DISPERSAL PATTERNS AND SUMMER OCEANIC DISTRIBUTION OF ADULT

DOLLY VARDEN FROM THE WULIK RIVER, ALASKA,

EVALUATED USING SATELLITE TELEMETRY

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A

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Abstract

In Arctic Alaska, Dolly Varden *Salvelinus malma* is highly valued as a subsistence fish; however, little is known about oceanic dispersal or ecology. This study addresses this knowledge gap, by using a fisheries independent method, pop-up satellite archival tags (PSATs). In spring of 2012 and 2013, we attached 52 PSATs to Dolly Varden in a river in northwestern Alaska, which flows into the Arctic Ocean, to examine the marine dispersal, behavior and habitat occupancy of this species. Tagged Dolly Varden demonstrated two types of dispersal, including offshore and nearshore dispersal. The offshore type was the first documented northwesterly dispersal and occupancy of Outer Continental Shelf (OCS) areas of the Russian Chukchi Sea. While occupying this area, tagged Dolly Varden demonstrated affinity for the first 5 m of the water column, diel patterns in depth occupancy, and dive depths of up to 50 m, while experiencing a thermal environment of generally 3–7°C. During the nearshore dispersal type, Dolly Varden transited in coastal areas of northwest Alaska, likely returning to their natal rivers to spawn. While in nearshore areas, tagged Dolly Varden always occupied shallow waters (< 6 m), and experienced a rapidly changing thermal environment $(\pm 15^{\circ}C)$, including some water temperatures cooler than -1°C. This study demonstrates that PSATs offer an alternative and effective platform with which to study several aspects of large adult Dolly Varden dispersal and ecology in areas where it is not practical or feasible to capture these fish, such as in coastal and offshore regions of Arctic Alaska. Additionally, the results of this study have increased our knowledge of the summer marine distribution, behavior and thermal environment of Dolly Varden in Arctic regions of Alaska, and this knowledge is important to several stake holders for the conservation of this important subsistence species.

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Introduction

Chars (*Salvelinus*) have a circumpolar distribution, and are widespread throughout northern latitude countries, including Japan, Russia, Norway, Iceland, Sweden, Canada, and the United States (Armstrong and Morrow 1980; Johnson 1980; Klemetsen et al. 2003). Species within this genus have received considerable attention, most notably because of their large variation in life history, complex movements, and phenotypic plasticity between and among species (Armstrong and Morrow 1980; Behnke 1980; Morrow 1980; Savvaitova 1980; DeCicco 1985; Klemetsen et al. 2003; Morita et al. 2011). While these large variations draw a certain level of biological fascination to the genus, it has also created much taxonomic debate of the species within this genus (Behnke 1980; Morrow 1980; Savvaitova 1980), as well as difficulty understanding their population dynamics and abundances, which is directly applicable to their management and conservation (Nordeng 1983; Armstrong 1984; DeCicco 1985; Lisac and Nelle 2000; Dunham et al. 2008; Klemetsen et al. 2003).

One char, the Dolly Varden, *Salvelinus malma*, is found throughout a wide range in northern North America and Asia and is widely distributed in Arctic regions of Alaska (Armstrong and Morrow 1980). In Arctic Alaska, at age of 2–5 years, anadromous Dolly Varden moves into the sea during the spring to feed (Armstrong and Morrow 1980; DeCicco 1985). In contrast to most anadromous salmonids, after the summer feeding season and regardless of maturity, Dolly Varden returns to freshwater in the fall to overwinter in lower reaches or spring fed areas of rivers (Armstrong and Morrow 1980; DeCicco 1985). After 2–3 marine summer feeding migrations, Dolly Varden reaches maturity, and typically spawns in headwaters springs in the fall (DeCicco 1985). Dolly Varden is iteroparous and can theoretically spawn every year

after maturation; however, it usually spawns every other year because it rarely acquires sufficient energy reserves to spawn in consecutive years (Furniss 1975; DeCicco 1989).

While not of commercial significance, the Dolly Varden is highly important as a subsistence resource and is thought to be the most frequently landed fish in many Arctic Alaska villages (Pedersen and Linn 2005; Magdanz et al. 2010). For example, in the village of Kaktovik located on the North Slope of Alaska, Dolly Varden comprises roughly 80% of all fish caught in subsistence fisheries (Pedersen and Linn 2005). In the villages of Kivalina and Noatak, located in northwestern Alaska, Dolly Varden landings in 2007 (30,761 fish) exceeded the landings of all species of Pacific salmon *Oncorhynchus* spp. combined (5,241 fish; Magdanz et al. 2010). In these fisheries, Dolly Varden is typically targeted with gillnets and beach seines in coastal regions and near river mouths during the spring and fall, and with hook in line through the ice during winters.

Since the development of oil and gas exploration and extraction off the coast of Alaska, as well as inland mining operations, Dolly Varden has been the subject of many studies throughout Arctic Alaska (Yoshihara 1972; Furniss 1975; Craig 1977; McCart 1980; DeCicco 1985, 1989, 1996). However, due to the logistic challenges in capturing fishes in the Arctic Ocean, as well as the lack of commercial fisheries there, most of this research has focused on the freshwater biology and ecology Dolly Varden. These studies have attempted to elucidate its spawning and overwintering sites, timing of freshwater immigration and emigration, geographic distribution, mixing of stocks, and relative abundance. Results of these studies, as well as more recent genetic studies, show that Dolly Varden in Arctic Alaska can be divided into two geographically distinct groups, the northwestern group and the North Slope group (Crane et al. 2004). The northwestern group is classified as those populations natal to rivers north of the

Seward Peninsula to the village of Point Hope, and the North Slope group are those populations natal to rivers east of Barrow. Perhaps the most important and interesting finding about Dolly Varden in Arctic Alaska is that within a group (e.g., northwestern group), individuals may show complex migration patterns, in which they may overwinter in non-natal rivers as mixed aggregates. As a result, there is often significant mixing of populations within groups during both its marine and freshwater phases, and subsistence fishers often target fish in these mixed aggregations. While there has been no evidence of interchange between these two groups (i.e., northwestern vs. North Slope), conventional tagging observations have documented interchange between the northwestern Alaska and Russian Far East groups (DeCicco 1992), and between the North Slope and Canadian groups (Craig 1977). Additionally, more recent genetic analyses have shown that there is significant mixing of Dolly Varden between North Slope and Canadian populations, in the Beaufort Sea during the summer (Krueger et al. 1999).

In contrast to the base of knowledge about the freshwater phase of Dolly Varden, much less is known about its marine spatial and temporal distribution, and ecology. Marine research on coastal fish communities in Arctic Alaska has mostly been conducted on the North Slope with passive gear types (e.g., gillnets and fyke nets) deployed within close proximity of shore (Craig and McCart 1976; Craig and Haldorson 1980; Craig 1984; Brown 2008). The general consensus from these studies was that while at sea, Dolly Varden generally remains in nearshore areas for summer feeding (Armstrong and Morrow 1980). However, given the sampling biases from these studies, they may not reflect the true spatial and temporal distribution of Dolly Varden when in the ocean. While it is unclear if Dolly Varden occupies offshore waters of the Arctic Ocean, there is growing evidence that this species may be widely distributed throughout offshore areas of the Pacific Ocean, including nearshore and offshore waters of the Japan Sea, Bering Sea,

Okhotsk Sea, and the Gulf of Alaska (Volkov et al. 1996; Morita et al. 2009). In addition to occupation of offshore waters, several studies have shown that Dolly Varden are capable of making long distance migrations, up to 1690 km, including transiting through marine offshore waters, such as when traveling from northwestern Alaska to freshwaters of the Russian Far East (DeCicco 1992; DeCicco 1997, Krueger et al. 1999).

Because Dolly Varden is a critical subsistence resource in Arctic Alaska, providing a more complete understanding of its oceanic dispersal and behavior in Arctic Alaska is important for assessing its potential interactions with emerging human activities. Such activities include oil and gas extraction and exploration, which currently take place in nearshore and offshore waters of the Arctic Ocean. Specifically, oil extraction is already taking place in nearshore marine areas adjacent to North Slope rivers with spawning populations of Dolly Varden. In addition to the proven hydrocarbon reserves that are currently being extracted, exploration activities have found an additional 400 potential oil and gas reserves north of the Arctic Circle (USGS 2008). Given this, there is potential for hydrocarbon exploration and extraction activities to increase in the future. One example is the recent U.S. Department of Interior's effort to expand current oil and gas exploration in the U.S. Federal lease area of the Outer Continental Shelf (OCS) waters of the Chukchi Sea portion of the Arctic Ocean adjacent to northwestern Alaska near Cape Lisburne (U.S. Department of the Interior 2010a, 2010b). Located in relative close proximity to this lease area is the Wulik River, which is thought to support the largest overwintering aggregation of Dolly Varden in Arctic Alaska (Scanlon 2011). Therefore, it is possible that anadromous Dolly Varden exit the Wulik River and occupy the federal lease area in the Chukchi Sea. If these Dolly Varden do occupy the lease area, these individuals may be directly exposed to habitat disturbance as a result of hydrocarbon exploration activities. Documenting whether this

important subsistence resource occupies areas that may be impacted by human activities is directly pertinent to several stakeholder groups (Holland-Bartels and Pierce 2011).

Because there are several knowledge gaps in the marine phase of its life history, natural resource managers are unable to assess whether Dolly Varden comes in close proximity to human activities such as oil and gas exploration. Given this, new methods and approaches are warranted for investigating the marine ecology of Dolly Varden. One such promising approach is pop-up satellite archival tags (PSATs), which now provide a fisheries independent opportunity to monitor the movements and habitat occupancy of fish while at sea. Until recently, the successful use of PSATs to study the movements of fishes was confined to large species such as tuna *Thunnus* spp. (Gunn and Block 2001), tiger sharks *Galeocerdo cuvier* (Holland et al. 2001), and Pacific halibut *Hippoglosus stenolepis* (Seitz et al. 2003), because of the large size of the tags. As the size of the tags has become smaller, PSATs have been successfully used to describe movements of smaller fishes such as the striped bass *Morone saxatilis* (Graves et al. 2009), Atlantic salmon *Salmo salar* (Chittenden et al. 2013; LaCroix 2013; Godfrey et al. 2015), and European eel *Anguilla anguilla* (Aarestrup et al. 2009). Because Dolly Varden in Arctic Alaska can attain sizes equivalent to those of striped bass and Atlantic salmon tagged in previous studies, PSATs may be an effective tool for collecting fishery-independent information about the oceanic ecology of this species of char.

The following thesis aims to address the aforementioned knowledge gaps in two standalone chapters. Chapter one describes the feasibility of using PSATs to examine the summer marine distribution and behavior of Dolly Varden in Arctic Ocean. Chapter two describes detailed information provided by the PSATs about the marine habitat occupancy and behaviors of Dolly Varden while in nearshore and offshore waters of the Arctic Ocean. These chapters

provide unprecedented information about the marine ecology of Dolly Varden in the Arctic Ocean. As such, these chapters are directly pertinent to assessing, managing and/or protecting a critical component of the natural resources of value to subsistence lifestyles.

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Chapter 1: Utility of pop-up satellite archival tags to study summer dispersal and habitat occupancy of Dolly Varden in Arctic Alaska¹

Abstract

In Arctic Alaska, Dolly Varden *Salvelinus malma* is highly valued as a subsistence fish; however, little is known about its oceanic ecology. New advances in electronic tagging, such as pop-up satellite archival tags (PSATs) potentially provide project investigators a fishery independent means of studying several aspects of this species movement and ecology. Therefore, we attached 52 PSATs to Dolly Varden in the Wulik River, which flows into the Chukchi Sea of the Arctic Ocean, to evaluate the utility of using this technology to study several aspects of the oceanic habits of this species. Overall, PSATs provided unprecedented information about summer dispersal of Dolly Varden, including the first evidence of offshore dispersal in the Chukchi Sea. In addition, we found no trends in deleterious effects of tags on fish as small as 62 cm. We conclude that PSATs offer an alternative and effective platform with which to study several aspects of Dolly Varden dispersal and ecology in areas where it is not practical or feasible to capture these fish, such as in coastal and offshore regions of Arctic Alaska.

¹Courtney MB, Scanlon BS, Rikardsen AH, Seitz AC (2015) Utility of pop-up satellite archival tags to study the summer dispersal and habitat occupancy of Dolly Varden in Arctic Alaska. Prepared for submission to Arctic.

Introduction

The Dolly Varden *Salvelinus malma* is found throughout a wide range in northern North America and Asia, and is widely distributed in Alaska. While Dolly Varden is not commercially important in Arctic Alaska, it is thought to be the most frequently landed fish in many Arctic Alaska villages (Pedersen and Linn 2005; Magdanz et al. 2010). For example, in the villages of Kivalina and Noatak, located in northwestern Alaska, Dolly Varden landings in 2007 (30,761 fish) exceeded the landings of all species of Pacific salmon *Oncorhynchus* spp. combined (5,241 fish; Magdanz et al. 2010).

In Arctic Alaska, Dolly Varden is classified as an anadromous fish. As such, once individuals reach age 2–5 years, they execute annual migrations to the ocean to feed in the summer, and then return to freshwater to overwinter and sometimes spawn (Armstrong and Morrow 1980). Due to the logistic challenges in capturing fishes in the Arctic Ocean, as well as a lack of commercial fisheries there, most Dolly Varden research has focused on its freshwater biology and ecology. Previous studies in northwestern Arctic Alaska have attempted to locate its spawning and overwintering sites, timing of freshwater immigration and emigration, geographic distribution, mixing of stocks, and relative abundance (DeCicco 1985, 1989, 1996, 1997; Crane et al. 2005; Schwanke 2013). Results from these early studies, as well as more recent genetic studies show that Dolly Varden displays complex migration patterns, in which individuals may overwinter in mixed stocks and exhibit transboundary movements among Alaska and the Russian Far East (DeCicco 1992, 1997; Crane et al. 2005). As a result, there is often significant mixing of stocks during both its marine and overwintering freshwater phase, and subsistence fishers often target fish natal to multiple drainages.

In contrast to the base of knowledge about the freshwater phase of Dolly Varden, little is known about its oceanic ecology. Initial studies suggested that Dolly Varden remain in nearshore habitats while in the ocean (Armstrong and Morrow 1980); however, several lines of evidence suggest that Dolly Varden may occupy offshore habitats (DeCicco 1992; Volkov et al. 1996; Fechhelm et al. 1997; Krueger et al. 1999; Morita et al. 2009). For example, bycatch data from offshore Pacific salmon research fisheries south of the Bering Strait indicate that Dolly Varden is distributed throughout a wide range of the Pacific Ocean, including nearshore and offshore waters of the Japan Sea, Bering Sea, Okhotsk Sea, and the Gulf of Alaska (Morita et. al. 2009). While it is known that Dolly Varden may occupy offshore areas in the Pacific Ocean, it is not known whether it occupies offshore areas of the Arctic Ocean, including the Chukchi and Beaufort seas.

Electronic fish tags provide opportunities to examine several aspects of oceanic ecology of fishes, including marine dispersal, behavior, habitat occupancy, and mortality (Arnold and Dewar 2001; Thorstad et al. 2013). One tag, the pop-up satellite archival tag (PSAT), measures and records depth, temperature and ambient light intensity while attached to a fish. On a preprogrammed date, the tag releases from a fish, floats to the surface of the ocean, and transmits the archived data to satellites, which can be retrieved by project investigators. Therefore, PSATs provide a valuable fisheries-independent method for examining several aspects of fish biology and ecology (Gunn and Block 2001; Seitz et al. 2003; Teo et al. 2007). Initially, PSATs were limited to large-bodied marine species, including Atlantic Bluefin tuna *Thunnus thynnus* (Block et al. 2005), white marlin *Tetrapturus albidus* (Horodysky et al. 2007), tiger sharks *Galeocerdo cuvier* (Holland et al. 2001), and Pacific halibut *Hippoglossus stenolepis* (Seitz et al. 2003), because of the large size and weight of the tags. As the size of the tags has become smaller,

PSATs have been successfully used to describe habitat occupancy and movements of smaller fishes such as the striped bass *Morone saxatilis* (Graves et al. 2009) and Atlantic Salmon *Salmo salar* (Chittenden et al. 2013b; Lacroix 2013; Godfrey et al. 2015).

Because Dolly Varden in Arctic Alaska can attain sizes equivalent to those of striped bass and Atlantic salmon tagged in previous studies, we hypothesized that PSATs may be an effective tool for collecting fishery-independent information about the oceanic ecology of this species of char. Fishery-independent data collection is critically important for understanding the marine distribution, habitat occupancy, and behaviors of Dolly Varden in Arctic Alaska, because there are very limited fisheries in the Chukchi and Beaufort seas in the summer in which to capture Dolly Varden. Therefore, the goal of this study is to evaluate the utility of using PSATs to study the marine spatial distribution, dispersal, and habitat occupancy of Dolly Varden in Arctic Alaska.

Methods

Study Site

Fish for this study were obtained from the Wulik River, located in northwestern Arctic Alaska [\(Fig. 1.1\)](#page-48-0). The Wulik River contains the largest known overwintering aggregation of Dolly Varden in Arctic Alaska, with annual abundance estimates produced by aerial surveys conducted in 1980–2010 ranging from 30,923 to 297,257 fish (Scanlon 2011). The Wulik River drainage is a clearwater system that drains a $3,891 \text{ km}^2$ watershed beginning at the Delong Mountains, after which it flows westward approximately 145 km before entering the Chukchi Sea, near the village of Kivalina, AK.

Fish capture and tag attachment

In early to mid-June of 2012 and 2013, 52 Dolly Varden that overwintered in the Wulik River were captured and tagged with PSATs. In 2012, Dolly Varden $(n = 20)$ were captured during $3-5$ June by beach seine (70 x 2.4 m, with 0.2 m mesh) in the mainstem of the Wulik River (67° 52' 40.91" N, 163° 40' 23.28" W), approximately 45 km upstream from where it enters Kivalina Lagoon [\(Table 1.](#page-45-0)1; [Fig. 1.2\)](#page-49-0). In 2013, to reduce the amount of tagged fish incidentally captured in subsistence and recreational fisheries before leaving the Wulik River, Dolly Varden (n = 32) were captured with gillnets in Kivalina Lagoon (67 \degree 43' 24" N, 164 \degree 31' 24" W; near the confluence of the lagoon and the Chukchi Sea) during 13–14 June [\(Table 1.](#page-45-0)1; [Fig. 1.2\)](#page-49-0). After capturing fish, large Dolly Varden (> 60 cm) that were deemed appropriate for tagging (i.e., no visible bleeding or injuries) were carefully removed from the seine net or gillnet with a knotless-mesh dipnet and placed in a small-mesh holding pen (1.2 x 2.4 m, 70 cm water depth), where their health was monitored for up to four hours before tagging. During this health assessment, each fish was monitored for signs of stress or abnormal behavior including, visual injuries and bleeding, loss of equilibrium, abnormal coloration, frayed fins, and rapid opercular movement. Only fish that were deemed to be healthy by these metrics were held for tagging. After accumulating several large fish in the holding pen, individuals were removed from the holding pen, placed into a custom-fabricated tagging cradle that contained river water, blindfolded, and PSAT-tagged in series.

Tags were attached to Dolly Varden using a "tag backpack" system [\(Fig. 1.3\)](#page-50-0). Backpack systems included two components: the "straps," and the "pack." The "straps" were a harness attachment system which was affixed through the dorsal musculature of the fish, and the "pack" was the transmitter, which was attached to the harness. The "straps" consisted of two custom-

fabricated plastic plates (1.0 cm wide x 5.0 cm long x 0.2 cm thick), each protected on one side by a 0.2-cm thick silicon pad, that were affixed to both ends of a 15 cm length of 80 lb. test Dacron fishing line. The middle of this line was then secured to a corrodible link on the PSAT tag (the "pack") using a cow hitch knot, thus forming the "tag backpack." Each "tag backpack" was affixed to a fish by placing the silicon-padded side of each plastic bar approximately 2 cm below and on opposite sides of the dorsal fin. Once in place, the "tag backpack" was secured by threading a 20-cm long U-shaped piece of stainless steel wire first through two small holes in one of the plastic bars, then through the dorsal musculature of the fish, and finally out two small holes in the second plastic bar on the opposite side of the fish. The ends of the wire were secured to each other using a haywire twist which was pushed to lie flat against the plastic bar to prevent detachment of the "tag backpack." After a PSAT tag was secured, the fish was returned to the mesh holding pen for observation while the remaining fish were tagged. Tagged fish were released simultaneously after it was determined that all fish were swimming satisfactorily. All field work was conducted under University of Alaska Fairbanks, Institution of Animal Care and Use Committee protocol (#308584) and State of Alaska Fisheries Research Permit (SF-ECP-2007-87).

PSAT tag specifications, settings, and data acquisition

Each PSAT tag (X-tag, Microwave Telemetry) weighed 40 g in air, had an overall length of 30.5 cm (maximum diameter 3.2 cm, antenna length 18.5 cm) and was slightly positively buoyant. The tags contained a lithium composite battery, temperature gauge, pressure sensor, light sensor, and a satellite transmitter. While externally attached to an animal, these tags measured and recorded depth (resolution 0.34–5.4 m, range 0–1296 m), temperature (resolution 0.16–0.23°C, range -4–40°C), and ambient light $(4 \times 10^{-5} \text{lux at } 555 \text{ nm})$ readings every two-

minutes. Because the exact timing of return to freshwater was unknown and the PSATs need to be in water that is at least 5 psu salinity for their release mechanism to function (galvanic corrosion), a staggered pop-up schedule was used in which tags were programmed to pop-up in two week intervals: 1 July to 1 September in 2012, and 1 July to 1 October in 2013. This pop-up schedule was developed as a compromise between maximizing the duration of tag data records and tag reporting rate.

On the predetermined dates, the tags released from the fish, floated to the surface of the sea and transmitted, via satellite, archived temperature and depth data, and daily sunrise and sunset times (based on light readings). While transmitting, the location of the tag was determined from the Doppler shift of the transmitted radio frequency in successive uplinks received during one Argos satellite pass (Keating 1995). Due to the large amount of data collected by the tags, limited data reception by Argos satellites, and short tag-battery life, only a subset of temperature and depth data recorded at 15-minute intervals was transmitted by the tags. However, if the tags were recovered while still attached to the fish (e.g., recaptured in subsistence or sport fisheries), the complete data set recorded at two-minute intervals was obtained. Transmitted daily sunrise and sunset times were used to calculate daily geolocation estimates by the tag manufacturer during post-processing of raw transmitted data.

Two types of end locations of tagged Dolly Varden were obtained. First, for tags that popped-up and transmitted to satellites on their scheduled date, end locations were considered as the first transmission with an Argos location class ≥ 1 , which translates into a position error of \lt 1.5 km. Second, in cases where fish were physically recaptured in subsistence and sport fisheries, Global Positioning System coordinates of the recapture site were used, resulting in a position error of < 0.2 km.

In two cases, tags appeared to prematurely release and wash up on shore days to weeks before the scheduled pop-up date. In these cases, depth and temperature records were used to infer that the tag washed up on shore shortly after prematurely releasing from the fish. Because these tags likely did not drift a considerable distance on the surface of the ocean between the dates of premature release and reporting to satellites, the location of the first transmission with an Argos location class ≥ 1 was assumed to be near the location of premature release from the fish and was assigned as the end location. In two other cases of premature tag release, PSATs released before the scheduled pop-up date and drifted on the surface of the ocean for several days (Chittenden et al. 2013a). In these cases, it was assumed that the tags likely drifted a considerable distance on the surface of the ocean between the dates of premature release and reporting to satellites. For these tags, end locations were back-calculated by subtracting the estimated distance traveled by the tag while drifting on the surface of the ocean during the days between premature release and reporting to satellites from the initial reporting position of the tag. In short, the direction and distance of the drifting tags were approximated by multiplying the number of days of tag drift on the surface by an average daily direction and distance of prevailing sea-surface currents (Woodgate et al. 2005) in the vicinity of the reporting position of the tag.

Mortality of fish was determined by tags which depth readings indicted that fish immediately sank to the bottom of the sea floor (15–50 m) and remained at this constant depth for at least 7 days ($n = 6$). In addition, recorded temperature data from several tags ($n = 3$) which transmitted from rivers, indicated that they tags had washed up on shore (LaCroix 2013). In these cases, it was assumed that tagged fish had experienced mortality, and that the tags had washed up on shore before the scheduled pop- up date. Although these results could be interpreted as tag
shedding, based on previous studies on Atlantic salmon using the same attachment system that showed no tag shedding for periods over one year (Rikardsen A.H, unpublished data), tag shedding was assumed to be negligible. End locations of presumed deceased fish whose tags reported from the ocean were assigned as the location of the first tag transmission with an Argos location class ≥ 1 , if the tag remained at a constant depth (15–50 m), after which the tag immediately floated to the surface and reported to satellites on the scheduled pop- up date ($n =$ 3). However, if tag recorded depth suggested that tags released from fish (i.e., tags were freed by fish decomposition), floated to the surface of the ocean, and drifted before reporting to satellites, the end locations and archived data, were excluded from the dispersal analyses $(n = 3)$, because the tags appeared to have drifted on the surface of the ocean for 1–2 months. Therefore, the location of first transmission to Argos satellites was likely considerably far away from the location of mortality and back-calculating an end location would likely be inaccurate. In cases where tags washed up on shore in rivers $(n = 3)$ the first transmission with an Argos location class ≥ 1 was assumed to be near the location of mortality and was assigned as the end location. *Data analyses*

To evaluate the utility of using PSATs to study Dolly Varden, several metrics were examined, including: reporting rates and percentage of retrieved depth and temperature data of tags; and summer distribution and dispersal patterns, and trends in behavior and survivorship of tagged fish. Tag reporting rate was determined by tabulating the percentage of tags for which end locations (recaptured + reported to Argos) could be determined. Percentage of retrieved depth and temperature data were calculated as the total number of individual depth and temperature readings received via Argos, divided by the hypothetical amount of data that should have been transmitted and received by satellites. Additionally, the reporting rate and percent data retrieved

were compared to total time at liberty among individual tagged fish, and end location habitat type (riverine, lagoon, oceanic).

Summer distribution and dispersal patterns of tagged Dolly Varden were described by examining minimum dispersal distance, end locations, and daily geolocation estimates. Minimum dispersal distance travelled 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. Distribution and dispersal patterns were qualitatively described by examining end locations in two week intervals in a GIS framework. In addition to the qualitative end location analysis, the efficacy of light based geolocation was assessed by tabulating the number of tags and the total number days from which sunrise and sunset could be calculated, and subsequently produce "plausible" daily geolocation estimates. Plausible daily geolocations, were defined as locations that were located in a body of water (i.e., not on land), and where daily tag-recorded sea-surface temperatures (SSTs; i.e., tag-recorded temperature < 2 m) was within $\pm 1^{\circ}$ C of satellite-derived SST (NOAA, Geo-Polar Blended SST Analysis 0.05° x 0.05°).

To understand the possible trends of PSAT tagging on Dolly Varden behavior and survivorship, two analyses were conducted. First, differences in mean size (FL) among fish who died while a tag was attached (n = 9), those that were alive on the pop-up date (n = 27), those that failed to provide an end location ($n=10$), and those that were considered missing ($n=6$) were examined through descriptive statistics, including means and bootstrapped (1000 replications) 95% confidence intervals. Second, a linear model (α = 0.05) was used to examine the relationship of fish length (FL) and the square root of minimum dispersal distance (km). All statistical tests were performed with the statistical software R (R Core Team 2014).

Results

Reporting rates

Tagged Dolly Varden ranged from 62.0 to 91.5 cm in length $(76.3 \pm 7.1 \text{ cm}, \text{mean} \pm \text{SD})$ and were at liberty for 2–127 days [\(Table 1.](#page-45-0)1). Of the 52 tags deployed, 33 (63% of the 52 total tags) provided end locations used in the dispersal analyses. Specifically, 24 (46% of the 52 total tags) provided end locations calculated by Argos satellites, and nine (17% of the 52 total tags) tags were recovered while still attached to fish in subsistence and recreational fisheries, and provided GPS end locations [\(Table 1.2\)](#page-47-0). The fates of the remaining 19 (37% of the 52 total tags) tags were as follows: ten tags transmitted, but failed to provide any end locations (19% of the 52 total tags), three prematurely released after death and drifted for 1–2 months, thus subsequent end locations were not used (6% of the 52 total tags), and six (12% of the 52 total tags) tags never reported and were considered missing [\(Table 1.2\)](#page-47-0).

Percentage of retrieved data

The percentage of archived temperature and depth data received from tags that transmitted to satellites varied from 0 to 100% [\(Table 1.](#page-45-0)1; [Fig. 1.4\)](#page-51-0). Most fish that reported from freshwater provided end locations, but failed to provide any substantial archived temperature and depth data (0–1%), except for three fish who presumably died, washed up, reported from freshwater rivers, and provided 17–54% of their archived data [\(Table 1.](#page-45-0)1; [Fig. 1.4\)](#page-51-0). In contrast, fish that reported from ocean provided 84–100% of the subset of archived data recorded at 15 minute intervals, and tags that were recaptured provided 100% of archived data recorded at 2 minute intervals [\(Table 1.](#page-45-0)1; [Fig. 1.4\)](#page-51-0). While there were large differences in the percentage of data retrieved between tags which reported from freshwater and saltwater, there was little observed correlation between time at liberty and the percentage of data retrieved [\(Fig. 1.4\)](#page-51-0).

Summer distribution and dispersal patterns

The tagged Dolly Varden had end locations in both marine and freshwater habitats, and dispersed a mean minimum distance $(\pm SD)$ of 206 ± 162 km (range 0–470 km; [Table 1.](#page-45-0)1). For tags with end locations in marine habitats, seven reported from the Russian Chukchi Sea approximately 100–200 km north of the Chukotka Peninsula, exhibiting minimum travel distances of 319–470 km from the tagging locations [\(Table 1.](#page-45-0)1; [Fig. 1.5\)](#page-52-0). Eight other tags had end locations in nearshore marine waters adjacent to Kotzebue Sound 40–135 km southwest of the tagging locations [\(Table 1.](#page-45-0)1; [Fig. 1.5\)](#page-52-0). For tags with end locations in freshwater areas, nine reported 40–362 km from the tagging sites in other river drainages including the Omikviorok, Rabbit, Buckland and Noatak drainages in northwestern Alaska [\(Table 1.](#page-45-0)1; [Fig. 1.5\)](#page-52-0). The other tagged fish with freshwater end locations showed less extensive dispersal and their tags had end locations in Kivalina Lagoon $(n = 3)$, and in lower and upper reaches of the Wulik River, near known overwintering and spawning areas ($n = 6$) [\(Table 1.](#page-45-0)1; [Fig. 1.5\)](#page-52-0). When examined in two week intervals, in early to late June, fish were located near the tagging sites (mouth and lower reaches of the Wulik River) and in nearshore areas within or adjacent to Kotzebue Sound [\(Fig.](#page-53-0) [1.6\)](#page-53-0). From early July to September some fish still occupied the Wulik River; however, tagged fish were more widely distributed and were located in the Chukchi Sea north of Russia, near Kotzebue Sound, and in other rivers [\(Fig. 1.6\)](#page-53-0).

In addition to end locations, ten (19% of the total 52 tags) PSATs provided limited daily light-based geolocation estimates. Daily geolocation estimates were calculated for a total of 30 days: 14 days in June, one day in July, and 15 days in August. Of the geolocation estimates provided in June and July (15 days from 10 PSATs), location estimates varied widely across the northern and southern hemisphere with none being validated as plausible, as 14 were on land and one location had a daily corresponding sea surface temperature that was $> 1^{\circ}C$ than the satellitederived SST in the same location. In August, two tags provided daily geolocation estimates (n=15 d, 6–14 August 2012). These tags reported just days later (15 August 2012) in the Russian Chukchi Sea. Of these daily estimates, 2 were on land, and the rest $(n = 13)$ had daily corresponding SSTs that were within $\pm 1^{\circ}$ C of satellite-derived SST, and thus were considered plausible. Of these plausible daily geolocations, all were broadly distributed in the Chukchi Sea in the vicinity (106 \pm 55km, mean \pm SD) of their respective end locations. For the remaining tags $(n = 42)$, light sensor saturation (i.e., light sensor was unable to distinguish any diel differences in light intensity) preventing the calculation of sunrise and sunset events, and subsequent calculation of daily geolocation estimates.

Trends in behavior and survivorship

Mortality was observed in fish ranging from 62–86 cm, which nearly spanned the entire range of fish tagged in this study [\(Table 1.](#page-45-0)1). Fish size did not appear to relate to whether a fish was alive or dead on its pop-up date, as mean sized differed only slightly between live and deceased fish [\(Fig. 1.7\)](#page-54-0). Similar to the lack of relationship between mortality and size, no relationship in mean length and dispersal patterns was observed. Specifically, while dispersal distance (0–470 km) varied among tagged Dolly Varden, a linear model showed no significant correlation between mean fish size and minimum distance travelled ($P = 0.57$; [Fig. 1.8\)](#page-55-0).

Discussion

PSATs offer an alternative and effective platform in which to study several aspects of large adult Dolly Varden behaviors and habitat occupancy in locations where it is not economically or logistically practical or even feasible to recapture fish, such as coastal and offshore regions of the Arctic. While attached to Dolly Varden, PSATs provided unprecedented

information about their dispersal patterns in Arctic Alaska, including the first evidence of offshore habitat occupation in the Arctic Ocean. Additionally, while undertaking these different dispersal types, PSATs collected depth and temperature, which may be used to be used to make inferences about the oceanic behaviors, habitat occupancy, and ecology of this species, fulfilling many knowledge gaps.

The overall reporting rate (recaptured $+$ Argos; 63%) from this study was lower than reporting rates (grand mean 79%; 95% CI = 76 to 82%) analyzed in a review of other PSAT tagging studies, in which 731 tags were deployed on 19 species of marine animals (Musyl et al. 2011). The relatively low reporting rate in this study is most likely attributable to the occupation of freshwater by tagged Dolly Varden on their pop-up dates. Given that the PSATs used in this study need 5 psu of salinity for the release mechanism to function properly, occupation of freshwater likely led to some failure of the release mechanism. However, some tags did report from freshwater, but instead of releasing from the fish, it is likely that the tags were still attached to the fish. While attached to the fish, the antennae periodically protruded above the surface of the water and were able to weakly transmit to satellites, thus providing sporadic transmissions that resulted in relatively few end locations and low data recovery rates. Additionally, occupation of freshwater on the scheduled pop-up date (i.e., the PSAT tag did not properly release or transmit), likely explains the tags that were either missing or failed to transmit an end location.

While occupation of freshwater lowered the tag reporting and data recovery rates, PSATs that reported from marine waters had relatively high data returns, and provided end locations where fisheries are not currently prosecuted, filling in knowledge gaps about the spatial and temporal summer ranges of Dolly Varden during its summer feeding season. When compared to the previously described dispersal of Dolly Varden in northwestern Alaska (reviewed in DeCicco

1997), our results demonstrate some similar movement patterns, including to other rivers and southerly marine nearshore movements. However, in contrast to these studies, several PSATs in this study provided the first documentation of a northwesterly offshore dispersal in the Russian Chukchi Sea. The lack of documentation of offshore dispersal in the Arctic Ocean in previous studies is likely because fisheries were not prosecuted in this region, thus there was no feasible method for physically recovering tagged fish. The occupation of offshore waters in the Arctic Ocean where no fisheries are conducted emphasizes the importance of using technology that does not rely on the physical recapture of tagged fish.

The lack of geolocation estimates in this study is likely due to the inability of the X-tag to detect changes in ambient irradiance during the Arctic summer when the sun does not set (June– mid-July), thus preventing the calculation of light-based geolocation estimates on most days. Even when tags provided limited daily geolocation estimates, most derived location estimates were not plausible until the middle of August. Given that Dolly Varden only spend a short time, up to three months, in the ocean each summer before returning to freshwater, the method of light-based geolocation used in this study does not appear to be an effective method for understanding the daily movements of fish occupying the Arctic Ocean during the summer. However, alternative location estimation models based on tag-recorded depth and temperatures may have the potential to provide valuable insights in the spatial and temporal distribution of Dolly Varden during the summer (Hayes et al. 2011; Chittenden et al. 2013a, 2013b).

Because there were no observed relationships among fish size, mortality, and dispersal patterns, PSATs appeared to have relatively little effect on the health and swimming ability of tagged Dolly Varden ≥ 62 cm. Specifically, while at liberty for up to 126 days, tagged Dolly Varden travelled up to 470 km, transited with speeds up to 60 km \cdot day \cdot ¹ (Chapter 2), suggesting

that the tag did not adversely impact the swimming ability of tagged fish. Given these results, 60 cm is likely an appropriate guideline for minimum PSAT tagging size of Dolly Varden, which is similar to that of another salmonid species, the Atlantic salmon (Lacroix 2013), in which individuals as small as 52 cm have been tagged and tracked with the same PSAT. However, a precise minimum size guideline is not known, and future laboratory studies studying the physiological effects of PSAT tagging salmonids, would be instrumental and provide a much better understanding.

Interpreting mortality events in this study is difficult, because it is impossible to discern natural from tag-induced mortality. Nevertheless, the low observed mortality, in conjunction with assumed negligible tag-induced mortality in similar studies on Atlantic salmon (Lacroix 2013, 2014), suggests that mortality of fish in this study may be at least partly assigned to natural mortality. While little is known about the causes and rates of natural mortality of Dolly Varden from Arctic Alaska, it is thought to be highly variable and dependent on environmental conditions (Arvey 1991). Past research has suggested that birds, and marine mammals, particularly spotted seals *Phoca largha*, may cause significant mortality of Dolly Varden in northwestern Alaska in some years (DeCicco 1985, 1996). Although the specific cause of mortality of fish in this study is unknown, most of the mortality events occurred in nearshore areas where marine mammals are common, possibly suggesting predation as the cause, which has been documented for Atlantic salmon (Lacroix 2014).

The pop-up schedule used in this study, while successful for ensuring that some fish would be in marine waters on the pop-up date and thus properly release and transmit data, could be refined in future studies. Based on the results from this study, pop-up dates scheduled between 15 July and 15 August will likely maximize the probability of retrieving data in future

experiments on Dolly Varden in northwestern Alaska. Therefore, future PSAT tagging studies on Dolly Varden and anadromous species should take into account the population-specific individual knowledge about the biology, ecology, and life history of the study species, to maximize data retrieved. Additionally, in the future, new alternative technology that does not rely on a galvanic corrosion release mechanism (e.g., allow for freshwater release) would be invaluable for studying anadromous fishes at high latitudes and allow researchers to obtain more data during the entire ice-free season.

In addition to Dolly Varden, PSATs may be valuable for studying other large-bodied fish in the Arctic Ocean, a place where few fisheries exist. The information gained from PSATs may provide valuable observations against which future studies may be compared. This is especially important in the Arctic where climate change and human development are predicted to have rapid and acute effects on the environment. For example, climate change may present significant challenges for fishes in the Arctic (Reist et al. 2006a), specifically, facultative anadromous species like chars (Reist et al. 2006b), likely changing their distribution, forage base, and habitat occupancy. In addition, natural resource development, such as oil and gas exploration, which is currently occurring in both offshore and nearshore areas of the Arctic Ocean, may also present challenges for fish communities. Based on these concerns, environmental observations such as those collected in this study will be directly pertinent for several stakeholders in assessing the vulnerability of a species to natural and anthropogenic environmental changes.

Table 1.1. Deployment and end location information for pop-up satellite archival tags attached to 52 Dolly Varden in the Wulik River, Alaska in June 2012 and 2013. End dates and locations represent when and where a fish reported to satellites or was physically recaptured.* represents fish that died prior to the pop-up date. Tags denoted as "Missing" never transmitted to satellites. "Failed" tags transmitted, but did not provide any end location estimates. "% data obtained" denotes total number of individual depth and temperature readings received via Argos, divided by the hypothetical amount of data that should have been transmitted and received by satellites.

Fish ID	Length (cm)	Tagging year	End date	Time at liberty (days)	Minimum dispersal (km)	% data obtained	End location
107988	78.0	2012	7/1/12	26	45	84	Kivalina Lagoon
107989	75.5	2012	7/7/12	32	13	100	Wulik River
107990	81.5	2012	7/1/12	26	319	100	Russian Chukchi
107991	78.0	2012	Failed	÷.	$\overline{}$	÷,	
107992	81.2	2012	7/15/12	40	383	100	Russian Chukchi
107993*	86.0	2012	7/4/12	29	138	99	Cape Espenberg
107994	81.5	2012	Failed	$\overline{}$	$-$	$\overline{}$	
107995	89.0	2012	7/4/12	29	135	100	Kotzebue Sound
107996	82.0	2012	7/12/12	37	306	100	Buckland River
107997	86.5	2012	Failed	$\overline{}$	$\overline{}$	÷,	
107998	85.5	2012	6/24/12	19	$\boldsymbol{0}$	100	Wulik River
107999	91.5	2012	6/7/12	$\overline{2}$	$\boldsymbol{0}$	100	Wulik River
108000	81.6	2012	8/15/12	71	381	98	Russian Chukchi
108001	78.5	2012	Missing	\blacksquare	$\overline{}$	÷,	
108002	75.5	2012	9/1/12	88	38	$\mathbf{1}$	Wulik River
108003	85.0	2012	8/15/12	71	359	97	Russian Chukchi
108004*	86.0	2012		$\overline{}$		96	
108005	79.0	2012	6/18/12	13	45	100	Kivalina Lagoon
108006	82.5	2012	Missing	$\overline{}$	$\overline{}$	$\overline{}$	\blacksquare
108007*	81.5	2012				54	
108030	69.0	2013	Missing	$\overline{}$			
108031	65.0	2013	Failed	$\frac{1}{2}$			
108032*	63.5	2013	6/26/13	14	102	96	Cape Espenberg
108033	65.5	2013	6/22/13	9	120	100	Sheshalik Spit
108034*	62.0	2013	6/25/13	13	38	84	Coast

-continued-

Fish ID	Length (cm)	Tagging year	End date	Time at liberty (days)	Minimum dispersal (km)	% data obtained	End location
108035	70.5	2013	7/25/13	42	308	$\mathbf{1}$	Noatak River
108036	67.0	2013	7/6/13	24	390	100	Russian Chukchi
108037	69.0	2013	6/27/13	14	140	99	Noatak Delta
108038	72.0	2013	7/15/13	33	40	τ	Rabbit Creek
108039	65.0	2013	7/15/13	32	470	97	Russian Chukchi
108040	67.5	2013	7/10/13	27	365	100	Russian Chukchi
108041	82.5	2013	Failed	$\overline{}$			
108042	79.0	2013	Failed				
108043	79.0	2013	6/16/13	3	6	29	Wulik River
108044	67.0	2013	Missing	-			
108045	70.0	2013	Missing	$\overline{}$			
108046	78.5	2013	Failed	$\overline{}$			
108047	76.0	2013	8/21/13	70	371	$\mathbf{1}$	Noatak River
108048	72.5	2013	8/22/13	70	70	9	Omikviorok River
108223	72.0	2013	9/3/13	83	362	$\overline{2}$	Noatak River
108224	71.0	2013	Failed	$\overline{}$			
108225	78.0	2013	Failed				
108226	80.0	2013	6/21/13	8	120	100	Sheshalik Spit
108227	71.5	2013	6/21/14	373	120	100	Sheshalik Spit
108228	73.5	2013	Failed	$\overline{}$			
108229	79.0	2013	Missing				
108230*	83.0	2013	9/3/13	83	362	54	Noatak River
108231*	68.0	2013	6/16/13	3	$\overline{\mathcal{L}}$	58	Kivalina Lagoon
108232	75.5	2013	9/15/13	94	228	3	Noatak River
108233*	81.0	2013		$\overline{}$	$\overline{}$	82	
108234	72.0	2013	10/17/13	127	45	$\overline{4}$	Wulik River
129838*	78.0	2013	7/27/13	44	191	17	Noatak River

Table 1.1. Continued

Table 1.2. Annual deployment summary of pop-up satellite archival tags attached to Dolly Varden in the Wulik River drainage. "Tagged" describes the number of tags deployed. "Recaptured" describes number of tags physically recaptured in sport and subsistence fisheries. "Argos end locations" describes the number of tags which provided end locations determined by Argos satellites. "Failed end locations" refers to number of tags which reported to satellites, but failed to provide end locations, likely because of weak transmission strength. "Missing" refers to the number of tags which never reported to satellites nor were recaptured in fisheries. "Mortality" refers to the number of fish whose archived data suggested that they died before the pre-programmed pop-up date of the tag.

Fig. 1.1. Prominent watersheds and landmarks in northwestern Alaska. The Wulik River, highlighted in blue, denotes the study site.

Fig. 1.2. Sampling locations (circles) where Dolly Varden were tagged in the Wulik River.

Fig. 1.3. X-tag attached to a Dolly Varden with a wire harness "tag backpack" attachment system.

Fig. 1.4. Percentage of retrieved data (total number of individual depth and temperature readings received via Argos divided by the hypothetical amount of data that should have been transmitted and received) compared to time at liberty (days) for fish whose tags reported to Argos satellites from three habitat types.

Fig. 1.5. End locations of pop-up satellite archival tagged Dolly Varden in the Wulik River in summers of 2012 (black dots) and 2013 (white dots). End locations were where a fish was physically recaptured or transmitted to satellites.

Fig. 1.6. Temporal distribution of pop-up satellite archival tagged Dolly Varden in the summers of 2012 and 2013. End locations were where a fish was physically recaptured while the tag was still attached or where a tag popped-up from a live fish and reported to satellites.

Fig. 1.7. Comparison of mean fork lengths and bootstrapped 95% confidence intervals of tagged Dolly Varden that were alive, dead, whose tags failed to transmit an end location to satellites, or were considered missing on their scheduled pop-up dates.

Fig. 1.8. Relationship between fork length of tagged Dolly Varden and square root of minimum dispersal distance (km).

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Chapter 2: Oceanic behavior and dispersal of an important subsistence fish in Arctic Alaska, the Dolly Varden¹

Abstract

In northwest Alaska near the Chukchi Sea region of the Arctic Ocean, Dolly Varden *Salvelinus malma* is highly valued as a subsistence fish and local residents harvest thousands of these fish each year. While in the ocean, very little is known about the dispersal, behavior, and habitat occupancy of Dolly Varden. Of particular interest, it is not known whether Dolly Varden occupy offshore areas of the Chukchi Sea, including several U.S. Outer Continental Shelf (OCS) Federal oil and gas lease areas. Therefore, we attached 52 pop-up satellite archival tags (PSATs) to Dolly Varden in the Wulik River, which flows into the Chukchi Sea, to examine the marine habitat occupancy and behavior of this species. Seven tagged fish demonstrated the first documented northwesterly dispersal to offshore areas of the Russian Chukchi Sea. While at sea, these fish dispersed up to 30–60 km·day⁻¹ and generally occupied relatively shallow water $\left($ < 15 m). Eight other fish likely occupied nearshore waters of northwestern Alaska. These nearshore dispersers all experienced highly fluctuating daily temperatures $(0-15^{\circ}C)$, shallow depths (< 6 m), and appeared to quickly transit in a southerly direction. Although there was no evidence of Dolly Varden occupying the U.S. OCS Federal oil and gas lease areas, Dolly Varden may be exposed to emerging human activities, such as hydrocarbon development and shipping because of its ability to rapidly transit broad areas of the Chukchi Sea, in addition to its frequent occupation of shallow water.

¹Courtney MB, Scanlon BS, Rikardsen AH, Seitz AC (2015) Oceanic behavior and dispersal of an important subsistence fish in Arctic Alaska, the Dolly Varden. Prepared for submission to Environmental Biology of Fishes.

Introduction

The Dolly Varden *Salvelinus malma* is found throughout a wide range in northern North America and Asia, and is widely distributed in Alaska. In some Arctic Alaska villages, which are mainly inhabited by Alaska Natives practicing subsistence-based lifestyles, Dolly Varden is the most frequently landed fish species and thousands are harvested annually (Pedersen and Linn 2005; Magdanz et al. 2010). For example, in the villages of Kivalina and Noatak, Dolly Varden landings in 2007 (30,761 fish) exceeded the landings of all species of Pacific salmon *Oncorhynchus* spp. combined (5,241 fish; Magdanz et al. 2010).

Dolly Varden in northwestern Alaska is classified as an anadromous fish. As such, once Dolly Varden reaches age 2–5 years, individuals execute annual migrations to the ocean to feed in the summer, and then return to freshwater to overwinter and sometimes spawn (Armstrong and Morrow 1980). While Dolly Varden is iteroparous and can theoretically spawn every year after maturation, adults normally spawn biennially because they rarely acquire sufficient energy reserves to spawn in consecutive years (DeCicco 1989). During spawning years, adults return to their natal stream to spawn and overwinter, while during non-spawning years, they typically overwinter in large mixed-stock aggregations in non-natal streams (DeCicco 1997). The largest known, and possibly the most important, overwintering site for adult Dolly Varden in northwestern Alaska is the Wulik River. Dolly Varden populations natal to many other drainages throughout northwestern Alaska, including the Noatak and Kobuk rivers [\(Fig. 2.1\)](#page-83-0), have all been shown to use the Wulik River as an overwintering site, and in some years over 100,000 overwintering fish have been counted via aerial surveys (Scanlon 2011).

While in the ocean, very little is known about the dispersal and behavior of Dolly Varden. Initial research suggested that Dolly Varden concentrates in nearshore habitats

(Armstrong and Morrow 1980). However, several lines of evidence suggest that Dolly Varden occupies or at least transits through offshore habitats (DeCicco 1992; Volkov et al. 1996; Fechhelm et al. 1997; Morita et al. 2009). First, in the late 1980s, two tagged Dolly Varden released in the Wulik River were recaptured 1560 and 1690 km away in the Anadyr River, Russia, up to 14 months after being released, implying that these fish had to transit through offshore areas (DeCicco 1992). Second, bycatch data from offshore Pacific salmon research fisheries south of the Bering Strait indicate that Dolly Varden is distributed throughout a wide range of the Pacific Ocean, including nearshore and offshore waters of the Japan Sea, Bering Sea, Okhotsk Sea, and the Gulf of Alaska (Morita et al. 2009). While it is known that Dolly Varden may occupy offshore areas in the Pacific Ocean (Morita et. al 2009), it is not known whether this species occupies offshore areas of the Chukchi Sea region of the Arctic Ocean, which is an important feeding area during the summer for many marine mammals, fishes, and seabirds (Smith 2010).

Understanding the oceanic distribution of Dolly Varden in northern Alaska is important for understanding the potential interactions between human activities and this fish species. Oil and gas exploration and development may be conducted in offshore areas of the Chukchi Sea, specifically in several U.S. Outer Continental Shelf (OCS) Federal lease areas. If anadromous Dolly Varden occupies these areas, these individuals may be directly exposed to habitat disturbance as a result of these human activities. Given this, understanding the oceanic dispersal and behavior of Dolly Varden is important for several stakeholder groups to assess its potential interactions with emerging human activities in the Chukchi Sea.

Because many rivers in northern Alaska that flow directly into the Chukchi Sea are home to large populations of Dolly Varden, we hypothesized that this species of char inhabits the

Chukchi Sea, including offshore areas, during the summer. To examine this hypothesis, we used pop-up archival satellite tags (PSATs) tags to describe the marine habitat occupancy and behaviors of adult Dolly Varden that overwinter in the Wulik River. Fishery-independent data collection is critically important for documenting the marine habitat occupancy, and behaviors of Dolly Varden in Arctic Alaska, because there are only very small fisheries conducted in relatively few nearshore areas of the Arctic Ocean in the summer, and virtually none conducted in offshore areas in which to capture Dolly Varden. Because of these very limited fisheries, traditional fishery dependent methods are insufficient for examining the marine habitat occupancy and behaviors of Dolly Varden in the Arctic Ocean.

Methods

Study site, fish capture and PSAT tagging

Fish for this study were obtained from the Wulik River, located in northwestern Alaska [\(Fig. 2.1\)](#page-83-0). The Wulik River drainage is a clearwater system that drains a 3,891 km^2 watershed beginning at the Delong Mountains, after which it flows westward approximately 145 km before entering the Chukchi Sea, near the village of Kivalina, AK. The mean annual discharge (1985– 2010) ranges from 13 to 50 $m^3 \cdot s^{-1}$ with average peak flows ranging from 179 to 960 $m^3 \cdot s^{-1}$.

In early to mid-June of 2012 and 2013, 52 Dolly Varden that overwintered in the Wulik River were captured and tagged with PSATs (X-tag, Microwave Telemetry; Chapter 1). While externally attached to a Dolly Varden, these tags measured and recorded depth, temperature, and ambient light intensity readings every two minutes. A staggered pop-up schedule was used in which tags were programmed to pop-up in two week intervals: 1 July to 1 September in 2012, and 1 July to 1 October in 2013. All field work was conducted under University of Alaska

Fairbanks Institutional Animal Care and Use Committee protocol (#308584) and State of Alaska Fisheries Research Permit (SF-ECP-2007-87).

Data acquisition

On the predetermined dates, the tags released from the fish, floated to the surface of the sea and transmitted, via satellite, archived temperature and depth data, as well as daily sunrise and sunset times (calculated from light readings). While transmitting, the location of the tag was determined from the Doppler shift of the transmitted radio frequency in successive uplinks received during one Argos satellite pass (Keating 1995). For this study, the end locations of tagged Dolly Varden were considered as the first transmission with an Argos location class \geq 1 (position error of < 1.5 km), unless it was determined that there was mortality or premature tag release before the pop-up date. In these cases, when possible, end locations were back calculated to obtain approximate end locations (Chapter 1). Because the behavior of fish which experienced mortality events did not appear to be qualitatively different from the behavior of the fish which were alive on the pop-up date, their depth and temperature records while alive were used in data analyses. In cases in which fish were physically recaptured in subsistence and sport fisheries, Global Positioning System coordinates of the recapture site were used, resulting in a positional error of < 0.2 km. Due to the large amount of data collected by the tags, limited data reception by Argos satellites, and short tag-battery life, only a subset of temperature and depth data recorded at 15 minute intervals was transmitted by the tags. However, if the tags were recovered while still attached to the fish (e.g., recaptured in subsistence or sport fisheries), the complete data set recorded at two minute intervals was obtained. Transmitted daily sunrise and sunset times were used to calculate daily geolocation estimates by the tag manufacturer during post-processing of raw transmitted data.

Data analyses

To qualitatively describe the marine habitat occupancy and behaviors of Dolly Varden in the summer, only fish whose tags had end locations in marine waters were analyzed. This filtering technique ensured that analyses were conducted on tags which provided near complete datasets (> 84% of archived temperature and depth), and provided oceanic depth and temperature occupancy of tagged fish (Chapter 1).

After a cursory examination of the tag data, patterns of occupied temperature and depth emerged, which were used to infer types of habitat occupation and behavior (e.g., Teo et al. 2011; Lacroix 2013) of Dolly Varden. These inferred habitat occupation and behavior types included river residency, ocean entry, marine residency, marine transit, and marine feeding. This inference was based on comparison of the depths and temperatures occupied by the tagged fish to possible depths and temperatures in riverine and oceanic habitats. Specifically, the habitat conditions in the Wulik River are relatively shallow and warm, and display relatively high variability in water temperatures on a diel basis. In contrast, the habitat conditions in the Chukchi Sea are relatively deep and cold, and display less variability in water temperature on a diel basis. Of particular note in the Chukchi Sea, is the zone of nearshore landfast ice where water temperature is $< 0^{\circ}$ C under the ice.

Following the rationale that riverine and oceanic habitats have different water depths and temperatures, periods when fish occupied relatively shallow and warm water were classified as inferred river residency. After this period of inferred river residency, some fish experienced brief periods of very cold water which was likely when tagged fish exited the mouth of the Wulik River and entered the ocean by swimming under the landfast ice in the coastal zone of the Chukchi Sea. Therefore, this transition from relatively warm freshwater to cool marine waters

was classified as inferred ocean entry. After inferred ocean entry, fish occupied water with slightly warmer temperatures than those experienced during ocean entry, but cooler than inferred river residency, and they occupied relatively shallow depths with little variability. Because it is thought that rapidly traveling salmonids typically do not undertake frequent diving behavior (e.g., Lacroix 2013), the period of occupation of relatively cool water and shallow depths was classified as inferred marine transit. After inferred marine transit, some tagged fish remained in relatively cool water, but occupied greater and more variable depths, and displayed oscillatory diving behavior. Under the assumption that feeding fish frequently demonstrate oscillatory diving behavior (Teo et al. 2007; Spares et al. 2012), this period of occupation of relatively cool water and deeper and more variable depths was defined as inferred marine feeding. Marine residency was defined as the combination of marine transit and marine feeding behaviors (i.e., all oceanic occupancy). Data 12 hours before and after a switch in habitat occupancy and/or behavior type were excluded from data analyses. Finally, dispersal types were assigned to fish based on end locations. Nearshore and offshore dispersers were defined as tagged fish with end locations less and more than 12 nautical miles from shore, respectively.

To describe depth and temperature occupancy of tagged fish, several metrics were calculated. First, for each behavior phase (e.g., marine residency, marine transit, and marine feeding) of each dispersal type (offshore and nearshore), individual minimum, maximum, and mean depth and temperatures, as well as grand mean (time-weighted) and standard deviation (time-weighted) were calculated. Second, grand mean (time-weighted) proportion of time spent at discrete depth (nearshore 1 m and offshore 5 m) and temperature intervals (1° C) were calculated in histograms for each behavior phase of each dispersal type. Time-weighted means and variance were used in the aforementioned analyses, because the number of days at liberty

and amount of data retrieved from tags differed between individual fish. Minimum transit times and speeds were estimated for both nearshore and offshore dispersers, by examining ocean entry and end location dates in relation to the minimum distance travelled.

To examine potential diel differences in habitat occupancy in both nearshore and offshore dispersers, occupied depth was categorized into periods of night and day. In northern Alaska, during late-May through approximately mid-July, the sun is continuously over the horizon and there is 24 hours of daylight. However, during this time there are daily differences in lightintensity throughout the 24 hour day, and many marine invertebrates demonstrate diel behaviors (Falkenhaug et al. 1997; Fortier et al. 2001). Given this, to understand daily differences in depth, in relation to light intensity, tag-recorded depth data were separated and classified as "night" and "day." Because light intensity should be at its lowest at local solar midnight, 00:00 hrs (UTC- $11:00$ hrs) \pm 2 hours was arbitrarily used to designate "night" and the remainder of time was "day," based on a cursory analysis of depth time series provided by tags attached to fish. Post hoc pairwise comparisons of the proportion of grand mean time spent by offshore dispersers at discrete depth intervals (i.e., $0-5$, $5-10$, $10-15$, $15-20$, $20-25$ m) between night and day periods was conducted using a χ^2 test of independence (Bonferroni adjusted $\alpha = 0.01$; McDonald 2014). Because of the shallow depth occupancy (-0) –6 m, described in results) and the depth resolution of the PSATs (0.34–5.4 m), an alternative statistical analysis was used to assess diel behaviors in nearshore dispersers (Godfrey et al. 2015). In these analyses, individual mean recorded depth from both night and day periods were calculated. These estimates were then compared with a Wilcoxon signed-ranked test to detect median differences in mean depth between periods of night and day (α = 0.05).

Summer distribution patterns of offshore and nearshore dispersers were described by calculating minimum dispersal distance, examining light-based geolocation estimates, and comparing tag-recorded water temperatures to satellite-derived water temperatures. Minimum dispersal distance travelled was calculated by measuring the great arc circle distance of a nonmeandering route that did not pass over land between tagging and end locations. Light-based daily geolocation estimates were explored using Microwave Telemetry's proprietary software that uses transmitted daily sunrise and sunset events to produce daily geolocation estimates. However, most tags failed to provide any daily geolocation estimates (Chapter 1), and thus, did not provide any appreciable insight into the movements of tagged fish.

As an alternative to light-based geolocation, a method similar to Chittenden et al. (2013) was developed to understand the weekly and monthly spatial distribution of tagged fish whose end locations were in offshore waters. Generally, to approximate possible distribution, the tagrecorded sea-surface temperature (SST; i.e., temperature experienced while the fish was in water depths < 2 m) was compared to satellite-derived SST (NOAA, Geo-Polar Blended SST Analysis 0.05° x 0.05°). Specifically, for individual fish, mean weekly tag-recorded SST was calculated and compared to mean weekly satellite-derived SST of the Chukchi and northern Bering seas. Polygons of possible weekly distribution for each individual fish were designated as areas where tag and satellite recorded SST overlapped $(\pm 0.5^{\circ}C)$. To provide a broader and more inclusive perspective on the spatial distribution of all tagged fish, grand mean monthly tag-recorded SST from all fish combined were compared to mean monthly satellite SST in the Chukchi and northern Bering seas. Polygons of possible monthly distribution of all combined fish were designated as areas where mean monthly tag and satellite SST temperatures overlapped $(±$ 1.0°C). While these analyses lacked the resolution to produce daily or fine-scale geolocation

estimates, they did provide weekly and monthly polygons of possible distribution of tagged fish, and perhaps more importantly in the context of this study, excluded areas that fish could not have inhabited.

Results

Tagged Dolly Varden ranged from 62.0 to 91.5 cm in length (76.3 \pm 7.1 cm, mean \pm SD) and were at liberty for 2–127 days. These fish exhibited many different summer dispersal patterns, including remaining in the Wulik River, movement to other rivers, movement to offshore waters of the Chukchi Sea, and southerly alongshore movements (Chapter 1). Of the 52 tags deployed, 15 had end locations in marine waters, and subsequently were used in the analyses in this study [\(Table 2.1\)](#page-82-0). Of these 15 tags, seven reported from the Russian Chukchi Sea and were termed offshore dispersers, while eight had end locations in nearshore areas in northwestern Alaska and were termed nearshore dispersers [\(Table 2.1\)](#page-82-0).

Offshore dispersers

Seven tagged Dolly Varden demonstrated offshore dispersal to the Russian Chukchi Sea, north of the Chukotka Peninsula, exhibiting minimum dispersal distances of 319–435 km (376 \pm 35 km; [Table 2.1;](#page-82-0) [Fig. 2.2\)](#page-84-0). These fish likely entered the ocean between 25 June and 2 July, during which they experienced cold water temperatures ranging from -1.3–2.5°C for periods of 0.25–13 hrs, after which they occupied deeper and warmer water [\(Fig. 2.3\)](#page-85-0). During marine residency, they were surface oriented, occupying mean depths ranging from 0.2–6.2 m (weighted grand mean 3.9 ± 6.9 m). This tendency of relatively shallow water occupancy led these tagged fish to spend 70.1% and 93.4% of the time in the top 5 and 15 m of the water column respectively [\(Fig. 2.4\)](#page-86-0). Also during marine residency, these fish experienced water temperatures ranging from -0.9–8.5°C (weighted-grand mean 5.4 ± 1.2 °C), and spent the majority of the time
in temperatures of 3–7°C [\(Fig. 2.5\)](#page-87-0). While occupying the ocean, the ambient temperature experienced by tagged fish increased throughout the summer. Specifically, tagged fish spent over 90% of their time in water temperatures of 3–7°C in July and 5–7°C in August [\(Fig. 2.6\)](#page-88-0).

During marine residency, inferred marine transit behavior lasted between 5 and 10 days and varied on an individual basis. Throughout inferred marine transit [\(Fig. 2.7\)](#page-89-0), tagged Dolly Varden experienced water temperatures of -0.9–8.5°C (weighted grand mean 4.6 ± 2.6 °C) while occupying relatively shallow depths with very little variability (weighted grand mean 2.2 ± 1.9) m, range 0–24 m). During transit, individual fish spent 78.8–99.6% (weighted grand mean 90.0 \pm 8.1%) and 99.1–100% (weighted grand mean 99.5 \pm 2.5%) of their time within the first 5 and 15 m of the water column respectively [\(Fig. 2.4\)](#page-86-0). One fish (#107990) likely entered the ocean on 25 June 2012 and its tag reported from the Russian Chukchi Sea 319 km away on 1 July 2012 [\(Table 2.1;](#page-82-0) [Fig. 2.2\)](#page-84-0), transiting an average of $\sim 60 \text{ km} \cdot \text{day}^{-1}$. Based on duration of inferred transiting behavior and minimum dispersal distance, six of the seven offshore dispersers immediately transited 30–60 km day⁻¹ after entering the ocean. In contrast to these six fish, one offshore disperser occupied greater and more variable depths for approximately 13 days between ocean entry and inferred marine transit behavior, suggesting a delay between ocean entry and transit to the offshore area of the Russian Chukchi Sea.

After inferred marine transit behavior, these fish began inferred marine feeding [\(Fig. 2.7\)](#page-89-0). During this time, oscillatory dives generally occurred between 0 and 15 m with maximum dive depths ranging between 13–51 m for individual fish [\(Fig. 2.8\)](#page-90-0). Although the variability in depth increased during inferred feeding, individual tagged Dolly Varden still spent 48.8–72.7% (weighted grand mean $58.6 \pm 6.9\%$) and $84.0 \text{--} 100\%$ (weighted grand mean $89.6 \pm 2.1\%$) of the time in the first 5 and 15 m of the water column, respectively [\(Fig. 2.4\)](#page-86-0).

Even though there was continuous daylight during the majority of their time at liberty, all offshore dispersers demonstrated a diel pattern in depth, in which they occupied shallow depths and remained near the surface between 2200–0200 on most days, with oscillatory diving occurring during the remainder of the day [\(Fig. 2.8\)](#page-90-0). Specifically, tagged Dolly Varden spent significantly more time in the first five m of the water at night than day, and conversely spent significantly more time at depths 5–25 m during the day than night $(\chi^2$ test of independence, *P* < 0.01; [Fig. 2.9\)](#page-91-0). This behavior was evident in all offshore dispersers and remained consistent throughout the inferred marine feeding phase.

During marine residency, mean monthly SSTs recorded by tags attached to offshore dispersers were 4.9–5.6°C (grand mean 5.4 ± 0.4 °C) in July 2012 and 6.7–6.8°C (grand mean 6.7 \pm 0.1 \degree C) in August 2012. When the mean weekly SSTs experienced by individual fish were compared to satellite-derived SSTs (\pm 0.5 \degree C) from the Chukchi and northern Bering seas, the possible distribution of tagged fish in July 2012 was confined to a relatively small band of water in the Chukchi Sea, mostly north of the Chukotka Peninsula of Russia, that generally progressed in a northwesterly direction throughout the summer [\(Fig. 2.10\)](#page-92-0). When the grand monthly mean SSTs for all offshore dispersers was compared to mean-monthly satellite-derived SSTs $(\pm 1.0^{\circ}C)$ for July 2012, possible fish distribution was confined to a band of water that stretched from Franklin Point, Alaska to the Chukotka Peninsula [\(Fig. 2.11\)](#page-93-0). For August 2012, the extent of possible distribution of fish increased and included the northwestern Chukchi Sea and northern Bering Sea [\(Fig. 2.11\)](#page-93-0). In 2013, the tags attached to offshore dispersers (n=3) all reported between 6 and 15 July. The mean monthly sea surface temperatures recorded by these tags was 6.3–7.7°C (grand mean 6.6 ± 0.3 °C), but no geolocation estimates were able to be approximated for these fish due to poor quality satellite-derived SST estimates for this time.

Nearshore dispersers

Eight tagged Dolly Varden had end locations in nearshore waters along the coast of the Chukchi Sea adjacent to northwestern Alaska, exhibiting minimum dispersal distances of 38–140 km (114 ± 33 km; [Table 2.1;](#page-82-0) [Fig. 2.2\)](#page-84-0) While exact outmigration dates to the ocean were generally indiscernible, these fish all appeared to leave the Wulik River and enter the Chukchi Sea approximately 18–24 June. During marine residency, all experienced highly fluctuating daily water temperatures (range $0.5-15.5^{\circ}\text{C}$; grand mean $7.4 \pm 1.8^{\circ}\text{C}$) and shallow depths (grand mean 2.0 ± 0.9 m) [\(Fig. 2.12\)](#page-94-0). This shallow water occupancy led nearshore dispersers to spend the majority ($> 90\%$) of their time within the first 4 m of the water column, and roughly, 45% of the time in a relatively discrete, 2–3 m deep, band of water [\(Fig. 2.13\)](#page-95-0). In contrast to offshore dispersers, diel patterns in diving or depth occupancy were less discernable [\(Fig. 2.14\)](#page-96-0). Specifically, there were no significant differences in mean recorded depths between periods of night and day (Wilcoxon signed-rank test, $P > 0.05$). Therefore, no foraging behavior was inferred by qualitative analyses of depth. Additionally, while there was large daily variation $(\pm$ 15°C) in temperatures experienced by fish as they occupied nearshore areas in northwestern Alaska, fish spent the majority of their time (59%) in water temperatures between 6–10°C [\(Fig.](#page-97-0) [2.15\)](#page-97-0). Based on time at liberty and minimum distance travelled, individual fish demonstrated transit speeds of 5–60 km·day⁻¹. Because of the high day to day variability in occupied water temperatures of nearshore dispersers, and highly course and interpolated satellite imagery, geolocation by comparing tag-recorded SSTs to satellite derived SSTs was not feasible.

Discussion

PSATs provided the first evidence of a northwesterly offshore dispersal of Dolly Varden to the Russian Chukchi Sea north of the Chukotka Peninsula, demonstrating that some Dolly

Varden from northwest Alaska occupy offshore areas of the Chukchi Sea during the summer feeding season. In addition, nearshore dispersal along northwestern Alaska, similar to that inferred in previous conventional tag studies, was documented (DeCicco 1985; DeCicco 1997). However, in contrast to previous research on Dolly Varden, tag-recorded occupied depth and temperature data provided information about the timing of outmigration into the ocean, spatial distribution and diving behaviors, all of which can be used to make inference about the summer habits of Dolly Varden in the Chukchi Sea.

Offshore dispersers

Distinct ocean entry events, as indicated by drastic declines in water temperature, were most apparent for the offshore dispersers. The timing of ocean entry by offshore dispersers was similar to the timing inferred for Dolly Varden previous conventional tagging studies in northwest Alaska (DeCicco 1985; DeCicco 1997). The water temperature experienced several tagged fish $(<$ -1 \degree C; for up to 12 hrs) is some of the coldest documented temperatures experienced by Dolly Varden. These results are similar to other recent electronic tagging studies which have documented Atlantic salmon *Salmo salar* (Reddin et al. 2011) experiencing temperatures as low as -1 °C, and 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 \sim -0.7°C (Pennell and Barton 1996). Previous research in a laboratory has shown that a closely related congener, Arctic char *Salvelinus alpinus,* is resistant to freezing and can survive temperatures of -0.99°C for up two hours in the presence of ice, and \geq 5 days at -1.2°C in the absence of ice (Fletcher et al. 1988). While there have been no reports of antifreeze compounds found in salmonids, changes in blood electrolyte balance, and the epidermis of Arctic char, have been hypothesized as serving as a barrier to ice nuclei formation in their flesh (Fletcher et al.

1988). These processes in Dolly Varden likely 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.

After ocean entry, the majority of offshore dispersers appeared to have rapidly transited to the area north of the Chukotka Peninsula of Russia. One fish that was 81.5 cm fork length had an end location in the Russian Chukchi sea approximately 300 km from its tagging location five days after leaving the Wulik River, indicating that it traveled approximately 60 km \cdot day⁻¹ for five days. Including mean northward prevailing ocean currents of $5-8$ cm \cdot sec⁻¹ (Woodgate et al. 2005), this rate of travel by this fish translates into a swimming speed that closely corresponds to the most energetically efficient swimming speed of other salmonids $(1.0$ body length \cdot sec⁻¹; Brett 1995). Considering the low variability in depth during this inferred marine transit period and the close similarity of the mean swimming speed of tagged Dolly Varden and the most energetically efficient cruising speed in other salmonids, it is likely that Dolly Varden are swimming in a relatively straight line between overwintering and offshore feeding areas. During this transit, it is likely that they forego other activities such as oscillatory diving and feeding, to minimize energy expenditure. Although most of the tagged Dolly Varden appeared to rapidly transit to offshore feeding areas immediately after ocean entry, one fish displayed oscillatory diving for approximately two weeks before its likely transit to the offshore feeding area in the Chukchi Sea. This suggests that some Dolly Varden may feed in nearshore waters of the Chukchi Sea adjacent to Alaska before moving to the offshore area in the Russian Chukchi Sea.

It is likely that the tagged Dolly Varden occupied this offshore area of the Russian Chukchi Sea throughout the summer. The end locations and the geolocation approximation based on SSTs support the idea that offshore dispersers tagged in 2012 quickly dispersed to and

remained in a relatively small area throughout the summer. Although the distribution of tagged fish could not be approximated in 2013, due to poor quality satellite-derived SST estimates, given that these fish were only in the ocean for approximately a few weeks before reporting to satellites approximately 365–435 km away from Kivalina Lagoon, it is likely that they swam directly to these areas, similar to fish in 2012. The most parsimonious explanation is that these tagged fish exited the Wulik River and swam immediately to the area north of Russia, and did not transit through or occupy the U.S. OCS Federal lease areas.

The diel depth occupancy and diving behavior displayed by the tagged Dolly Varden while in the Chukchi Sea north of Russia is similar to diving behavior of most other salmonids documented by archival tags, including Arctic char (Rikardsen et al. 2007), chum salmon *Oncorhynchus keta* (Yukimasa et al. 2001; Walker et al. 2005), steelhead *Oncorhynchus mykiss* (Nielsen et al. 2011), sockeye salmon *Oncorhynchus nerka* (Walker et al. 2007), and Atlantic salmon (Lacroix 2013). While literature on the oceanic feeding behavior of Dolly Varden is scarce, the diet of Dolly Varden occupying the Bering Sea is thought to be comprised mainly of invertebrates including euphausiids, copepods and hyperiids (Volkov et al. 1996). These invertebrates demonstrate diel vertical migrations in which they occupy deeper water during the day and shallow water at night, offering a likely explanation for the diel depth patterns observed in this studies tagged fish.

Because the tagged Dolly Varden remained in this region of the Russian Chukchi Sea during their summer feeding season and displayed oscillatory diving behaviors typically associated with feeding, it is highly likely that this location is an important feeding area for Dolly Varden in the Chukchi Sea for most of the summer. The possible importance of this area for feeding is corroborated by studies on another upper-trophic level planktivore, the bowhead whale

Balaena mysticetus, which occupies this same area off the northern coast of the Chukotka Peninsula in the fall (Moore et al. 1995; Citta et al. 2014). Feeding in this area by bowhead whales was first documented in the early 1990s, on what appeared to be large aggregations of euphausiids (Moore et al. 1995). More recently, this area has been designated to be a core use area of the bowhead whale during its fall feeding season (Citta et al. 2014). The importance of this feeding area is thought to be a result of high densities of zooplankton (primarily copepods and euphausiids) being aggregated at a pronounced salinity gradient off the coast of the Chukotka Peninsula, which occurs between the cold, fresh southeastward flowing Siberian coastal current and the warmer, saltier, nutrient rich water from the Bering Sea (Weingartner et al. 1999; Weingartner et al. 2005; Berline et al. 2008; Citta et al. 2014).

Nearshore dispersers

The nearshore dispersers documented in this study likely were non-natal fish that used the Wulik River as an overwintering site. Previous studies indicate that fish from several rivers in northwest Alaska (e.g., Noatak, Kobuk, Kivalina, and northern Norton Sound rivers) and Russia form mixed-stock overwintering aggregations in the Wulik River (DeCicco 1997). This affinity for Dolly Varden to overwinter in the Wulik River is likely because of its relatively high habitat availability, which in northern Alaska during the winter is scarce because of severe freezing conditions and low runoff (Craig 1989). In the spring, it is thought that these non-natal fish leave the Wulik River, forego summer feeding and swim directly to their natal rivers to spawn (DeCicco 1989; DeCicco 1997). Considering these previous studies, as well as the lack of evidence of feeding, relatively quick transits, and end locations only occurring in nearshore areas early in the summer in this study, the nearshore dispersers were likely all non-natal to the Wulik River. Instead of conducting offshore feeding migrations, these fish were likely transiting in

nearshore waters, while foregoing feeding, to their natal rivers to spawn in the upcoming fall (DeCicco 1997). Interestingly, these fish all appeared to leave Kivalina Lagoon during 18–24 of June, possibly indicating that nearshore dispersers may exit the Wulik River earlier than offshore dispersers.

While at liberty, the fish that transited through nearshore areas experienced large daily fluctuations in temperature, including relatively warm temperatures not observed in the ocean. These rapid changes in water temperatures suggest that while transiting in nearshore habitats, they may occasionally swim into the lower reaches of several freshwater drainages. Similar behavior has been found in a closely related congener, the White Spotted Char *Salvelinus leucomaenis* in Japan (Morita et al. 2013), and is thought to be an "exploring" or "probing" behavior (Burger et al. 1995) to locate natal spawning rivers or to assess the suitability of overwintering habitat.

Summary and Conclusion

This study has produced new qualitative insights into the marine habitat occupancy and behaviors of Dolly Varden in the Arctic Ocean. Specifically, it provides the first evidence that Dolly Varden undertake relatively long offshore movements in the Chukchi Sea and feed on the OCS north of the Chukotka Peninsula of Russia. These fish are likely drawn to this area because of its relatively high biological productivity and is therefore likely an important summer feeding location for Dolly Varden. In addition, Dolly Varden disperse in nearshore areas of the Chukchi Sea, most likely while returning to natal streams to spawn (DeCicco 1997). However, while tagged fish occupied both offshore and nearshore habitats, this study did not provide any evidence of a northeasterly dispersal or occupation through or near active U.S. OCS Federal lease areas in the Chukchi Sea.

Because the tagged Dolly Varden spent the majority of their time near the surface of the Chukchi Sea, and most human activities such as oil and gas exploration and development, and marine shipping are surface-based, this increases the likelihood of interactions among Dolly Varden and human activities. For example, in the case of an oil spill, crude oil typically floats and prevailing wind and currents may widely disperse the oil across surface waters of the ocean. Depending on the direction of the prevailing winds and currents, Dolly Varden may be exposed to floating pollutants, even if individual fish do not occupy U.S. OCS Federal lease areas. Recently, exposure to pollutants has been shown to affect cardiac function of fishes (Brette et al. 2014), leading to population declines in fish species in which a large proportion of individuals undertake relatively arduous migrations, such as Dolly Varden.

In addition to anthropogenic interactions, climate change may present significant challenges for chars, and other species in the Arctic (Reist 2006a; Reist 2006b). While the implications of climate change are not clear, predictions include warming of the ocean, increased precipitation, permafrost degradation, and contracted winter seasons (Prowse et al. 2006; Martin et al. 2009). These climate changes are likely to cause changes in distribution and habitat occupancy of fishes (Reist et al. 2006b). Based on these concerns, biological datasets, such as those collected this study, will be directly pertinent for several stakeholders in assessing the vulnerability of this species and ecological implications to these future environmental changes (Drenner et al. 2012).

This study was conducted on only a small subset of large adult Dolly Varden overwintering in one river drainage of northwestern Alaska. There is likely more behavioral variability among and within populations of Dolly Varden throughout northern Alaska than was captured in this study. Given this variability, it is likely that the summer spatial distribution of

Dolly Varden is much larger than reported in this study, and may extend into areas, including U.S OCS Federal lease areas. Future studies on Dolly Varden which have much larger sample sizes, and include other drainages throughout northwestern and northern Alaska, have the potential to collect more information about Dolly Varden and subsequently improve our understanding of its marine habitat occupancy and behaviors. This improved understanding of the oceanic ecology of Dolly Varden should inform future management considerations by subsistence users, biological resource managers, and mineral and energy developers and regulators.

Fish ID	Length	Year	Dispersal	End location	Minimum
	(cm)		type		dispersal (km)
107990	81.5	2012	Offshore	Russian Chukchi	319
107992	81.2	2012	Offshore	Russian Chukchi	383
107993*	86.0	2012	Nearshore	Cape Espenberg	138
107995	89.0	2012	Nearshore	Kotzebue Sound	135
108000	81.6	2012	Offshore	Russian Chukchi	381
108003	85.0	2012	Offshore	Russian Chukchi	359
108032*	63.5	2013	Nearshore	Cape Espenberg	102
108033	65.5	2013	Nearshore	Sheshalik Spit	120
108034*	62.0	2013	Nearshore	Coast	38
108036	67.0	2013	Offshore	Russian Chukchi	435
108037	69.0	2013	Nearshore	Noatak Delta	140
108039	65.0	2013	Offshore	Russian Chukchi	390
108040	67.5	2013	Offshore	Russian Chukchi	365
108226	80.0	2013	Nearshore	Sheshalik Spit	120
108227	71.5	2013	Nearshore	Sheshalik Spit	120

Table 2.1. Fork length, year tagged, dispersal type, end location, and minimum distance travelled while at liberty of the 15 pop-up satellite archival tagged Dolly Varden used for data analyses in this Chapter. * represents fish that died prior to the pop-up date.

Fig. 2.1. Prominent watersheds and landmarks in northwestern Alaska. The Wulik River, highlighted in blue, denotes the study site.

Fig. 2.2. End locations of pop-up satellite archival tagged Dolly Varden tagged in the Wulik River in summers of 2012 and 2013. End locations may be where a fish was physically recaptured while the tag was still attached to a fish, or where a tag popped-off a live fish and reported to satellites. Black and white dots indicate offshore and nearshore dispersers, respectively.

Fig. 2.3. Example of temperature occupied by a tagged Dolly Varden (#108000), recorded every 15 minutes, which experienced sustained (> 12 hours) cold temperatures < -1.0°C on 25 June 2012. Inferred ocean entry is noted.

Fig. 2.4. Proportion (time-weighted mean \pm SD) of time spent in 5 m depth-bins by tagged Dolly Varden $(n = 7)$ that demonstrated offshore dispersal. Depth occupation is for overall marine residency (transit + feeding), in addition to two inferred behaviors while in the ocean, marine transit and marine feeding.

Fig. 2.5. Proportion of time (time-weighted mean \pm SD) spent in 1°C temperature-bins while in the ocean (transit + feeding) by Dolly Varden ($n = 7$) that demonstrated offshore dispersal.

Fig. 2.6. Proportion of time (time-weighted mean \pm SD) by month spent in 1^oC temperature-bins while in the ocean (transit + feeding) by Dolly Varden ($n = 7$) that demonstrated offshore dispersal.

Fig. 2.7. An example of depths and temperatures occupied by a tagged Dolly Varden (#108000) that exhibited typical inferred marine transit and feeding behaviors in July 2012. Depth (black line) and temperature (grey line) values were recorded every 15 minutes.

Fig. 2.8. Example of diel diving behaviors over a seven-day period in July (top panel) and August (bottom panel) 2012 by two Dolly Varden whose tags reported from the Russian Chukchi Sea. Depth (black line) and temperature (grey line) values were recorded every 15 minutes. Grey bars denote the hours of 2200–0200 (UTC -11:00 hrs).

Fig. 2.9. Diel patterns in the proportion (time-weighted mean \pm SD) of time spent in 5 m depthbins by tagged Dolly Varden ($n = 7$) that reported from offshore areas of the Chukchi Sea in 2012 and 2013. Shaded and hollow bars reflect night (2200–0159 hrs) and day time (0200–2159 hrs) depth occupancy, respectively (UTC- 11:00 hrs).

Fig. 2.10. Example of geolocation approximation of one tagged Dolly Varden (#108000) which reported to satellites on 15 August 2012. Shaded polygons are proposed to represent the possible weekly distribution of the tagged fish by depicting the region of the Chukchi Sea where mean weekly sea surface temperatures (SSTs) measured by the tag attached to the fish were similar $(±$ 0.5°C) to satellite-derived SSTs. Because we inferred that this fish spent the majority of its time at-liberty near the end location (black dot), it is included in each two-week panel for reference purposes. The U.S. OCS Federal Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

Fig. 2.11. Shaded polygons are proposed to indicate the extent of possible offshore distribution of tagged Dolly Varden during the summer of 2012 by depicting the region of the Chukchi Sea where mean monthly sea surface temperatures measured by all tags attached to Dolly Varden and by satellites were similar $(\pm 1.0^{\circ}C)$ in July (top panel) and August (bottom panel). Because we inferred that all fish spent the majority of their time at-liberty near their end locations (black dots), they are included in both panels for reference purposes. The U.S. OCS Federal Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

Fig. 2.12. Example of occupied depth and temperatures of one tagged Dolly Varden (#107995) released in the Wulik River (45 km upstream from the mouth) and recaptured near Kotzebue, AK on 4 July 2012, which exhibited southerly nearshore dispersal. Depth (black line) and temperature (grey line) values were recorded every 2 minutes. Inferred river residency and marine residency are noted.

Fig. 2.13. Proportion (time-weighted mean \pm SD) of time spent in 1 m depth-bins by tagged Dolly Varden $(n = 8)$ that reported from nearshore areas of northwestern Alaska in 2012 and 2013.

Fig. 2.14. Diel patterns in the proportion (time-weighted mean ± SD) of time spent in 1 m depthbins by tagged Dolly Varden $(n = 8)$ that reported from nearshore areas of northwestern Alaska in 2012 and 2013. Shaded and hollow bars reflect night (2200–0159 hrs) and day time (0200– 2159 hrs) depth occupancy, respectively (UTC- 11:00 hrs).

Fig. 2.15. Proportion of time (time-weighted mean \pm SD) spent in 1°C temperature-bins after entering the ocean by Dolly Varden $(n = 8)$ that reported from nearshore areas of the Chukchi Sea in 2012 and 2013.

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Conclusion

This study increased our knowledge about the summer marine distribution of Dolly Varden in Arctic regions of Alaska. In chapter one, we tested the feasibility of using a fisheries independent method of studying fishes in the ocean, pop-up satellite archival tags (PSATs), to examine the summer marine ecology of Dolly Varden in Arctic Alaska. Provided that PSATs were in saltwater during the schedule pop-up date, the tags provided nearly all of their archived depth and temperature data, as well as a relatively accurate $(\pm 1.5 \text{ km})$ end locations. In addition, we found no trends in deleterious effects of tagged Dolly Varden as small as 62 cm. Overall, PSATs provided unprecedented information about summer dispersal of Dolly Varden, including the first evidence of offshore dispersal in the Chukchi Sea. In summary, we conclude that PSATs offer an alternative and effective platform with which to study several aspects of Dolly Varden behaviors and ecology, in addition to other large anadromous fish species in coastal and offshore regions of Arctic Alaska.

In chapter two, we investigated the marine habitat occupancy and behaviors of Dolly Varden which reported from marine waters of the Arctic Ocean, and provided the majority of their archived data. This chapter produced new qualitative insights into Dolly Varden ecology, specifically that Dolly Varden quickly disperse to and occupy the Outer Continental Shelf (OCS) of Chukchi Sea, north of the Chukotka Peninsula of Russia for up to 45 days. While occupying these offshore waters, tagged Dolly Varden demonstrated diel patterns in depth occupancy, dive depths to 50 m, and affinity for the first 5 m of surface waters, while generally occupying water temperatures of 3–7 °C. In addition to offshore dispersal, this study validated that some Dolly Varden quickly migrate in nearshore waters of the Chukchi Sea during the summer, most likely returning to their natal river to spawn in the upcoming fall. While occupying these nearshore

waters, tagged Dolly Varden experienced a rapidly changing thermal environment, including waters temperatures down to -1°C.

Some tagged Dolly Varden in this study occupied a relatively small offshore area of Russian Chukchi Sea, thus highlighting its possible importance. While occupying this area, tagged Dolly Varden spent most of their time in a thermal environment cooler than that reported for optimal growth (Larsson and Berglund 2005). This suggests that prey availability and abundance may influence this dispersal behavior, although several other mechanisms (e.g., interspecific competition and predator avoidance) may also be influential. Regardless, for the ultimate or proximate reasons of occupation of this area, this study emphasizes that this area may be an important foraging location to Dolly Varden in Arctic regions of Alaska, which, to date, has never been proposed. Future research describing the physical characteristics and species composition of this area may provide valuable information on the importance and reasons for occupation of this area north of the Chukotka Peninsula.

One important limitation of this study is that it was only conducted a small subset of Dolly Varden that overwintered in one river drainage of northwestern Alaska. Because other populations of Dolly Varden in Arctic Alaska are genetically and geographically distinct from those tagged in this study (i.e., northwestern vs. North Slope), Dolly Varden natal to other drainages in northwestern Alaska and North Slope may demonstrate different dispersal and behaviors. Another limitation was that due to tag-size constraints, this study only sampled the oldest cohorts of Dolly Varden in the Wulik River, and therefore the inferred information on movements and occupied habitat may not be representative of the entire population. Given this, it is likely that the summer spatial distribution of Dolly Varden is much larger than reported in this study, and perhaps may extend into U.S. OCS Federal lease areas. Because of the possible

variability not documented in this study, future research similar to this study should be conducted in other drainages in Arctic Alaska, which may provide a more holistic understanding of Dolly Varden ecology in Arctic Alaska.

Regardless of whether Dolly Varden directly transits through or occupies the U.S OCS Federal lease area, this study demonstrates that Dolly Varden is highly surface oriented spending most of its time in the surface waters, increasing the likelihood of interactions between future, emerging, and ongoing human activities in the Arctic. For example, in the case of a catastrophic oil spill, floating crude oil may disperse widely across the Chukchi Sea, depending on prevailing winds and currents, directly exposing Dolly Varden to this pollutant. Exposure to this pollutant has recently been shown to affect the cardiac function of fishes (Brette et al. 2014), which may lead to population declines in fish species. Given this, the results from this study describing the marine depth distribution of Dolly Varden is directly pertinent to several stake holder groups, including biological resource managers, and mineral and gas developers and regulators in assessing its vulnerability and interactions with anthropogenic activities.

In addition to horizontal and vertical distribution information, this study provided valuable information on the marine thermal environment occupied by Dolly Varden, including some of the coldest occupied temperatures ever documented ($\langle O^{\circ}C \rangle$ for this species. In addition to these cold water temperatures, some tagged fish experienced drastic fluctuations in water temperatures $(\pm 15^{\circ}C)$, sometimes on less than an hourly basis, while occupying inferred nearshore waters. These results are similar other recent archival studies of other closely related species (Jensen and Rikardsen 2012; Morita et al. 2013) and suggest that Dolly Varden may be more tolerant to cold saline waters and rapid changes in temperature and salinities than previously conveyed (Fletcher et al. 1988; Dempson 1993), and may be an important mechanism

for its resiliency to climate change. While the magnitude of climate change is largely unknown, the Arctic has reached its warmest temperatures in over 400 years (Overpeck et al. 1997), and is one of the fastest warming regions on the planet (Martin et al. 2009). While results from this study did suggest that Dolly Varden may be tolerant of a wide range of temperatures and likely salinities, climate change is also likely to cause changes distribution of prey fields, predators, and competitors (Reist et al. 2006a; Reist 2006b). Given this, it is difficult to assess how climate change may affect populations of Dolly Varden in the future. However, collecting baseline observations, as in this study, which can be compared to future observations, may be useful to understanding these changes.

Although this study provided a much better understanding of Dolly Varden ecology, many research priorities remain. These priorities include examining the marine dispersal and habitat occupancy of younger cohorts, including immature postsmolts. Using acoustic telemetry and small archival tags may provide some insights on these research questions (e.g., Hayes et al. 2011; Spares et al. 2012). While these options will be financially and logistically costly, they are necessary, given the current lack of information about this life history stage and its potential vulnerability to anthropogenic changes in the marine environment. Another research priority that is more financial and logistical friendly, and of equal-importance, is the accurate assessment of overwintering Dolly Varden population abundances. One method that has the potential to address this question is the use of Dual Frequency Identification Sonar (DIDSON). While this method has recently been used to characterize immigration timing and estimate population abundances in Arctic Alaska, it is still in its trial phase, and it is currently unclear if this is a feasible endeavor (Osborne and Melegari 2008; Schwanke 2013). If DIDSON technology is a feasible method to accurately identify and enumerate immigrating/emigrating Dolly Varden, it
will be extremely valuable to fisheries managers, who have traditionally relied on coarse-scale abundance estimates from aerial and mark and recapture surveys (DeCicco 1996; Viavant 2005; Scanlon 2011). The aforementioned research will be invaluable to the conservation of this important subsistence species, upon which residents of Alaska have relied for millennia.

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Appendix A

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April 11, 2012

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

This action is included on the April 24, 2012 IACUC Agenda.

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

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

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