine to the hypothesis that Dolly Varden occupy offshore areas of the Beaufort Sea during the summer feeding season.

Methods

Study site

The physical oceanography of the nearshore waters of the Beaufort Sea is dictated by geological, climate, and tidal factors (Dunton et al. 2006; McClelland et al. 2012; Harris et al. 2017). A prominent geological characteristic of the Beaufort Sea continental shelf (~ 80 km wide in the study area) is a discontinuous network of barrier islands that form estuarine lagoons (Dunton et al. 2006). The Arctic climate shows extreme seasonal air temperature fluctuations (~ -50 to 20 °C), which influences water temperatures in rivers and in the ocean, as well as the presence or absence of river and sea ice (Harris et al. 2017). Tidal fluctuations in the region are relatively small (< 30 cm), but influence temperature and salinity of the lagoons. Ice break-up in lagoons and nearshore waters typically occurs between late May and early June with lagoons being icefree by early July (McClelland et al. 2012). Over 50% of the annual freshwater discharge from rivers near these lagoons occurs in a two-week period following ice break-up (Harris et al. 2017). This freshwater input creates a generally warm (~ 5–10 °C), but thermally dynamic (range ~ < 0–15 °C), brackish (10-25 psu) estuarine band of water that spills into nearshore marine areas ~ 0.5-2 km from shore (Craig 1984; Craig et al. 1985; Craig 1989; Dunton et al. 2006; Harris et al. 2017). The persistence and extent of this nearshore water mass depends on river discharge and prevailing wind and surface currents (Craig et al. 1985). Adjacent to the lagoon/nearshore habitat is the typically cold ($\sim < 6$ °C), saline (27-32 psu) offshore marine water of the Beaufort Sea (Craig 1984, 1989; Dunton et al. 2006).

Fish capture and tagging

Dolly Varden reported in this manuscript (n = 10) were captured and tagged during summers of 2015 and 2016, in nearshore marine waters of the Beaufort Sea near Kaktovik, AK (Fig. 1). Capture methods included angling and monitored gillnets, following the same sampling and fish handling protocols of Courtney et al. (2016b). In short, after capture, PSATs were attached to large adult (> 54 cm) Dolly Varden using a harness system (Courtney et al. 2016b). After a PSAT was secured, each tagged fish was immediately released back into the water at its capture location. All field work was conducted under University of Alaska Fairbanks Institution of Animal Care and Use Committee assurance 572670 and State of Alaska Fisheries Research Permits SF2014-202, SF-2015-158, and CF-16-061.

Tag data and acquisition

While attached to a fish, the PSATs (Microwave Telemetry's HR X-tag [n = 9], or X-tag [n = 1]), measured and recorded depth, and temperature, and light intensity every 2 min. Specifications for each tag model can be found on the manufacturer's website (http://www.microwavetelemet ry.com). On pre-programmed dates throughout the summer, the tags released from the fish, floated to the surface of the ocean, and transmitted archived data (2-min resolution for HR X-tag and 15-min resolution for X-tag) to the Argos satellite system (http://www.argos-system.org). While transmitting, a location (Argos location class 1–3; positional error < 1.5 km) of each tag was determined by the satellites, the first of which was considered a tagged fish's end location.

Data analyses were conducted by examining end locations, dispersal distance, and depth and temperature records of tagged fish. First, distribution of tagged Dolly Varden was qualitatively described by examining end locations in a GIS framework (ArcMap 10.1, Redlands, CA). Second, minimum dispersal distance traveled between tagging and end locations was calculated by measuring the great arc circle distance of a non-meandering route that did not pass over land between tagging and end locations (Courtney et al. 2016b). Third, depth and temperature of individual tagged fish were qualitatively described by visually examining time-series plots and calculating minimum, maximum, and mean depths $(\pm SD)$ and temperatures. Fourth, overall mean $(\pm SD)$ proportion of time that tagged Dolly Varden spent at depth and temperature intervals was calculated by aggregating data among all individuals.

Depth and temperature experienced by Dolly Varden were used to infer occupied water masses in the Beaufort Sea. In the context of this study, lagoon/nearshore habitat is characterized by shallow (0–5 m), generally warm (> 5 °C), but thermally dynamic water (range < 0-17 °C). In contrast, offshore marine water is characterized as deeper (> 10 m), generally colder, and a more thermally stable water mass (3–6 °C). It is important to note that the coastal and offshore habitats we describe are dynamic and constantly changing with the weather, wind, freshwater flow, and marine currents, defying any fixed geographic boundaries between lagoon/nearshore and offshore marine waters (e.g., Harris et al. 2017).

To understand the spatial distribution of tagged fish in relation to the physical oceanography and anthropogenic activities of the Beaufort Sea, end locations and tag-recorded sea-surface temperature (SST) were interpreted in the context of satellite-derived SST (1 km resolution; http://ouro cean.jpl.nasa.gov/SST/), sea ice extent (http://nsidc.org/data/masie/), and locations of active U.S. Federal Outer Continental Shelf (OCS) oil and gas leases (https://www.boem.gov/Alaska-Region/). Daily tag-recorded SST for each tag was calculated as the mean daily temperature at a depth of < 2 m. While this analysis did not provide fine scale Dolly Varden distribution information, it did provide information on the possible extent of offshore occupation, habitats that they likely did not occupy, and whether they transited through or

occupied areas near active U.S. Federal oil and gas leases of the Beaufort Sea. Daily light-based geolocation was not examined because HR X-tags (n = 9) do not provide daily geolocation estimates, and the one PSAT that processed light intensity data was unable to detect changes in ambient irradiance due to light sensor saturation during the Arctic summer (Courtney et al. 2016b).

Results

Marine habitat occupancy

Ten tagged Dolly Varden (54–65 cm fork length) provided a total of 146 days of detailed data about the marine behavior and distribution of Dolly Varden in the Beaufort Sea (Table 1). During their marine residency, including occupation of both lagoon/nearshore waters and offshore waters up to 69 km from shore, tagged Dolly Varden were generally surface oriented. While occupying mean depths of 0.1–2.2 m (grand mean 1.0 ± 1.3 m; range 0–18.8 m; Table 1), they spent 86% of their time in the first 2 m of the water column (Fig. 2a), and occupied water temperatures of mostly (70%

 Table 1
 Summary of depth and temperature measurements recorded by pop-up satellite archival tags attached to Dolly Varden Salvelinus malma

 that reported from marine waters of the Beaufort Sea in the summers of 2015 and 2016

ID	Fork length (cm)	Deployment date	Reporting date	Liberty (days)	Temperature (°C) ^a	Depth (m) ^a	Dispersal (km) ^b	% Data retrieved ^c
148486	59	7/01/15	7/16/15	14	1.9 ± 2.8 (- 1.4-13.4)	0.1 ± 0.6 (0-18.8)	39 (12)	97 (17712)
148491	59	7/03/15	7/18/15	14	3.9 ± 2.3 (- 0.4-11.8)	0.9 ± 1.2 (0-14.8)	72 (69)	98 (17862)
148492	62	7/04/15	7/19/15	14	2.7 ± 3.8 (- 1.4–15.6)	0.9 ± 1.6 (0-18.8)	27 (9)	83 (15174)
148714	54	7/09/15	7/20/15	10	7.0 ± 2.8 (- 0.0-12.9)	0.3 ± 0.9 (0-10.8)	2 (2)	100 (2048)
159700	60	6/26/16	7/10/16	14	7.3 ± 3.1 (0.3–17.0)	0.9 ± 0.9 (0-9.4)	15 (14)	86 (15786)
136527 ^d	59	6/27/16	7/11/16	14	(2.4–15.4)	(0–9.4)	55 (40)	4 (792)
159701 ^d	65	6/27/16	7/12/16	14	(2.7–12.1)	(0–9.4)	46 (38)	3 (576)
136525	62	6/27/16	7/12/16	15	5.7 ± 1.6 (0.8–13.7)	2.2 ± 1.1 (0-6.7)	55 (50)	94 (17244)
136529 ^d	57	6/27/16	7/14/16	16	(3.2–10.4)	(0-12.1)	62 (6)	8 (1386)
159702	60	6/27/16	7/15/16	18	5.6 ± 0.9 (1.9-8.1)	1.5 ± 1.9 (0-13.4)	84 (65)	41 (7578)

^aTemperature and depth are reported as mean \pm standard deviation. Parentheses denote range of temperature and depths experienced by individual fish

^bDispersal is reported as minimum distance traveled by tagged fish while at liberty, followed by the approximate straight line distance between each tag's end location and shore

^cPercent data retrieved are reported as the % data successfully transmitted to satellites, with the total unique temperature and depth readings in parentheses

^dDenotes tags which did not successfully transmit most of their archived data. Mean \pm standard deviation temperatures and depths are not reported for these tags



Fig. 2 Mean proportion of time spent at **a** depth and **b** temperature by tagged Dolly Varden *Salvelinus malma* in lagoon/nearshore (black bars), marine offshore waters (gray bars), and all marine waters combined (white bars) in the Beaufort Sea (n = 10). Whiskers represent the standard deviation of individual means

of the time) 2–8 °C (grand mean 4.5 \pm 3.3 °C; Table 1; Fig. 2b).

When individual tag records were examined, shifts in habitat between relatively warm lagoon/nearshore water and relatively cold offshore water were apparent (Fig. 3). Dolly Varden occupied lagoon/nearshore waters for 1-13 days after tagging, before transiting to offshore marine water (Fig. 3). During times when tagged fish were inferred to occupy lagoon/nearshore water, they generally occupied the top 1 m of the water column and experienced a thermal environment of 4-12 °C (Figs. 2, 3). However, variable temperatures of 0-15 °C were found on a daily basis in some records (Fig. 3). When tagged fish were inferred to have occupied offshore marine water, they remained surface oriented and spent most of their time in the top 4 m of the water column. The offshore environment, however, was much colder (~ 3-6 °C) and more thermally stable than the nearshore habitat (Figs. 2b, 3). While in offshore water, most dives were relatively shallow (< 10 m; Fig. 3). For example, several fish whose tags reported approximately 40–69 km from shore in the Beaufort Sea, where the water depth was ~ 40-100 m, usually only occupied depths < 5 m. Visual qualitative analyses of depth time series data revealed no observable depth-specific behaviors (e.g., diel diving behavior; Courtney et al. 2016a).

Analyses of tag-recorded SST, satellite-derived SST, and sea-ice extent provided additional context to the spatial distribution of tagged Dolly Varden. In summer 2015, fish whose tags' end locations were ~ 2-69 km from shore generally experienced cooler SSTs that those tagged in 2016 whose tags' end locations were ~ 6-65 km from shore (Fig. 4). Similar SSTs recorded by the tags and satellites near the reported end locations suggest that the extent of movement of tagged fish was not considerably farther offshore than the extent of end locations in each year; therefore, the end locations are likely representative of the extent of offshore dispersal. Of note is that end locations in 2016 suggest that several tagged fish were in close proximity to a pronounced thermal break in offshore water of the Beaufort Sea. However, fish showed no affinity for occupying waters near the ice edge during summer melting in either year. Finally, end locations and inferred spatial distribution of the tagged Dolly Varden suggest that tagged fish occupied waters in close proximity to hydrocarbon exploration and extraction activities (Fig. 4).

Discussion

PSATs provide evidence of offshore dispersal of Dolly Varden in the Beaufort Sea, suggesting that this species is widely distributed and may utilize offshore marine waters throughout its range (Volkov et al. 1996; Morita et al. 2009; Courtney et al. 2016a). This finding challenges a commonly held assumption that while occupying the Beaufort Sea, anadromous fishes, including Dolly Varden, are assumed to optimize energetic and physiological processes by utilizing warm, brackish waters found nearshore, and forego movements to relatively deep, cold, and saline marine waters (Craig 1984; Craig et al. 1985; Craig 1989). Findings from several studies support this assumption by reporting higher catches inside lagoons compared to the ocean-side of barrier islands, as well as declining catches with increasing distance from shore (Craig and McCart 1976; Griffiths et al. 1977; Craig and Haldorson 1981; Craig 1984). In addition to these findings from passive gear sampling, Jarvela and Thorsteinson (1997) tracked acoustic tagged Dolly Varden in nearshore areas of the Beaufort Sea, and found that fish appeared to closely follow the shoreline. However, as this study had a small sample size (n = 6) and a very short tracking period (2-21 h), it may have only documented post-tagging effects, or the limited period of time fish spent in nearshore waters, before making offshore movements. Additionally, most marine research on coastal fish in Arctic Alaska has been conducted within close proximity (< 10 km) of shore (Craig and McCart 1976; Griffiths et al. 1977; Craig and Haldorson 1981; Craig 1984; Craig et al. 1985), or used sampling procedures that would not likely catch a strong swimming fish (Logerwell et al. 2010). By design, these sampling procedures would fail to document offshore habitation by Dolly Varden.





Fig. 3 Examples of marine depth and habitat occupancy of Dolly Varden Salvelinus malma whose tags (n = 6) reported in marine offshore waters of the Beaufort Sea. Time periods of inferred lagoon/ nearshore (black bar) and marine offshore (gray bar) occupancy are denoted at the top of each panel. Tag identification numbers is provided for reference purposes. In the context of this study, lagoon/

While the reasons for Dolly Varden occupying offshore areas are not clear, it is likely based on a combination of factors, including prey availability and abundance, interspecific competition, and predator avoidance. However, in the case of the Beaufort Sea, occupancy of offshore regions is likely related to the high abundance of epipelagic zooplankton and forage fishes, particularly along oceanographic fronts (Smith 2010). Offshore occupation of the Beaufort Sea for the purpose of feeding has been documented for other upper trophic level vertebrates. For example, the bowhead whale has been documented in large aggregations in the central Beaufort Sea approximately ~ 70 km from shore in water < 50 m deep (Clarke et al. 2017; Okkonen et al. 2016). These aggregations of bowhead whales are thought to result from upwelling events that transport zooplankton prey to prominent oceanographic fronts that form dense prey fields (Okkonen et al. 2016). Similarly, other forage fish species, including arctic cod Boreogadus saida and capelin Mallotus villosus, are known to feed on epipelagic zooplankton (e.g., copepods, euphausiids, and amphipods) in offshore

nearshore habitat was characterized by shallow (0-5 m), generally warm (> 5 °C), but thermally dynamic water (range < 0-17 °C). In contrast, marine offshore habitat was characterized as a deeper (> 10 m), generally colder, and more thermally stable water mass (3-6 °C)

waters of the Beaufort Sea (Pirtle and Meuter 2011; Rand et al. 2013; Gray et al. 2016). The findings from this study in conjunction with previous findings about other fishes and whales suggest that offshore areas of the Beaufort Sea may be important feeding locations for Dolly Varden during the summer.

The fact that at least some large Dolly Varden migrate considerable distances offshore in the Beaufort Sea does not diminish the known importance of coastal habitats for rearing and feeding. For example, tagged Dolly Varden captured in this study were located in or transited through these environments for brief periods of time, some of which were expelling stomach contents consisting of undigested invertebrates upon capture (Author's personal observation). This corroborates and supports inferred and documented feeding by Dolly Varden in previous studies in nearshore areas of the Beaufort Sea (Griffiths et al. 1977; Craig and Haldorson 1981; West and Wiswar 1985). We surmise that Dolly Varden may use the nearshore/lagoon waters for foraging and/or a migration pathway to and from natal and



Fig. 4 Satellite-derived sea-surface temperature (SST) and sea-ice extent (white polygon) in the Beaufort Sea on a 1 August 2015 and b 20 July 2016. Black dots represent tag end locations. c Mean daily

tag-recorded SST experienced by individual tags in 2015 (black dots) and 2016 (gray dots). Gray squares denote active U.S. Federal oil and gas lease areas

overwintering freshwater rivers, as previously documented, but also note the potential importance of offshore marine waters for foraging.

The water temperatures experienced by several tagged fish (< -1 °C; tag temperature resolution 0.16–0.23 °C) are some of the coldest documented habitats occupied by Dolly Varden, and likely represent fish transiting areas adjacent to landfast sea-ice and sea-ice floes (Courtney et al. 2016a). These results are similar to other recent electronic tagging studies that have documented Dolly Varden in northwest Alaska (Courtney et al. 2016a) and Atlantic salmon Salmo salar (Reddin et al. 2011) experiencing temperatures as low as -1.3 °C. These results suggest that Dolly Varden have some tolerance to freezing in saline waters, as the hypothetical freezing point of a salmonid with no anti-freeze compounds is approximately -0.7 °C (Pennell and Barton 1996). Past research in a laboratory has shown that a closely related species, Arctic char Salvelinus alpinus, is resistant to freezing and can survive temperatures of -0.99 °C for up 2 h in the presence of ice and ≥ 5 days at - 1.2 °C in the absence of ice (Fletcher et al. 1988). While there have been no documentation of antifreeze compounds found in salmonids, changes in blood electrolyte balance and the epidermis of Arctic char have been hypothesized to serve as preventative mechanisms to ice nuclei formation in their flesh. If these processes are present, in Dolly Varden, they possibly serve a similar function, but future research is needed to describe the physiological processes involved in the ability of Dolly Varden to survive extremely cold temperatures (Courtney et al. 2016a).

Because of this species' cultural and nutritional importance to indigenous peoples who inhabit Arctic regions of both the U.S. and Canada, the increased understanding of Dolly Varden biology and ecology provided by this study is important for management and impact assessment applications. For example, while estimates of catch and harvest of Dolly Varden from the U.S. Beaufort Sea and its adjacent freshwater drainages suggest a sustainable level of use (Scanlon 2015), anadromous populations in northwestern Canada, just across the U.S. border, are listed as a species of concern by the Committee on the Status for Endangered Wildlife in Canada (COSEWIC; http://www.cosewic. gc.ca/). As such, threats such as occupying areas close to U.S. Outer Continental Shelf (OCS) Federal lease areas in the Beaufort Sea may expose them to potential risks. In the future, we suggest further PSAT studies northern Alaska and

northwestern Canada on Dolly Varden to provide increased sample sizes. Synergistically, this information will help both American and Canadian agencies better understand transboundary movements of Dolly Varden, which is a comanagement priority in Canada. It will also provide a more complete conceptual life history model of Dolly Varden in the northeastern extent of its range, which will further aid in understanding potential impacts of human activities and environmental changes.

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