



Dispersal Patterns and Summer Ocean Distribution of Adult Dolly Varden From the Wulik River, Alaska, Evaluated Using Satellite Telemetry

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Abstract

In northwest Alaska, Dolly Varden charr *Salvelinus malma* is highly valued as a subsistence fish and local residents harvest thousands of these fish each year. Because the Chukchi Sea is biologically productive in the summer, we hypothesized that Dolly Varden inhabit this sea, including offshore areas, during the summer. Therefore, we attached 52 Pop-up Satellite Archival Transmitting (PSAT) tags to Dolly Varden in the Wulik River, which flows into the Chukchi Sea, to examine their oceanic dispersal and behavior. PSAT tags provided the first evidence of a northwesterly offshore dispersal of Dolly Varden (n=8) 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. While at sea, they dispersed up to $60 \text{ km} \cdot \text{day}^{-1}$ and frequently occupied relatively shallow water (<15 m). Two of the fish likely occupied this area of the Chukchi Sea for at least 45 days; therefore, we infer that offshore areas of the continental shelf of the Chukchi Sea may be an important feeding area for Dolly Varden. Although there was no evidence of Dolly Varden occupying the U.S. Federal Outer Continental Shelf lease areas, because of its frequent occupation of shallow water in the Chukchi Sea, Dolly Varden may be exposed to emerging human activities there, such as potential offshore oil and gas exploration and development and shipping.

Introduction

Background

The Dolly Varden charr *Salvelinus malma* is found throughout a wide range in northern North America and Asia, and is widely distributed in Alaska (Fig. 1; Fig. 2). Total subsistence harvest of Dolly Varden in northern regions of Alaska is largely unknown (Scanlon 2011), though it is thought to be the most frequently landed fish (Magdanz et al. 2010) in some northwestern Alaska villages (Magdanz et al. 2010). For example, in the villages of Kivalina and Noatak, Dolly Varden landings in 2007 (30,761 fish; Magdanz et al. 2010) exceeded the landings of all species of Pacific salmon *Oncorhynchus* spp. combined (5,241; Magdanz et al. 2010).

Dolly Varden in northwestern Alaska are classified as anadromous fishes. As such, once individuals reach age 2–5, they execute annual migrations to the ocean to feed in the summer, and then return to freshwater to overwinter and sometimes spawn (Johnson 1980). While Dolly Varden are iteroparous and can theoretically spawn every year after maturation, they normally spawn biennially because they rarely acquire sufficient energy reserves to spawn in consecutive years (DeCicco 1997). During spawning years, adult Dolly Varden return to their natal stream to spawn and overwinter, while during non-spawning years, Dolly Varden typically overwinter in large mixed-stock aggregations in non-natal streams (DeCicco 1997). An important, and possibly the largest, overwintering site for Dolly Varden in northwestern Alaska is the Wulik River. Fish natal to the Noatak, Kivalina, Wulik, Kobuk, and Pilgrim rivers have all been shown to use the Wulik River as an overwintering site, and in some years >100,000 overwintering fish have been counted via aerial surveys (Scanlon 2011).

The Dolly Varden that overwinter in the Wulik River demonstrate complex and highly variable summer dispersal. Previous research suggests that the summer dispersal of Dolly Varden that overwinter in the Wulik River can be categorized into four main groups (DeCicco 1996). The fish in the first group, which comprises the vast majority of the Dolly Varden in the Wulik River, are immature, non-spawning fish natal to a variety of rivers in Alaska, and perhaps Russia, that will migrate to the ocean in the spring to feed. The second group contains pre-spawning fish natal to the Wulik River that will forego migration to sea prior to spawning in this river in August. The third group is pre-spawning fish natal to other rivers in Alaska, and perhaps Russia, that will move to sea in the spring. However, they will not likely occupy the ocean for an extended period of time, but rather will swim directly to their natal spawning grounds. The fourth group is post-spawned fish natal to the Wulik River that spawned the previous fall and will out-migrate to the ocean where they will feed during the summer to rebuild energy reserves.

Very little is known about the dispersal and behavior of Dolly Varden while they are in the ocean. Initial studies suggested that Dolly Varden concentrate in nearshore habitats, defined in this study as the United Nations Convention on the Law of the Sea territorial seas (<12 nm from shore). However, two lines of evidence suggest that Dolly Varden occupy or at least transit through offshore habitats (>12 nautical miles from shore). First, in the late 1980s, two conventionally-tagged Dolly Varden released in the Wulik River transited through offshore areas and were recaptured 1,560 and 1,690 km away in the Anadyr River, Russia, up to 14 months after being released (DeCicco 1992). Second, bycatch data from offshore Pacific salmon research fisheries south of the Bering Strait indicate that Dolly Varden are 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).

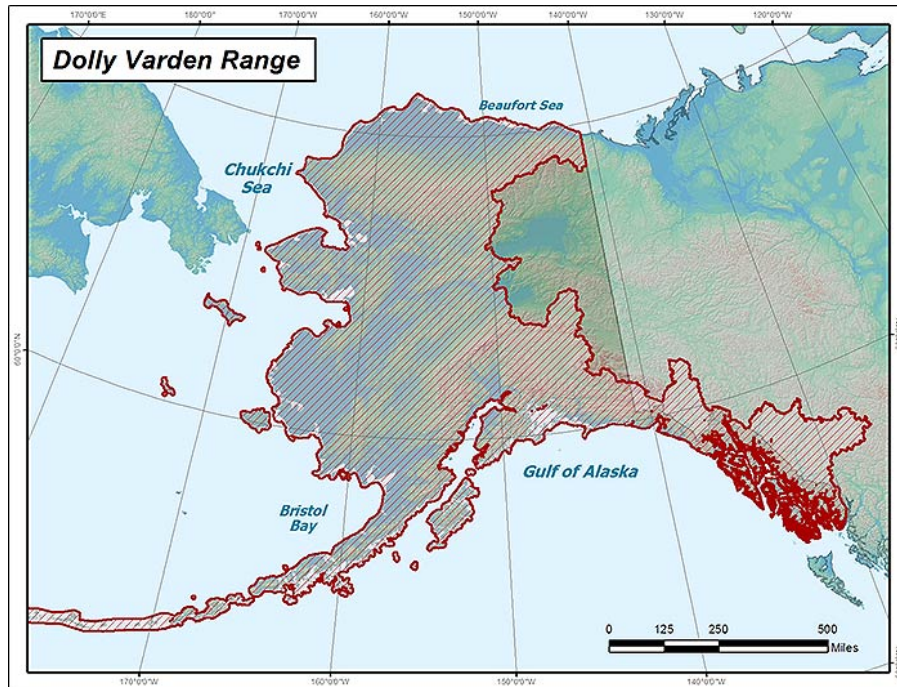


Figure 1. Freshwater and coastal distribution of Dolly Varden in Alaska (from Alaska Department of Fish and Game, species profile).

While it is known that Dolly Varden may occupy offshore areas in the Pacific Ocean (Morita et al. 2009), it is not known whether they occupy offshore areas of the Chukchi Sea, which is a biologically important feeding area during the summer for many marine mammals, fish, and seabirds (Smith 2010). Their wide oceanic distribution in the North Pacific Ocean, complex movements, and the fact that they overwinter in several rivers that drain into the Chukchi Sea, all suggest that at least some individual Dolly Varden occupy offshore areas in the Chukchi Sea.

Electronic fish tags provide researchers opportunities to examine marine dispersal, behavior and habitat occupancy of fishes. One type of tag, the Pop-up Satellite Archival Transmitting (PSAT) tag, measures and records depth, temperature and ambient light intensity while attached to a fish. On a pre-programmed date, the tag releases from a fish, pops-up to the surface of the ocean, and transmits the archived data, which can be retrieved by project investigators, thus providing a valuable fisheries-independent method for examining several aspects of fish biology and ecology (Gunn and Block 2001; Seitz 2003; Teo et al. 2007). Fisheries independence is critically important for recovering tag data from fish species that occupy areas where there are no fisheries, such as in offshore areas of the Chukchi Sea. Therefore, in this study we used PSAT tags to study the summer dispersal and behavior of adult Dolly Varden that overwinter in the Wulik River.

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

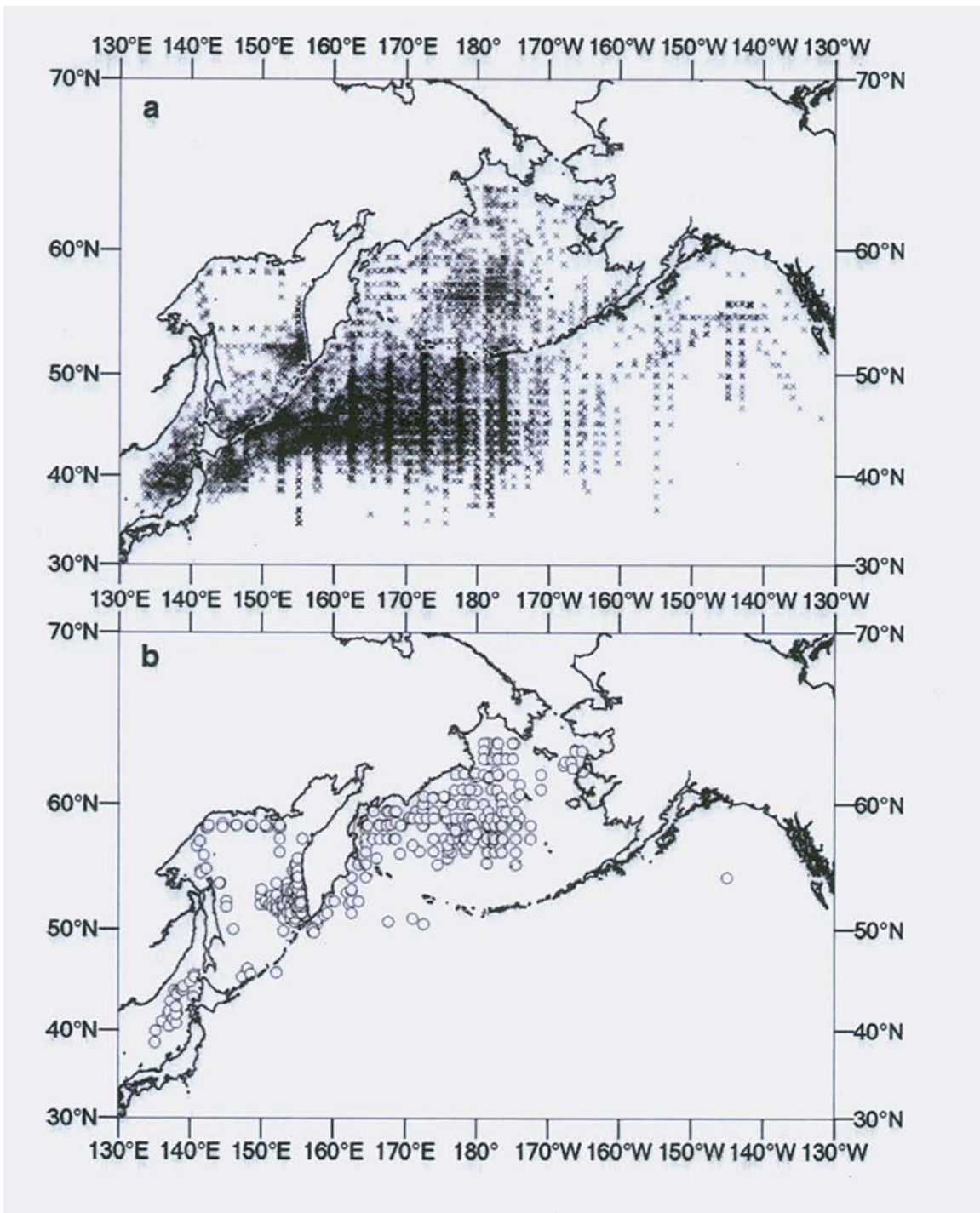


Figure 2. (a) Distribution of Japanese high seas salmon research fishing stations by all fishing gear types (gillnets, longlines, trawls) and (b) the fishing stations where Dolly Varden were captured over a 35-year period (1960-1962 and 1972-2007; from Morita et al. 2009).

Hypothesis

Dolly Varden that overwinter in the Wulik River will feed during the summer in marine areas that may be explored and developed for oil and gas in outer continental shelf areas in the Chukchi, Bering and/or Beaufort Seas.

Objectives

To examine the previous hypothesis, we accomplished the following objectives:

1. Describe baseline ecological information about Dolly Varden tagged in the Wulik River, Alaska, including:
 - a. Timing of outmigration from the Wulik River to the Chukchi, Bering and/or Beaufort Seas
 - b. Summer dispersal
 - c. Temporal and spatial distribution
 - d. Depth and temperature occupancy
2. Describe temporal and spatial distribution in outer continental shelf areas to provide information to the public, biological resource managers and marine gas and oil resource managers to better understand potential interactions among Dolly Varden and exploration and development activities in the Chukchi, Bering and/or Beaufort Seas.

Methods

Study site

The Wulik River drains a 3,891 km² 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 (Fig. 3). The mean annual discharge (1985–2010) ranges from 13 to 50 m³·s⁻¹ with average peak flows ranging from 179 to 960 m³·s⁻¹.

Fish capture, tag attachment and data acquisition

In early to mid-June of 2012 and 2013, 52 Dolly Varden that overwintered in the Wulik River were captured and tagged with PSAT tags. 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 joins the Kivalina Lagoon (Table 1). 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°43'24" N, 164°31'24" W; near the mouth of the Wulik River) during 13–14 June (Table 1). 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). Their health was screened for up to four hours before tagging, with each fish being 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, placed into a custom-fabricated tagging cradle that contained river water, blindfolded, and PSAT-tagged in series.

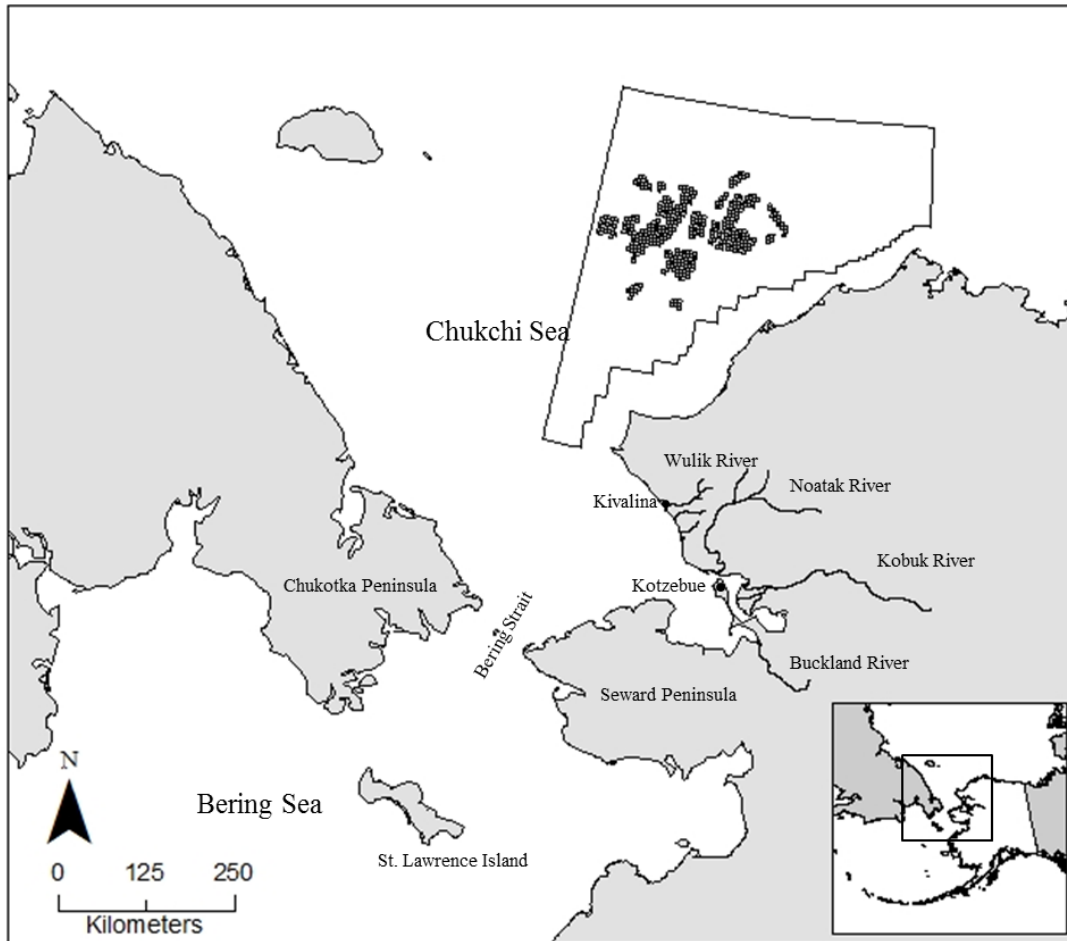


Figure 3. Prominent watersheds and landmarks in northwestern Alaska and eastern Russia. The U.S. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

Tags were attached to Dolly Varden using a “tag backpack” system (Fig. 4; A. Rikardsen, personal communication). Backpack systems included two components: the “straps,” and the “pack.” The “straps” were a harness attachment system, 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 bars (1 cm wide x 5 cm long x 0.2 cm thick), each protected on one side by a 0.2 cm thick silicon pad, affixed by marine epoxy to both ends of a 15 cm length of 80 lb test Dacron fishing line. The middle of the line was secured to a corrodible link on the PSAT tag (the “pack”) using a cow hitch, thus forming the “tag backpack.” Each “tag backpack” was affixed to a fish by placing the silicon-padded side of each plastic bar on a fish’s skin on opposite sides of the dorsal fin, approximately 2 cm below the fin’s insertion in the body. 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.” Once a PSAT tag was secured, the fish was returned to the mesh holding pen for observation. Tagged fish were released simultaneously after it was determined that all fish were swimming satisfactorily. All field work was conducted under UAF IACUC Assurance 308584 and State of Alaska Fisheries Research Permit (SF-ECP-2007-87).



Figure 4. Microwave Telemetry’s X-tag, attached to a Dolly Varden with a wire harness “tag backpack” attachment system. Photo courtesy of Andy Seitz.

Each PSAT tag (Microwave Telemetry’s X-tag) 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 at liberty (i.e. externally attached to fish between the tagging and pop-up dates), PSAT tags measured and recorded depth (resolution 0.34–5.4, range 0–1296 m), temperature (resolution 0.16–0.23°C, range -4–40°C,) and ambient light (4×10^{-5} lux at 555 nm) readings every two minutes. Because the exact timing of the fishes’ return to freshwater was unknown and the PSAT tags need to be in water that is at least 5 psu salinity for their release mechanism to function, 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, the pop-up position and archived temperature and depth data, as well as daily geolocation estimates. 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. Frequently, extrinsic factors such as biofouling compromised tag transmission strength and led to incomplete reception of the entire archived temperature and depth data sets. Therefore, to quantify the amount of archived temperature and depth data retrieved from individual tags, the percentage of archived data retrieved was calculated by dividing the actual amount of temperature and depth data received via Argos by the hypothetical amount of depth and temperature data that should have been received via Argos under ideal transmission conditions. Specifically, for one tag, the total number of individual depth and temperature readings received via Argos was divided by the product of the number of days at liberty and 192 (8 depth and temperature readings per hour x 24 hours). 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.

Three types of end locations were obtained. First, for tags that popped-up and transmitted to satellites on their scheduled date, end locations were 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 ≥ 1 ($n=24$), which translates into a position error of <1.5 km. Second, if a tag popped-up, but a position was not obtained while transmitting ($n=3$), end locations were calculated by Service Argos, Inc. using Kalman reprocessing of archived satellite transmissions, resulting in a positional error of 1.0–15.0 km. However, in one case of Kalman reprocessing, no error estimate could be provided (#107994). Third, in cases where fish were physically recaptured in subsistence and sport fisheries ($n=9$), Global Positioning System coordinates of the recapture site were used, resulting in a positional error of <0.2 km.

Two tags appeared to prematurely release early in the summer of 2013 (13–27 June) and wash up on shore 2–12 weeks before the scheduled pop-up date. In these cases, depth and temperature records were used to infer that the tags washed up on shore shortly after prematurely releasing from the fish and likely had minimal drift on the surface of the ocean between the dates of premature release and reporting to satellites. For these tags, 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. Additionally, in two cases, tags prematurely released ($n=2$, 2013) from the fish before the scheduled pop-up date and drifted on the surface of the ocean for 5 and 10 days. In these cases, it was assumed that the tags 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 reporting position of the tag. 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 sea-surface currents. Because the surface currents before and after reporting to satellites were assumed to be similar, the average daily direction and distance of sea-surface currents were estimated from multiple daily locations (>10) of the tags as they transmitted to Argos satellites after the scheduled pop-up date.

Table 1. Deployment and end location information for 52 Dolly Varden PSAT-tagged 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 the percentage of depth and temperature data actually obtained compared to the amount of these data collected by the tags.

| Fish ID | Length (cm) | Tagging location and year | End date | Time at liberty (days) | Minimum distance (km) | % data obtained | End location |
|---------|-------------|---------------------------|----------|------------------------|-----------------------|-----------------|------------------|
| 107988 | 78.0 | Wulik 2012 | 7/1/12 | 26 | 45 | 84 | Kivalina Lagoon |
| 107989 | 75.5 | Wulik 2012 | 7/7/12 | 32 | 13 | 100 | Wulik River |
| 107990 | 81.5 | Wulik 2012 | 7/1/12 | 26 | 319 | 100 | Russian Chukchi |
| 107991 | 78.0 | Wulik 2012 | 7/7/12 | 32 | 403 | 0 | Russian Chukchi |
| 107992 | 81.2 | Wulik 2012 | 7/15/12 | 40 | 383 | 100 | Russian Chukchi |
| 107993* | 86.0 | Wulik 2012 | 7/4/12 | 29 | 138 | 99 | Cape Espenburg |
| 107994 | 81.5 | Wulik 2012 | 7/24/12 | 49 | 565 | 0 | Amguema River |
| 107995 | 89.0 | Wulik 2012 | 7/4/12 | 29 | 135 | 100 | Kotzebue Sound |
| 107996 | 82.0 | Wulik 2012 | 7/12/12 | 37 | 306 | 100 | Buckland River |
| 107997 | 86.5 | Wulik 2012 | 8/1/12 | 57 | 286 | 0 | Noatak River |
| 107998 | 85.5 | Wulik 2012 | 6/24/12 | 19 | 0 | 100 | Wulik River |
| 107999 | 91.5 | Wulik 2012 | 6/7/12 | 2 | 0 | 100 | Wulik River |
| 108000 | 81.6 | Wulik 2012 | 8/15/12 | 71 | 381 | 98 | Russian Chukchi |
| 108001 | 78.5 | Wulik 2012 | Missing | - | - | - | - |
| 108002 | 75.5 | Wulik 2012 | 9/1/12 | 88 | 38 | 1 | Wulik River |
| 108003 | 85.0 | Wulik 2012 | 8/15/12 | 71 | 359 | 97 | Russian Chukchi |
| 108004* | 86.0 | Wulik 2012 | 6/27/12 | - | - | 96 | - |
| 108005 | 79.0 | Wulik 2012 | 6/18/12 | 13 | 45 | 100 | Kivalina Lagoon |
| 108006 | 82.5 | Wulik 2012 | Missing | - | - | - | - |
| 108007* | 81.5 | Wulik 2012 | 7/16/12 | - | - | 54 | - |
| 108030 | 69.0 | Kivalina 2013 | Missing | - | - | - | - |
| 108031 | 65.0 | Kivalina 2013 | Failed | - | - | - | - |
| 108032* | 63.5 | Kivalina 2013 | 6/26/13 | 14 | 102 | 96 | Cape Espenburg |
| 108033 | 65.5 | Kivalina 2013 | 6/22/13 | 9 | 120 | 100 | Sheshalik Spit |
| 108034* | 62.0 | Kivalina 2013 | 6/25/13 | 13 | 38 | 84 | Coast |
| 108035 | 70.5 | Kivalina 2013 | 7/25/13 | 42 | 308 | 1 | Noatak River |
| 108036 | 67.0 | Kivalina 2013 | 7/6/13 | 24 | 435 | 100 | Russian Chukchi |
| 108037 | 69.0 | Kivalina 2013 | 6/27/13 | 14 | 140 | 99 | Noatak Delta |
| 108038 | 72.0 | Kivalina 2013 | 7/15/13 | 33 | 40 | 7 | Rabbit Creek |
| 108039 | 65.0 | Kivalina 2013 | 7/15/13 | 32 | 470 | 97 | Russian Chukchi |
| 108040 | 67.5 | Kivalina 2013 | 7/10/13 | 27 | 450 | 100 | Russian Chukchi |
| 108041 | 82.5 | Kivalina 2013 | Failed | - | - | - | - |
| 108042 | 79.0 | Kivalina 2013 | Failed | - | - | - | - |
| 108043 | 79.0 | Kivalina 2013 | 8/1/13 | 49 | 6 | 29 | Wulik River |
| 108044 | 67.0 | Kivalina 2013 | Missing | - | - | - | - |
| 108045 | 70.0 | Kivalina 2013 | Missing | - | - | - | - |
| 108046 | 78.5 | Kivalina 2013 | Failed | - | - | - | - |
| 108047 | 76.0 | Kivalina 2013 | 8/21/13 | 70 | 371 | 1 | Noatak River |
| 108048 | 72.5 | Kivalina 2013 | 8/22/13 | 70 | 70 | 9 | Omivirorok River |
| 108223 | 72.0 | Kivalina 2013 | 9/3/13 | 83 | 362 | 2 | Noatak River |
| 108224 | 71.0 | Kivalina 2013 | Failed | - | - | - | - |
| 108225 | 78.0 | Kivalina 2013 | Failed | - | - | - | - |
| 108226 | 80.0 | Kivalina 2013 | 6/21/13 | 8 | 120 | 100 | Sheshalik Spit |
| 108227 | 71.5 | Kivalina 2013 | 6/21/13 | 8 | 120 | 100 | Sheshalik Spit |
| 108228 | 73.5 | Kivalina 2013 | Failed | - | - | - | - |
| 108229 | 79.0 | Kivalina 2013 | Missing | - | - | - | - |
| 108230 | 83.0 | Kivalina 2013 | 9/15/13 | 95 | 362 | 54 | Noatak River |
| 108231 | 68.0 | Kivalina 2013 | 6/16/13 | 3 | 4 | 58 | Kivalina Lagoon |
| 108232 | 75.5 | Kivalina 2013 | 9/15/13 | 94 | 228 | 3 | Noatak River |
| 108233* | 81.0 | Kivalina 2013 | 6/25/13 | - | - | 82 | - |
| 108234 | 72.0 | Kivalina 2013 | 10/17/13 | 127 | 45 | 4 | Wulik River |
| 129838 | 78.0 | Kivalina 2013 | 10/1/13 | 110 | 191 | 17 | Noatak River |

Data analyses

Movement of tagged Dolly Varden was described by examining end locations and dispersal distance. First, distribution and dispersal patterns were qualitatively described by examining end locations in two week intervals in a GIS framework. Second, minimum dispersal distance was calculated by one of two different methods, depending on each individual tag's end location. If the tag reported from the ocean, minimum dispersal was the great circle distance from the river mouth to the tag's end position. For fish tagged in 2012, the distance between the tagging location and the river mouth (45 river kilometers) was added to the great circle distance. In cases when a tag's end location was in another river, a minimum distance route that included travel through the Wulik River, the ocean, and the destination river was created in GIS software, so that the minimum distance path did not pass over land.

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 (Teo et al. 2011; Lacroix 2013). Inferred behavior types included river residency, ocean entry, marine residency, marine transit, and marine feeding (Fig. 5). This inference was based on comparison of the depths and temperatures occupied by the tagged fish to possible depths and temperatures in river and ocean 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 $<0^{\circ}\text{C}$ 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 (Fig. 5). 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 (Fig. 5). 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 rapidly traveling fish typically do not undertake frequent diving behavior, the periods of occupation of relatively cool water and shallow depths were classified as inferred marine transit (Fig. 5). After inferred marine transit, tagged fish remained in relatively cool water, but occupied greater and more variable depths, consistent with oscillatory diving behavior. Because feeding fish frequently demonstrate oscillatory diving behavior, these periods of occupation of relatively cool water and deeper and more variable depths were defined as inferred marine feeding (Fig. 5). Marine residency was defined as the combination of marine transit and marine feeding behaviors (i.e., all oceanic occupancy).

For data analyses, these inferred behaviors were separated by a 24 hour period from one another. For inferred river residency, marine transit, and marine feeding, minimum and maximum temperatures and depths as well as their individual and grand means ($\pm\text{SD}$), were calculated. For fish that were inferred to occupy the ocean, the mean percentage of time spent in 5-m depth and 1°C temperature bins were also calculated.

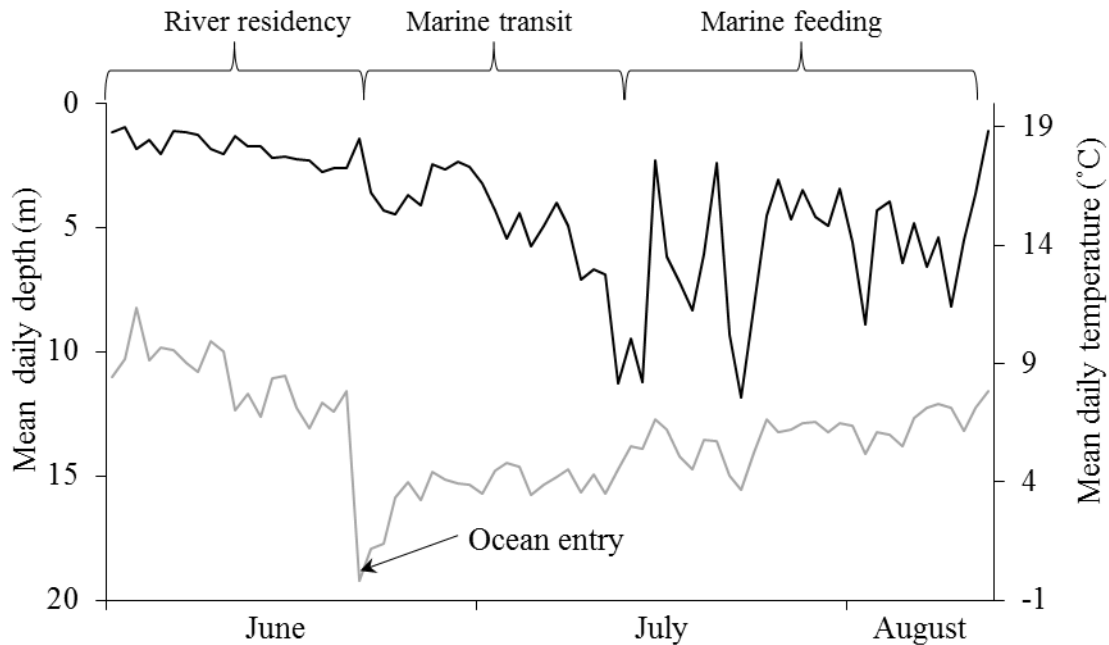


Figure 5. Example of daily average depth (black line) and water temperature (grey line) for one PSAT tagged Dolly Varden (#108000), whose tag popped-up in the Chukchi Sea north of Russia on 15 August 2012. Inferred dispersal phases including river residency, ocean entry, marine transit, and marine feeding are noted.

Mortality of fish was determined by tags that remained at a constant depth >0 m (i.e., the bottom) for at least 10 days ($n=6$). For three of these tags, depth and temperature remained constant until the pop-up date, at which time the tag floated to the surface and reported to satellites. End locations of these fish were assigned as the location of the first tag transmission with an Argos location class ≥ 1 , as there was little to no movement of the tag between dates of death and reporting (Lacroix 2013). However, in the other three cases of mortality, fish died early in the summer (25 June–17 July), and after a period of 1–2 weeks of constant depth readings >0 m, the tags were freed from the fish (i.e., fish decomposition), floated to the surface of the ocean, and drifted for 1–2 months before reporting to satellites. Because of the large temporal gap between floating to the surface and reporting to satellites, these end locations ($n=3$) were excluded from the dispersal analyses because the location of first transmission to Argos satellites was likely considerably far away from the location of the death of the fish. However, because behavior of these fish while alive did not appear to be qualitatively different from the behavior of the fish that were alive on the pop-up date, their depth and temperature records while alive were used in data analyses.

Light-based daily geolocation estimates were explored using Microwave Telemetry's proprietary software that uses ambient light level data to produce daily longitude and latitude estimates. Specifically, the tags' software estimates longitude by finding the point of symmetry in diel fluctuations in ambient light intensity, also known as local noon, and identifying sunrise and sunset times to estimate latitude. Two tags provided very limited light-based geolocation estimates after 6–8 August in 2012. However, because both of these tags reported to satellite on 15 August 2012 (accuracy < 1.5 km), the light-based geolocation estimates (accuracy $\pm \sim 100$

km) did not provide any appreciable insight into the movement of these fish during the week before the pop-up date. For the remaining tags, light sensor saturation (i.e. the tags' light sensor was unable to distinguish any diel differences in light intensity) resulting from constant levels of relatively high ambient light intensity during the Arctic summer, prevented calculation of any light-based daily geolocation estimates.

As an alternative to light-based geolocation, a novel method similar to Chittenden et al. (2013) was developed to understand the spatial distribution of tagged fish whose end locations were in the Russian Chukchi Sea. In general, to approximate possible distribution, the tag-recorded sea-surface temperature (i.e., temperature experienced while the fish was in water depths <2 m) was compared to satellite-derived sea-surface temperature (NOAA Daily 5 km blended). Specifically, for individual fish, mean weekly tag-recorded sea-surface temperature was calculated and compared to mean weekly satellite-derived sea-surface temperatures 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 sea-surface temperatures overlapped ($\pm 0.5^{\circ}\text{C}$). To provide a broader and more inclusive perspective on the spatial distribution of all tagged fish, grand mean monthly tag-recorded sea-surface temperature from all fish combined were compared to mean monthly satellite sea-surface temperatures 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 sea-surface recorded temperatures overlapped ($\pm 1.0^{\circ}\text{C}$). 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

Summary

Tagged Dolly Varden ranged from 62.0 to 91.5 cm (76.3 ± 7.1 cm, mean \pm SD) and were at liberty for 2–127 days (Table 1). Of the 52 tags deployed, 48 (88%) either transmitted to satellites or were physically recaptured. Of these 48 tags, 36 (69% of the 52 total tags) provided end locations used in the dispersal analyses (Table 2). Specifically, 27 (52% of the 52 total tags) transmitted to satellites, and nine (17% of the 52 total tags) tags were recovered while still attached to fish in subsistence and recreational fisheries. The remaining 16 (31% of the 52 total tags) tags either transmitted, but failed to provide any end locations ($n=7$; 13% of the 52 total tags), or prematurely released after death and drifted for 1–2 months ($n=3$; 6% of the 52 total tags), thus subsequent end locations were not used. Lastly, six (12% of the 52 total tags) tags never reported and were considered missing (Table 2).

The percentage of archived temperature and depth data received from tags that transmitted to satellites varied from 0 to 100% (Table 1). Most fish that reported from freshwater provided end locations, but failed to provide any substantial archived temperature and depth data (0–1% of the subset of temperature, light, and pressure data recorded), except for two fish whose tags reported from the Noatak River and provided 54 and 58% of their archived data (Table 1). In contrast, most 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). In total, 25 (48%) of the 52 tags deployed tags provided the vast

majority of depth and temperature data that were used in dispersal and behavior analyses (Table 2).

Table 2. Annual deployment summary of PSAT 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. “End locations” describes the number of tags that provided end locations, either determined by Argos satellites for tags the popped-up and transmitted, or by Geographic Positioning System for tags that were physically recovered. “Transmitted” refers to number of tags that reported to satellites, but failed to provide end locations, likely because of weak transmission strength. “Missing” refers to the number of tags that never reported to satellites nor were recaptured in fisheries. “Mortality” refers to the number of fish whose depth data suggested that they died before the pre-programmed pop-up date of the tag. Finally, the “>50% data” column describes the number of tags that provided the majority of their archived temperature and depth data.

| Year | Tagged | Recaptured | End locations | Transmitted | Missing | Mortality | >50% data |
|-------|--------|------------|---------------|-------------|------------|-----------|------------|
| 2012 | 20 | 6 (30.0%) | 18 (90.0%) | 0 (0.0%) | 2 (10.0%) | 3 (15.0%) | 13 (65.0%) |
| 2013 | 32 | 3 (9.4%) | 18 (56.3%) | 7 (21.9%) | 4 (12.5 %) | 3 (9.4%) | 12 (37.5%) |
| Total | 52 | 9 (17.3%) | 36 (69.2%) | 7 (13.5%) | 6 (11.5%) | 6 (11.5%) | 25 (48.1%) |

Summer dispersal

The tagged Dolly Varden had end locations in both marine and freshwater habitats and dispersed a mean minimum distance of 210.1 ± 167.6 km (range 0–565 km; Table 1). For tags with end locations in marine habitat, eight reported from the Russian Chukchi Sea approximately 100–200 km north of the Chukotka Peninsula, exhibiting minimum travel distances of 319–470 km from their tagging locations (Table 1; Fig. 6). Eight other tags had end locations in marine waters 40–135 km southwest of their tagging locations in nearshore waters adjacent to Kotzebue Sound (Table 1; Fig. 6). For tags with end locations in freshwater areas, 11 reported 40–565 km from the tagging site in other rivers including the Omikviorok, Rabbit, Buckland and Noatak Rivers in northwestern Alaska, and the mouth of the Amguema River in Russia (Fig. 6; Table 1). 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; Fig. 6). 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. 7). 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. 7).

River residency

Occupation of the Wulik River was demonstrated by eighteen fish in 2012. Of these fish, six fish spent their entire time at liberty (2–31 days) in the Wulik River and the remaining 12 fish resided in the Wulik River 20–27 days before swimming to the ocean. During river residency, fish occupied relatively shallow water (grand mean 0.9 ± 0.7 m, range 0–5.7 m), and typically occupied deeper water during the day and shallower depths during the night (Fig. 8). During

river residency, water temperatures ranged from -0.2 – 15.4°C (grand mean 9.4 ± 2.6 ; Fig. 9). For fish that were recaptured or whose tag reported to satellites from near or upstream of the tagging site, mean water temperature increased from June ($10.2\pm 1.9^{\circ}\text{C}$, range 6.3 – 14.2°C) to July ($11.7\pm 1.9^{\circ}\text{C}$, range 7.9 – 15.4°C) and typically displayed diel fluctuations of 4 to 6°C during the summer (Fig. 8). In contrast, fish whose end locations were in the lower river and lagoon displayed diel water temperature fluctuations of up to 10°C , with minimum temperatures occasionally $<0^{\circ}\text{C}$, likely as a result of brief periods (<1 hr) of occupation of brackish water in the lagoon (Fig. 9).

While most fish whose end locations were in other rivers failed to provide any substantial archived data (0 – 1%), one fish was recaptured in the Buckland River and provided 100% of its archived data, and two tags that reported from the Noatak River provided 54 – 58% of their archived data (Table 1). However, because of large fluctuations in daily temperatures, we were unable to discern precise freshwater reentry dates, and subsequent characteristics of freshwater residency in other rivers after returning from salt water.

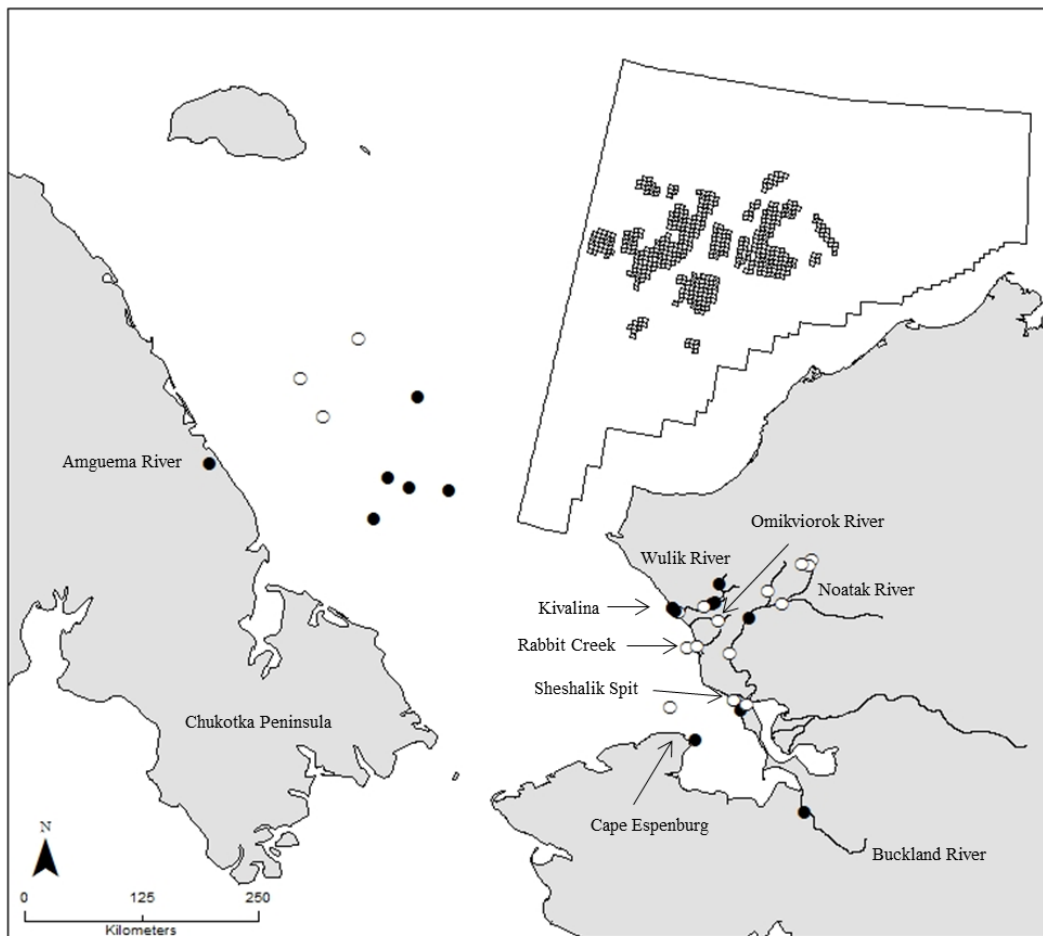


Figure 6. End locations of Dolly Varden tagged in the Wulik River in summers of 2012 (black dots) and 2013 (white dots). End locations may be where a fish was physically recaptured while the tag was still attached to a fish, or where a tag popped-off a live fish and reported to satellites. The U.S. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

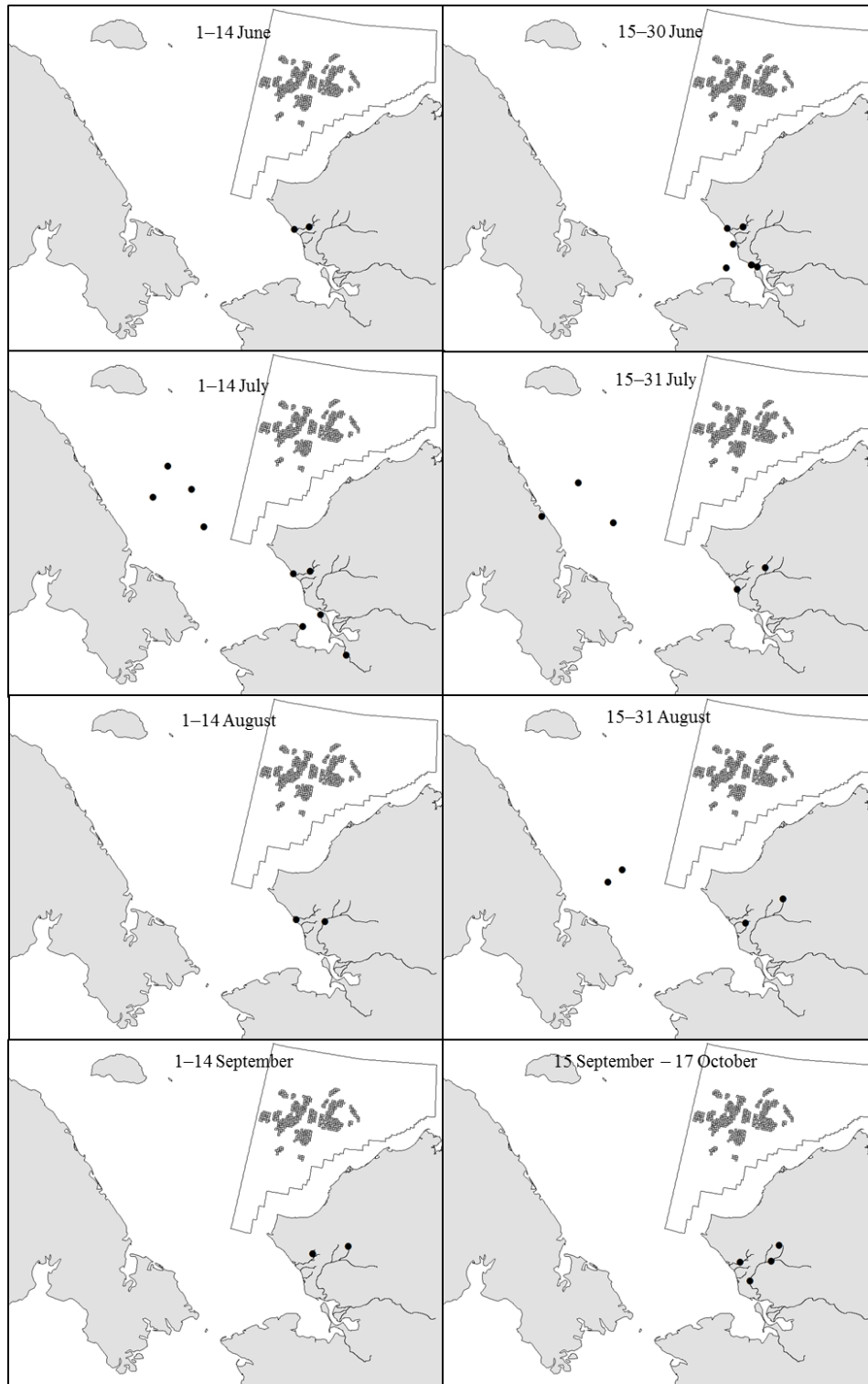


Figure 7. End locations of PSAT-tagged Dolly Varden throughout the summers of 2012 and 2013 combined. End locations may be where a fish was physically recaptured while the tag was still attached or where a tag popped-up from a live fish and reported to satellites. The U.S. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares

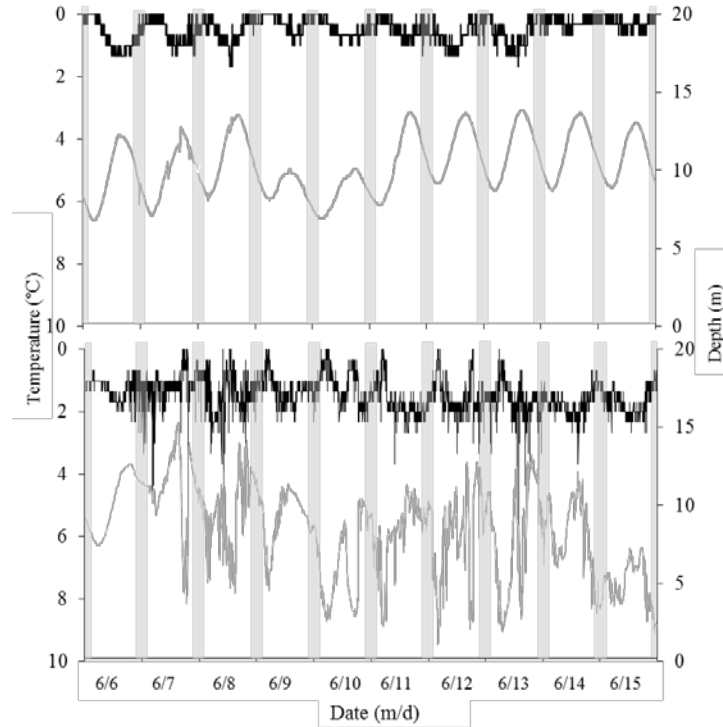


Figure 8. Riverine depth (black line) and temperature (grey line) data for Fish #107989 (top panel), which was recaptured near the tagging location in the Wulik River, and Fish #108005 (bottom panel), which was recaptured at the river mouth in June 2012. Depth and temperature were recorded every two minutes. Grey bars denote 2200–0200 hours Alaska Standard Time.

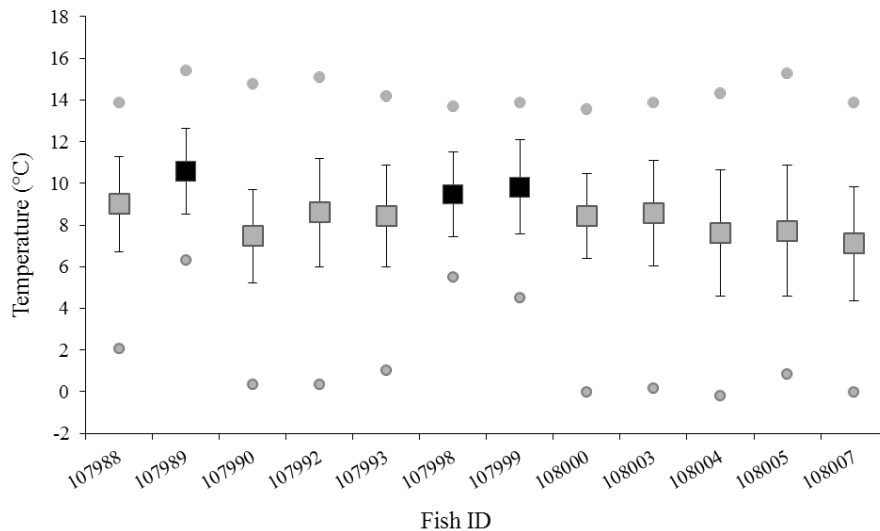


Figure 9. Box and whisker plots of riverine water temperatures experienced by Dolly Varden (n=12) in the Wulik River in 2012 and 2013. Boxes are the mean, whiskers are \pm SD and circles are minimum and maximum water temperatures. Black boxes denote tagged fish that remained in upstream reaches, and gray boxes denote tagged fish that demonstrated downstream movements to Kivalina Lagoon.

Marine residency

In 2012 and 2013, several fish ($n=8$), demonstrated offshore dispersal to the Russian Chukchi Sea, north of the Chukotka Peninsula. These fish inferably 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 0.25–13.0 hrs, after which they occupied deeper and warmer water (Fig. 10). During marine residency, they spent 76.3% and 96.4% of the time in the top 5 and 15 meters of the water column (Fig. 11). Also during marine residency, these fish experienced water temperatures ranging from -0.9 – 8.5°C (grand mean 5.2 ± 1.6), and spent the majority of the time in temperatures of 3 – 7°C (Fig. 12). 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. 13).

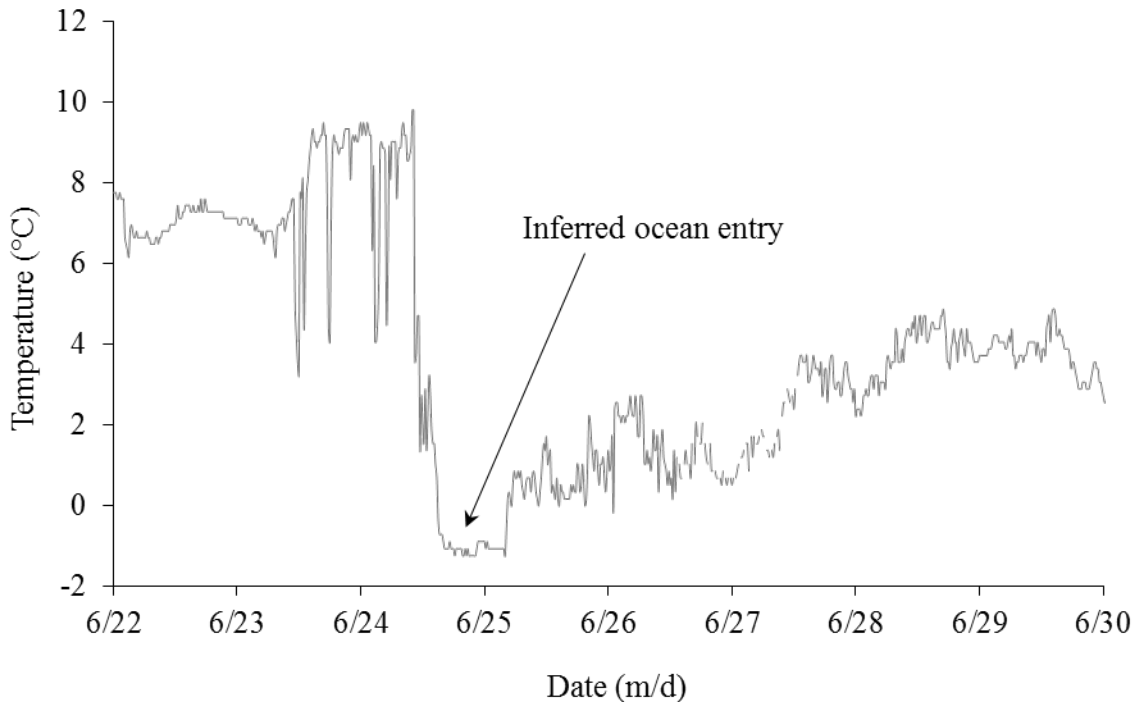


Figure 10. Temperatures (at 15 minute intervals) occupied by a tagged Dolly Varden (#108000) experiencing sustained (>12 hours) cold temperatures $<-1.0^{\circ}\text{C}$ on 25 June 2012.

After ocean entry, the marine residency period of these eight fish whose tags reported from the Russian Chukchi Sea was divided into two phases, marine transit and marine feeding, based on occupied depth. Inferred marine transit behavior lasted between 5 and 10 days and varied on an individual basis. During inferred marine transit (Fig. 14), tagged Dolly Varden experienced water temperatures of -0.9 – 8.5°C (grand mean 5.2 ± 1.8) while occupying relatively shallow depths with very little variability (1.6 ± 2.9 m, range 0–23.5 m). During transit, individual fish spent 76.6–99.6% (grand mean $88.6\pm 7.4\%$) and 99.1–100% (grand mean $99.8\pm 0.5\%$) of their time within the first 5 and 15 meters of the water column respectively (Fig. 11). One fish (#107990) inferably entered the ocean on 25 June 2012 and its tag reported from the Russian

Chukchi Sea 319 km away on 1 July 2012 (Table 1), transiting an average of $60 \text{ km} \cdot \text{day}^{-1}$. Based on duration of inferred transiting behavior and minimum dispersal distance, seven of the eight fish whose tags reported from the Russian Chukchi Sea immediately transited $30\text{--}60 \text{ km} \cdot \text{day}^{-1}$ after entering the ocean. In contrast to these seven fish who immediately displayed inferred marine transit behavior after ocean entry, one fish whose tag reported from the Russian Chukchi Sea 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.

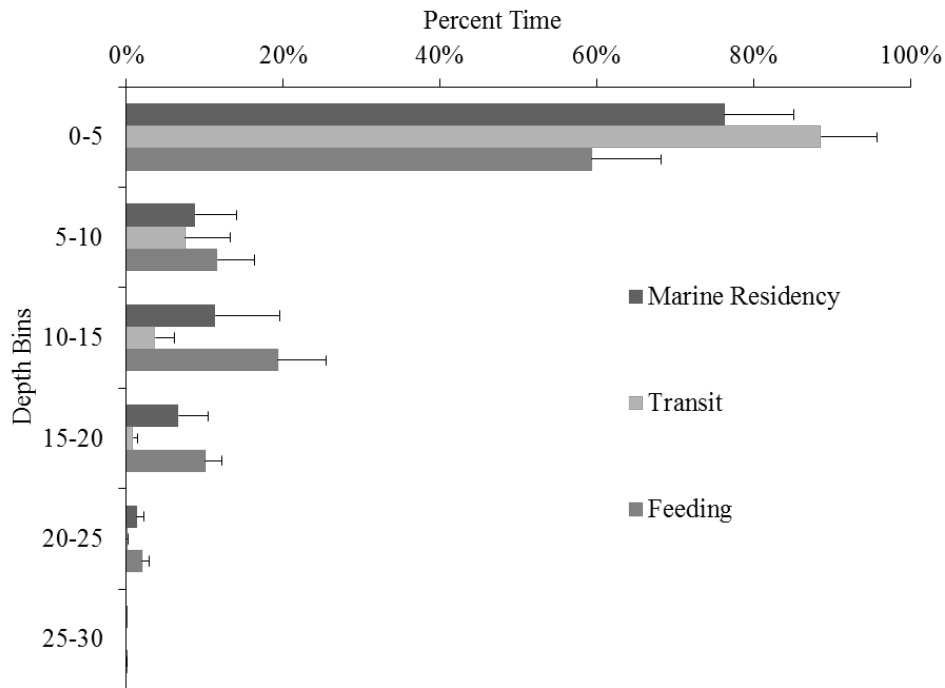


Figure 11. Percentage (mean \pm SD) of time spent in 5 m depth-bins by tagged Dolly Varden (n=8) that reported from the Russian Chukchi Sea in 2012 and 2013. Depth occupation is for overall marine residency (transit + feeding), in addition to two inferred behaviors while in the ocean, marine transit and marine feeding.

After inferred marine transit behavior, these fish began their second inferred behavioral phase, marine feeding, which was characterized by relatively consistent oscillatory diving behavior (Fig. 14; Fig. 15). These oscillatory dives generally occurred between 0 and 15 m with maximum dive depths ranging between 12.5–51.1 m for individual fish. Although the variability in depth increased during inferred feeding, individual tagged Dolly Varden still spent 48.8–72.7% (grand mean $59.4 \pm 8.9\%$) and 84.0–100% (grand mean $90.3 \pm 2.1\%$) of the time in the first 5 and 15 meters of the water column respectively (Fig. 11). Even though there was continuous daylight during the majority of their time at liberty, all tagged Dolly Varden whose tags reported from the Russian Chukchi Sea demonstrated a diel pattern in oscillatory diving behavior, in which they occupied shallow depths and did not dive between 2200–0200 on most days, with oscillatory diving occurring during the remainder of the day (Fig. 15).

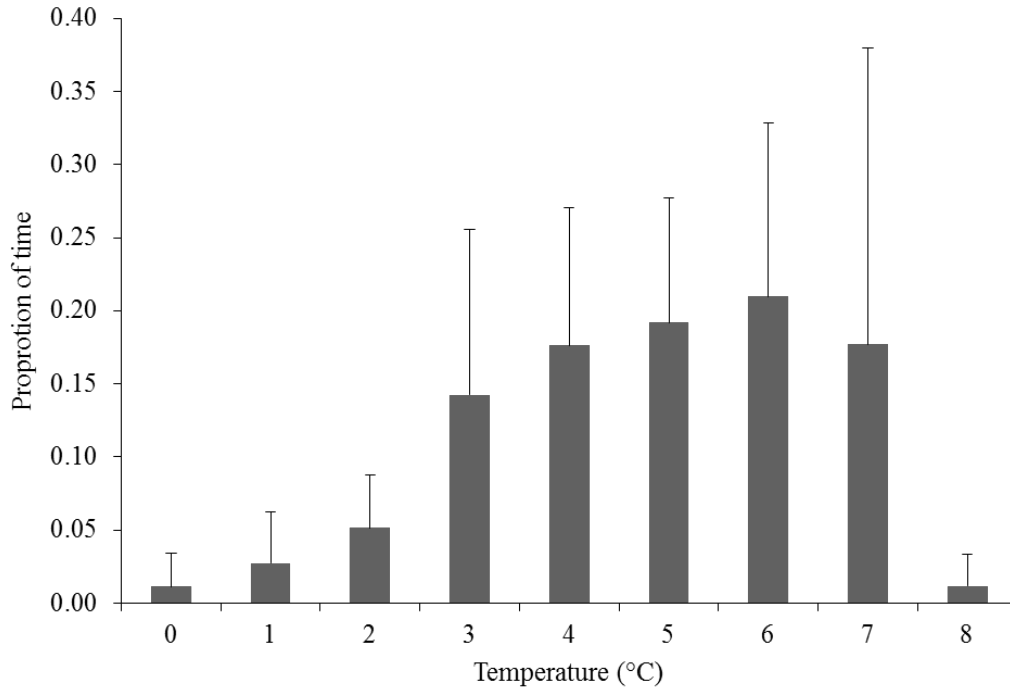


Figure 12. Proportion of time (mean±SD) spent in 1°C temperature-bins while in the ocean (transit + feeding) by Dolly Varden (n=8) that reported from the Russian Chukchi Sea in 2012 and 2013.

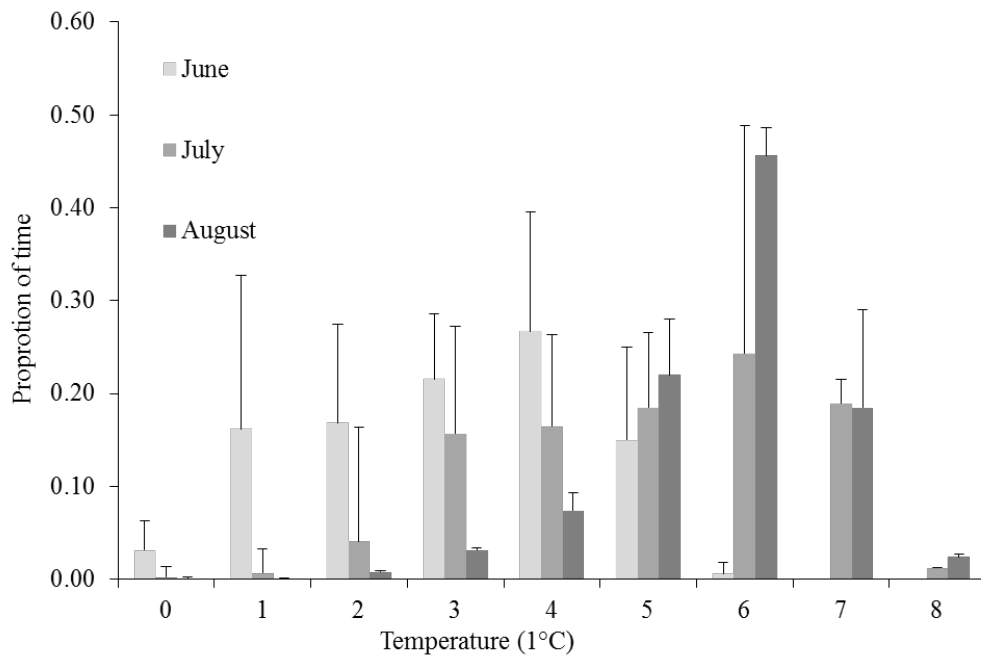


Figure 13. Proportion of time (mean±SD) by month spent in 1°C temperature-bins while in the ocean (transit + feeding) by Dolly Varden (n=8) that reported from the Russian Chukchi Sea.

During marine residency (transit + feeding) of the fish whose tags reported from the Russian Chukchi Sea, tag-recorded mean monthly sea-surface temperatures 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±0.1°C) in August 2012. When the sea-surface temperatures experienced by individual fish (mean weekly) were compared to satellite-derived sea-surface temperatures (±0.5°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 northwestern direction throughout the summer (Fig. 16). When all fish that reported from the Russian Chukchi Sea (grand monthly mean tag-recorded sea-surface temperatures) were compared to mean-monthly satellite-derived sea-surface temperature (±1.0°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. 17; Fig. 18). For August 2012, the extent of possible distribution of fish increased and was in the northwestern Chukchi Sea and northern Bering Sea (Fig. 17; Fig.18). In 2013, tags with end locations in offshore regions of the Chukchi Sea (n=3) all reported between 7 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), but no geolocation estimates could be approximated for these fish due to poor data quality of satellite imagery for this time.

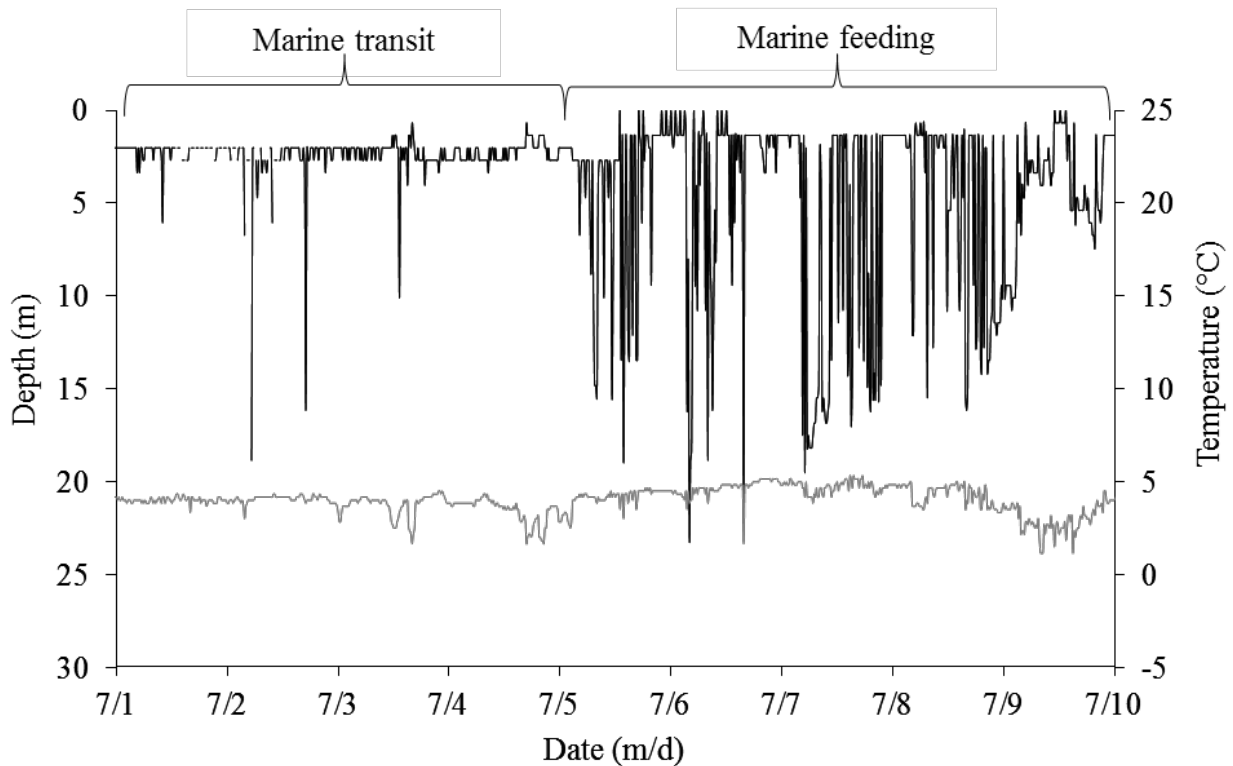


Figure 14. An example of depths and temperatures occupied by a tagged Dolly Varden (#108000) that exhibited typical inferred marine transit and feeding behaviors in July 2012. Depth (black line) and temperature (grey line) values were recorded every 15 minutes.

For fish that demonstrated southerly nearshore movements, all experienced highly fluctuating daily temperatures (0.5–15.5°C) and shallow depths (<6 m), and did not demonstrate oscillatory

diving behavior while in nearshore areas (Fig. 19). Given the lack of clear patterns in their depth and temperature records, distinct behavioral patterns such as ocean entry, transit behavior, and feeding could not be discerned.

Mortality

Six fish (11.5%) appeared to have died in the ocean, as indicated by constant depth readings >0 m before the pop-up date of the tag (Table 2). One fish whose tag reported from the Russian Chukchi Sea exhibited behaviors similar to other tagged fish in region (i.e., oscillatory diving behavior) before dying on 16 July. Four fishes whose tags reported from nearshore areas adjacent Kotzebue experienced highly fluctuating daily temperatures ranging up to -0.6–15.3°C, relatively shallow depths <6 m, and little oscillatory diving before dying between 25 June and 4 July. One fish whose tag reported from the Beaufort Sea appears to have died immediately after ocean entry on 27 June, after which the tag floated to the surface of the ocean on 26 July, and drifted in a northeasterly direction until reporting to satellites on 1 September.

Discussion

PSAT tags 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. Other dispersal types including Wulik River residency, nearshore dispersal along northwestern Alaska, and movement to other rivers, were also documented, similar to previous conventional tag studies (DeCicco 1985; DeCicco 1997). While undertaking these different dispersal types, 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.

Ocean entry

Drastic declines in water temperature, indicating exiting the Wulik River and entry into the ocean, were most apparent for the eight fish that dispersed to the Russian Chukchi Sea. Similarly to previous studies (DeCicco 1985; DeCicco 1997), these fish appear to have entered the ocean in late June to early July. During outmigration, fish experienced temperatures down to -1.4°C, with one fish experiencing temperatures <-1.0°C for >12 hr. These are the coldest documented temperatures occupied by Dolly Varden, 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 -0.7°C (Pennell and Barton 1996). Previous research in a laboratory has shown that a closely related congener, Arctic charr, *Salvelinus alpinus*, is resistant to freezing and can survive temperatures of -0.99°C for up two hours in the presence of ice, and ≥ 5 days at -1.2°C in the absence of ice (Fletcher et al. 1988). While there have been no reports of antifreeze compounds in salmonids, it is hypothesized that the epidermis of Arctic charr serves as a barrier to ice nuclei formation in their flesh (Fletcher et al. 1988). The epidermis of Dolly Varden may 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.

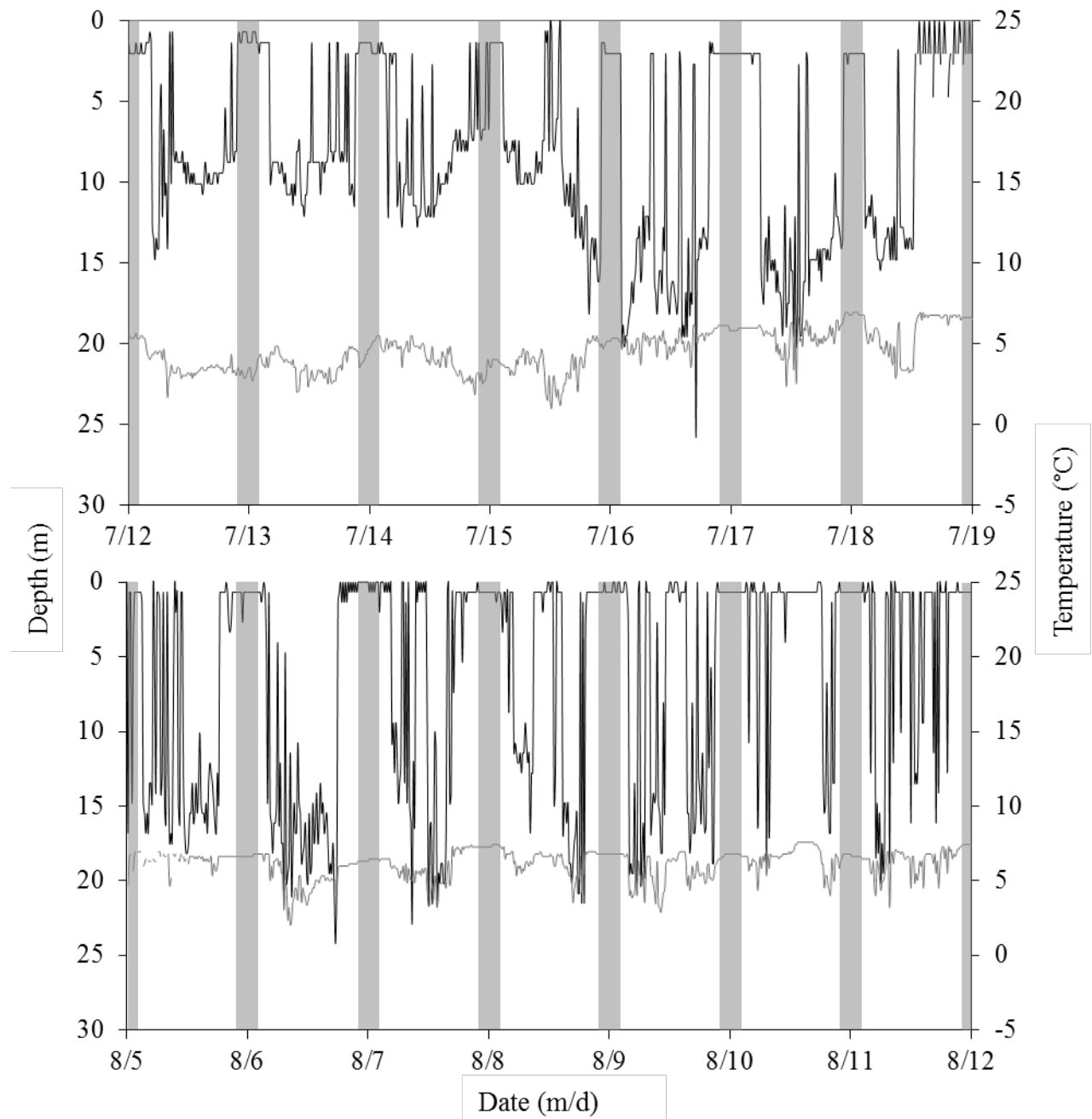


Figure 15. Example of diurnal diving behaviors over a seven-day period in July (top panel) and August (bottom panel) 2012 by two Dolly Varden whose tags reported from the Russian Chukchi Sea. Depth (black line) and temperature (grey line) values were recorded every 15 minutes. Grey bars denote the hours of 2200–0200 Alaska Standard Time.

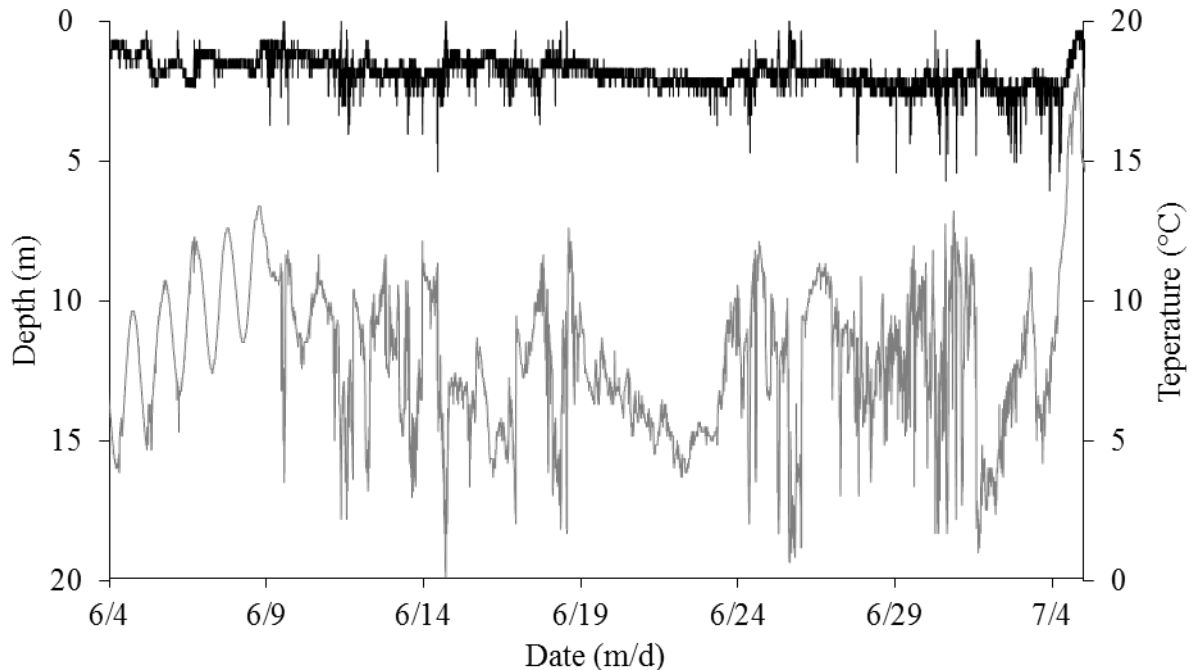


Figure 16. Example of occupied depths and temperatures of one tagged Dolly Varden (#107995) that exhibited southerly nearshore dispersal. Fish was released in the Wulik River (45 km upstream from the mouth) and recaptured near Kotzebue, AK on 4 July 2012. Depth (black line) and temperature (grey line) values were recorded every 2 minutes.

Marine residency

After ocean entry, the majority of fish whose tags reported from the Russian Chukchi Sea appeared to have rapidly transited to this area, based on their inferred transit behavior after ocean entry and estimation of geolocation by comparing sea surface temperatures measured by the tags and satellites. 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 $60 \text{ km}\cdot\text{day}^{-1}$ for five days. Including mean northward prevailing ocean currents of $\sim 8.0 \text{ cm}\cdot\text{sec}^{-1}$ (Weingartner et al. 2005), this rate of travel by this fish translates into a mean swimming speed, which closely corresponds to the most energetically efficient swimming speed of other salmonids ($1.0 \text{ body length}\cdot\text{sec}^{-1}$; 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 inferably transiting 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 feeding area in the Russian Chukchi Sea.

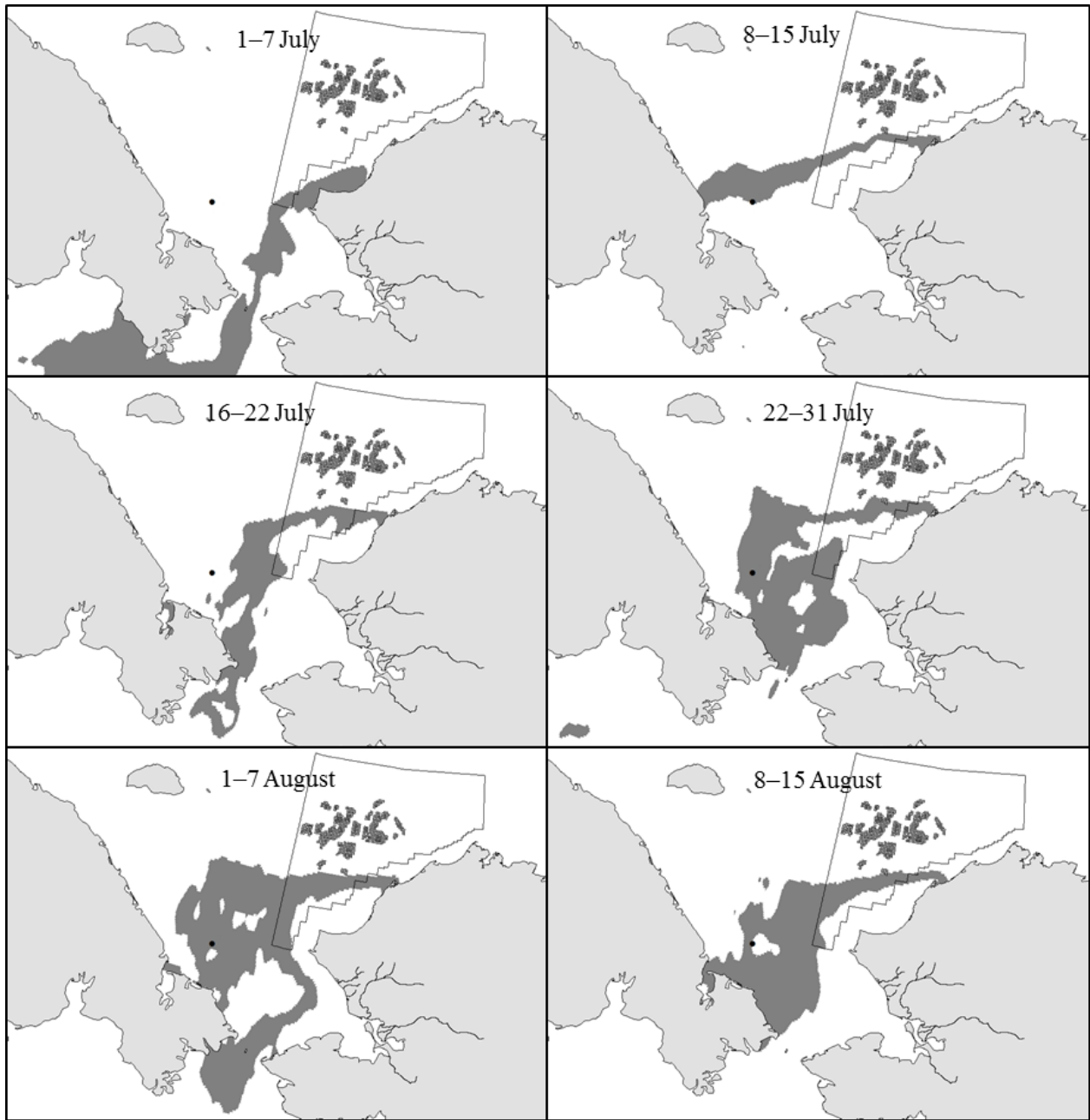


Figure 17. Example of geolocation approximation of one tagged Dolly Varden (#108000) which reported to satellites on 15 August 2012. Shaded polygons are proposed to represent the possible weekly distribution of the tagged fish by depicting the region of the Chukchi Sea where mean weekly sea surface temperatures measured by the tag attached to the fish were similar ($\pm 0.5^{\circ}\text{C}$) to satellite-derived sea-surface temperatures. 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. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

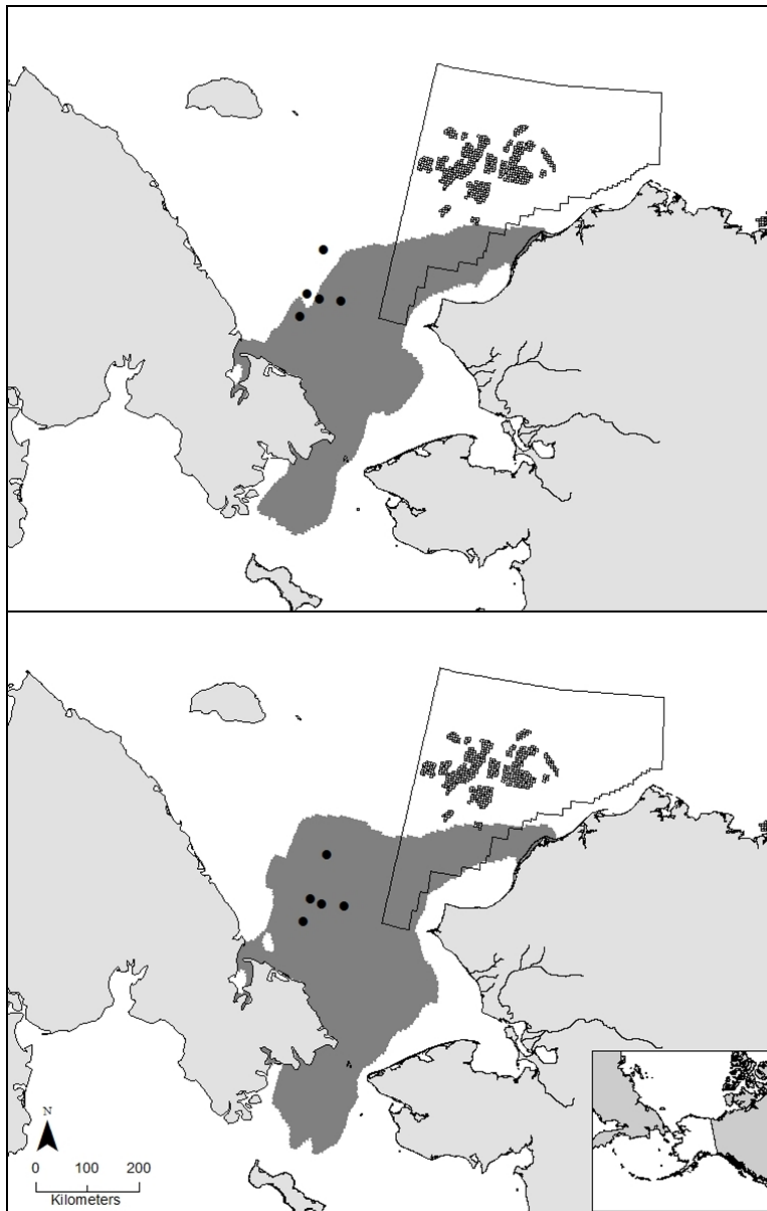


Figure 18. Shaded polygons are proposed to indicate the extent of possible offshore distribution of tagged Dolly Varden during July and August of 2012 by depicting the region of the Chukchi Sea where mean monthly sea surface temperatures measured by all tags attached to Dolly Varden and by satellites were similar ($\pm 1.0^{\circ}\text{C}$) (top panel, July; bottom panel, August). 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. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

All eight fish whose tags reported from the Russian Chukchi Sea were located in a relatively small area from 1 July to 15 August, so it is likely that the tagged Dolly Varden occupied this area throughout the summer. Even though light-based geolocation was ineffective and unable to provide additional evidence for this claim, an alternative analysis based on comparing sea-surface temperatures measured by the tags and satellites supports the idea that fish tagged in

2012 quickly dispersed to and remained in the area throughout the summer. Specifically, occupation of this area of the Russian Chukchi Sea provides the most parsimonious explanation for the observed matches between sea surface temperatures measured by the tags and satellites. In 2013, due to poor data quality we were unable to approximate geolocation on any tagged fish that reported in offshore regions of the Chukchi Sea using this alternative method. As mentioned in the results, due to large gaps in sea-surface temperature data resulting from environmental conditions (e.g. cloud cover) it was necessary to use NOAA's Blended (5 km daily) data which are highly interpolated. Even the blended sea-surface temperature imagery was too poor to address the plausible distribution of fish in 2013. However, given that these fish were only in the ocean for approximately two weeks (1-15 July) before reporting to satellites from approximately 450 km away from Kivalina Lagoon, it is likely that they swam directly to these areas, similar to fish in 2012. As a corollary to occupying this region of the Russian Chukchi Sea, it is unlikely that the tagged fish exhibited any northeasterly nearshore or offshore movements, particularly through the U.S. OCS Federal Lease Areas. Additionally, it is also unlikely that fish showed any movement or occupied any regions of the Bering or Beaufort Seas while at liberty.

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, therefore, it is highly likely that this location is an important feeding area for Dolly Varden in the Chukchi Sea for most of the summer. This supposition is corroborated by the diel diving behavior displayed by the tagged Dolly Varden in which they consistently occupied shallow depths between the hours of 2200–0200 hours, with rapid oscillatory diving to approximately 15 m during the remainder of the day. This diel pattern is similar to diving behavior of most other feeding salmonids including Arctic charr (Rikardsen et al 2007), chum salmon *Oncorhynchus keta* (Yukimasa et al. 2001; Walker et al. 2005), steelhead *Oncorhynchus mykiss* (Nielsen et al. 2011), Chinook salmon *Oncorhynchus tshawytscha* (Walker et al. 2005; Walker and Myers 2009), and Atlantic salmon *Salmo salar* (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 our tagged fish and the main motivation for occupying this area in the Russian Chukchi Sea. 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, likely because it is a biologically productive area (Moore et al. 1995).

Even though the tagged Dolly Varden did display oscillatory diving behavior, they spent the vast majority of their time near the surface while transiting and feeding in the ocean. While other oceanic depth data on Dolly Varden is scarce, the shallow depths inhabited by this species are similar to some other salmonid species including steelhead off the coast of California (Teo et al. 2011) and Alaska (Nielsen et al. 2011), as well as anadromous Arctic charr and brown trout *Salmo trutta* near Norway (Rikardsen et al. 2007). Chum Salmon also tend to occupy shallow depths, especially during periods of darkness (Yukimasa 2001).

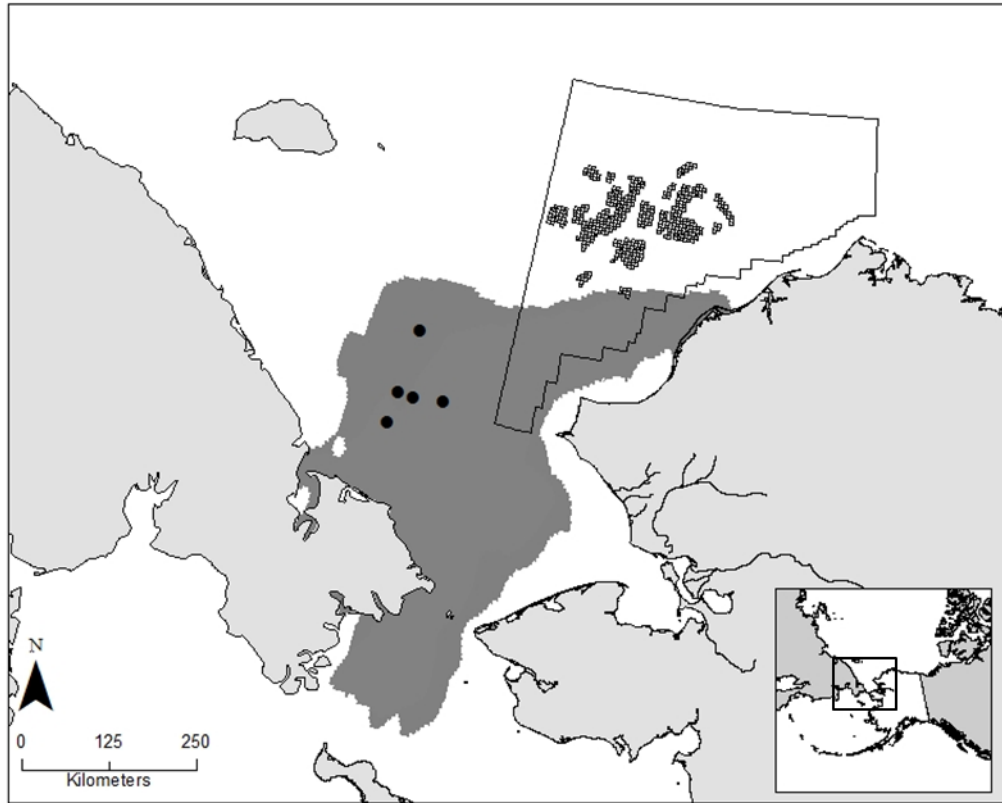


Figure 19. Shaded polygons are proposed to indicate the extent of possible offshore distribution of tagged Dolly Varden during the summer (1 July – 15 August) of 2012 by depicting the region of the Chukchi Sea where mean monthly sea surface temperatures measured by all tags attached to Dolly Varden and by satellites were similar ($\pm 1.0^{\circ}\text{C}$). We inferred that all fish spent the majority of their time at-liberty near their end locations (black dots), which are included here for reference purposes. The U.S. Federal OCS Chukchi Sea lease sale area is denoted by the black outline, and sold leases are denoted by shaded squares.

Wulik River residency

Other dispersal and behavioral types demonstrated by Dolly Varden in this study have been documented previously in several conventional tag studies (DeCicco 1985; DeCicco 1997). End locations of fish that occurred near the tagging site throughout the entire summer indicate that some Dolly Varden forego an oceanic migration and remain in freshwater for the entire summer. These fish are likely natal to the Wulik River and will spawn in locations upstream of their overwintering locations in late August and September, after which they will immediately move downstream to mix with non-spawners in overwintering locations (DeCicco 1997). In contrast to Dolly Varden that remained in upstream locations during the summer, other fish had end locations at the mouth of the Wulik River. Because these downstream end locations only occurred in June and early July, it is likely that Dolly Varden generally do not reside at the mouth of the river for the entire summer, rather the fish with end locations at the mouth of the river were likely intercepted in the Wulik River/Kivalina Lagoon subsistence fishery while dispersing to offshore feeding locations or to other rivers. Further evidence for Dolly Varden not

occupying the river mouth during the entire summer is provided by subsistence catches of Dolly Varden at the mouth of the Wulik River, which typically end in early July and do not begin again until August (DeCicco 1996).

Movement to other rivers

In addition to the Wulik River, end locations of tagged Dolly Varden were in nearshore areas of Alaska south of the Wulik River (Kotzebue Sound area) and in other Alaskan rivers (Noatak, Buckland, Omikviorok, and Rabbit rivers). Additionally, of particular note is the first documentation of a Dolly Varden traveling from northwestern Alaska to a river on the northern coast of the Chukotka Peninsula (Amguema River, Russia). Unfortunately, depth and temperature patterns of fish that traveled in nearshore areas and to other rivers were not as discernable as the patterns observed in the fish that migrated to the offshore area. However, some data from recovered tags in this study, as well as previous studies on Dolly Varden in northwest Alaska are useful for inferring the behavior of these fish whose end locations were in nearshore areas and other rivers. Previous studies indicate that fish from several rivers in northwest Alaska (e.g. Noatak, Kobuk, Kivalina, and Pilgrim rivers) and Russia form mixed-stock overwintering aggregations in the Wulik River (DeCicco 1996; Scanlon 2011). 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 and swim directly to their natal rivers to spawn (DeCicco 1989; DeCicco 1997). Considering these previous studies and data from this study (e.g., tagging and end locations, and the lack of oscillatory diving observed in the depth records), the fish in this study whose end locations were in other rivers and nearshore waters adjacent to Kotzebue were likely all non-natal to the Wulik River. Instead of dispersing to offshore feeding areas, these fish were likely transiting in nearshore waters, while foregoing feeding, to their natal rivers to spawn in the upcoming fall. These fish all appeared to leave Kivalina Lagoon 15–19 June, possibly indicating that fish transiting to their natal spawning areas may exit the Wulik River earlier than fish moving to the offshore feeding area in the Russian Chukchi Sea. While at liberty, the fish that transited through nearshore areas experienced large daily fluctuations in temperature, including warmer temperatures not observed in the ocean, suggesting that while transiting in nearshore habitats, they may occasionally swim into the lower end 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 documented in Pacific salmon (Burger et al. 1995) to locate natal spawning rivers or to assess the suitability of overwintering habitat.

Mortality

Several fish in this study appeared to have died prior to the pre-programmed pop-up date of the tag. Unfortunately, we are unable to determine whether these fish died from tag-induced mortality or natural mortality. While little is known about the causes and rates of natural mortality of Dolly Varden from northern Alaska, it is thought to be highly variable and dependent of environmental conditions (Arvey 1991). The causes of natural mortality are not clear, though 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). Even less is known about natural mortality rates, but in one

study of Dolly Varden from the Canning River on the North Slope of Alaska, average annual mortality of age 8–14 Dolly Varden, the same age as the tagged fish in this study (based on length), was estimated to be approximately 49% (Craig 1977). Given this, the mortality rate (11.5%) in this study, while not an annual rate, is still relatively small, and suggests that tag-induced mortality is most likely relatively small compared to natural mortality. Tag-induced mortality also has been shown to be small in similar PSAT tagging studies on another salmonid, the Atlantic salmon *Salmo salar* (Lacroix 2013).

Project evaluation

Overall, PSAT tags provided unprecedented information about the oceanic habits and behavior of Dolly Varden that overwinter in northwestern Alaska. Generally, tags that popped-up and transmitted from marine areas provided relatively high rates of temperature and depth data recovery (84–100%), leading to new insights into the oceanic ecology of this fish species. Previous conventional tagging research in the early 1980's and mid 1990's by the Alaska Department of Fish and Game was unable to directly address questions related to the oceanic ecology of this species and therefore focused on the freshwater ecology of Dolly Varden. This focus on freshwater studies was because recovery of conventional tagged fish relied upon physically recapturing tags in fisheries, which only existed in rivers and their mouths. It is likely that many of these fish studied in the 1980s and 1990s also dispersed to inferred offshore feeding areas in the Chukchi Sea; however, this dispersal and feeding behavior were never documented due to a lack of fisheries in which to capture these fish.

Although the tag data provided many novel insights into the oceanic ecology of Dolly Varden, the data also raised many unanswered questions. Foremost, the percentage of tags that provided the majority (>50%) of their archived temperature and depth data was lower than expected (>80%) when the project was conceived. Additionally, there was large interannual variability in the percentage of tags that provided end locations (90% in 2012 and 56.3% in 2013). The reasons for the lower-than-expected data recovery rate and the discrepancy between the percentages of end locations provided in 2012 and 2013 are unknown, but they may be related to the observation that a relatively large proportion of tagged fish in 2013 appeared to have moved immediately to other rivers. Because the tags need 5 psu to function properly, tags reporting from freshwater likely did not actually release and pop-up, rather they were still likely attached to the fish. However, because these fish occupied shallow water depths in rivers, we surmise that while still attached to the fish, the tags' antenna periodically protruded above the surface of the water and were able to weakly transmit to satellites, thus providing sporadic transmissions. Because these transmissions were sporadic, tags located in freshwater on their pop-up date generally provided few high accuracy end locations and low temperature and depth data recovery rates. Occupation of freshwater on the schedule pop-up date of the tags may also explain the tags that either failed to transmit or provide any end locations.

Even though occupation of freshwater may have decreased the efficacy of these tags in some cases, PSAT tags still were a valuable tool for studying Dolly Varden. The overall temperature and depth data recovery rate from PSAT tags in this study was greater than that of other electronic tagging studies on salmonids that all relied on physical recapture of data storage tags (Hinke et al. 2005; Walker and Myers 2009; Hayes et al. 2011; Nielsen et al. 2011; Teo et al. 2011). Additionally, the PSAT tags provided a much greater percentage of end locations than previous conventional tagging studies on Dolly Varden in which 8,695 individuals were tagged

and only 364 (4%) were recaptured (reviewed in DeCicco 1997). Of the end locations in this study, many were located where fisheries are not prosecuted, highlighting the importance of using a fisheries independent tagging methodology, such as PSAT tags, to examine the oceanic ecology and behavior of Dolly Varden and other similar species at high latitudes.

Results from this project will allow refinement of similar studies in the future. One such refinement is tag pop-up schedules. Our staggered pop-up dates proved valuable to ensure that at least some tags provided data. This is because the timing of freshwater re-entry of Dolly Varden is highly uncertain and tags in freshwater provided relatively low recovery rates of end locations and depth and temperature data. Therefore, a staggered schedule hedges bets against individual variability in dispersal characteristics, so that some fish will be in marine waters on the pop-up date of the tag attached to them. Unfortunately, it is impossible to know individual fish's fates and accordingly tailor pop-up dates around when individuals will be in the ocean. However, based on our results, pop-up dates scheduled between 15 July and 15 August will likely maximize the probability of retrieving data in future experiments. In the future, new technology that does not rely on a galvanic corrosion release mechanism would be invaluable for studying anadromous fishes at high latitudes. By not using a galvanic corrosion release mechanism, the tags could pop-up in freshwater, allowing researchers to obtain more data during the entire ice-free season.

In addition to informing tag pop-up schedules in future experiments, this project provided valuable information about the appropriate minimum size for PSAT tagging Dolly Varden, reporting some of the smallest fish tagged with PSAT tags to date. During the first year (2012) of tagging, we used 75 cm FL as a relatively conservative minimum size for tagging fish. We based this minimum size on the relative length and weight of the tag compared to the Dolly Varden. Upon receiving data from these first-year tags, there was no indication that the smallest tagged fish behaved different than the largest tagged fish; therefore we reduced our minimum size threshold for tagging to 60 cm FL in 2013. After examining our results from both years, mortality rates were relatively low, and there was no apparent relationship between fish size, mortality or dispersal distance. Given these results, we believe that 60 cm is likely an appropriate guideline for minimum PSAT tagging size of Dolly Varden, however the absolute minimum size threshold is not known. This minimum size guideline is similar to that of another salmonid species, the Atlantic salmon (Lacroix 2013), in which individuals as small as 52 cm have been tagged with the same PSAT tag. Given these results on Atlantic salmon, smaller Dolly Varden (50–60 cm) may be an appropriate size for X-tag deployments, however caution should be taken, as the effects (weight and drag) on fish behavior of this size are not known.

Conclusion

This study has produced new qualitative insights into the oceanic ecology of Dolly Varden in the Chukchi Sea. Specifically, it provides the first evidence that Dolly Varden execute relatively long offshore movements in the Chukchi Sea and feed on the outer continental shelf 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.

While in the Chukchi Sea, they spent the vast majority of their time near the surface of the ocean in the summer. 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.

This study was conducted on 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 likely variability, future studies on Dolly Varden, including in other drainages throughout northwestern and northern Alaska, have the potential to collect more information about Dolly Varden and subsequently improve our understanding of their oceanic ecology. 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.

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