Estuarine, Coastal and Shelf Science 262 (2021) 107609

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Ocean-entry timing and marine habitat-use of Canadian Dolly Varden: Dispersal among conservation, hydrocarbon exploration, and shipping areas in the Beaufort Sea

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ARTICLE INFO

Keywords:
Marine ecology
Biotelemetry
Offshore
Anadromous migration
Remote sensing
Salvelinus malma

ABSTRACT

Conservation and management of anadromous salmonids are enhanced by understanding timing, spatial extent, and occupied depths and temperatures in marine feeding habitats. We examined ocean-entry timing and marine habitat-use, and their association with environmental conditions (e.g., sea-ice and sea-surface temperatures (SSTs)) of anadromous Dolly Varden (*Salvelinus malma malma*) from the Canadian Arctic using pop-up satellite archival tags (PSAT) and data storage tags. Using this information, we evaluated the extent tagged fish occupied offshore (>5 km) habitats, and their proximity to a marine protected area (MPA) and areas of potential threats in the Canadian Beaufort Sea. Ocean-entry by tagged fish using the western Mackenzie Delta for freshwater migration occurred approximately mid-June (range = 8–26 June) and closely followed landfast sea-ice break-up based on satellite imagery. While at sea, fish predominately occupied surface waters (<2 m) at SSTs of 5–10 °C. PSAT end-locations were 37–152 km offshore, typically near the sea-ice edge, greatly extending previously reported distances from shore in the Alaskan Beaufort Sea. The spatial extent of offshore dispersal by Dolly Varden is likely influenced by SSTs and sea-ice conditions, and the physical properties of the Mackenzie River plume (e.g., turbidity), which extends preferred temperatures farther from shore. In relatively cooler years characterized by later sea-ice breakup and a summer sea-ice margin situated closer to shore, fish spent more time in nearshore than offshore habitats (51.7% vs. 48.3%) compared to warmer years (12.6% vs. 87.5%). Furthermore, fish typically occupied shallower offshore mean depths (2.2 m vs. 3.4 m) of the water column and experienced colder mean water temperatures (5.1 °C vs. 7.4 °C) in cooler versus warmer years. Dolly Varden were found within or adjacent to hydrocarbon lease areas and shipping lanes, and may be vulnerable to threats associated with these activities. Although PSATs reported outside of the MPA boundaries, which are situated adjacent to the Mackenzie Delta, occupancy in spring was inferred during ocean-entry and while transitioning to offshore areas. This first study to describe how environmental conditions influence marine distribution of Canadian Dolly Varden together with their proximity to anthropogenic threats is relevant for assessing impacts of climate change and future development.

1. Introduction

Conservation and management of anadromous fishes are enhanced by understanding timing of migratory movements and geographically delineating freshwater breeding and marine foraging habitats (Reist et al., 2013; Skaala et al., 2014; Hertz et al., 2019). While migration tactics within a population can be complex (e.g., partial migration), migration among habitats in seasonally predictable patterns provides opportunities to access spatially or temporally available resources that can improve survival and lifetime fitness (Hendry et al., 2004; Chapman et al., 2012). Protecting marine feeding areas of anadromous fishes is important given that habitat quality is consequential for energy needed for maintenance, growth, and reproduction, ultimately influencing population productivity and the fisheries they support (Thorstad et al.,

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https://doi.org/10.1016/j.ecss.2021.107609
Received 1 July 2021; Received in revised form 15 September 2021; Accepted 27 September 2021
Available online 2 October 2021

2016; Jensen et al., 2018). Anthropogenic threats to anadromous fishes in marine ecosystems include, among others, overfishing, habitat loss and degradation, and pollution (Arthington et al., 2016). In particular, climate change could not only affect migration prevalence (Finstad and Hein, 2012) and timing in anadromous fishes (Jonsson and Jonsson, 2009; Quinn et al., 2016), but also alter ecosystem characteristics through changes in water temperatures and other abiotic factors. These include shifts in species composition (e.g., loss of endemic species and range expansions of non-endemic species) and associated impacts on marine trophic interactions (Nielsen et al., 2013). Climate change is expected to disproportionately affect the Arctic where reductions in marine sea-ice are expected to increase shipping traffic and access for resource extraction (Dawson et al., 2018; Bindoff et al., 2019). Therefore, characterizing migration timing and habitat-use (e.g., spatial and thermal) of anadromous salmonids in Arctic marine ecosystems is necessary for conservation and management particularly given the dearth of scientific information on this topic (although see Rikardsen et al., 2007; Spares et al., 2012, Bond and Quinn, 2013; Gilbert et al., 2016, Courtney et al., 2016a; Harris et al., 2020).

The northern form of Dolly Varden (*Salvelinus malma malma*) is a cold-adapted, facultatively anadromous iteroparous salmonid, distributed north of the Alaska Peninsula (USA) to the Mackenzie Delta (Canada) (Armstrong and Morrow, 1980; DeCicco, 1989; Phillips et al., 1999; Maier et al., 2021). In Arctic North America, anadromous Dolly Varden is important for the subsistence and culture of Inupiat, Inuvialuit, and Gwich'in peoples who fish coastally in the summer and in rivers during migration in late-summer and fall. Seasonal migrations between freshwater (spawning and overwintering) and marine (feeding) habitats by anadromous individuals typically begin after rearing in natal streams for 2–5 years and can be quite complex (Gallagher et al., 2018; Morrison et al., 2019). Recent radio and satellite telemetry studies in Alaska have provided insights into the migration timing and marine habitat-use of Dolly Varden, including marine depths and temperatures occupied, and the first documentation of offshore habitat-use in both the Alaskan Chukchi and Beaufort seas (Courtney et al., 2016a, 2016b, 2018; Brown et al., 2019). However, data on ocean migration timing, marine habitat-use, and their environmental drivers are limited for Canadian populations. This is a notable gap given northern Dolly Varden in Canada is listed as 'Special Concern' (i.e., may become threatened or endangered because of a combination of biological characteristics and identified threats) under the federal *Species At Risk Act* legislation and is considered a priority species by Canadian co-management partners given their history of declines in abundance and importance to subsistence fisheries (DFO et al., 2019). Characterizing timing of ocean-entry and investigating possible offshore habitat-use by Dolly Varden populations in Canadian waters is relevant for understanding potential exposure to, and cumulative effects from, increasing environmental stressors in the Beaufort Sea.

Stressors identified for the Canadian Beaufort Sea include hydrocarbon exploration and production, shipping, fisheries, aquatic invasive species, contaminants, and climate change (Cobb et al., 2008; Stephenson and Hartwig, 2009; DFO et al., 2014; Ayles et al., 2016) each of which may act independently or synergistically. There has been a longstanding focus on hydrocarbon exploration in the Beaufort Sea since the 1970s (Hnatiuk, 1983; Banet, 1991). In Canada, there are 1,868,687 ha of Exploration Licenses and 224,523 ha of Significant Discovery Licenses situated up to ~120 km offshore north of the Yukon Territory North Slope and Mackenzie Delta between the Tuktoyaktuk Peninsula to the U.S.A./Canada border (CIRNAC, 2020) (Fig. 1). Although major production drilling has yet to occur and current exploration is inactive, hundreds of seismic programs have been conducted and over 250 wells have been drilled in the offshore area and Mackenzie Delta over past decades (Cobb et al., 2008). Concerns persist regarding oil spills, contaminants, seismic operations, infrastructure development (e.g., drilling

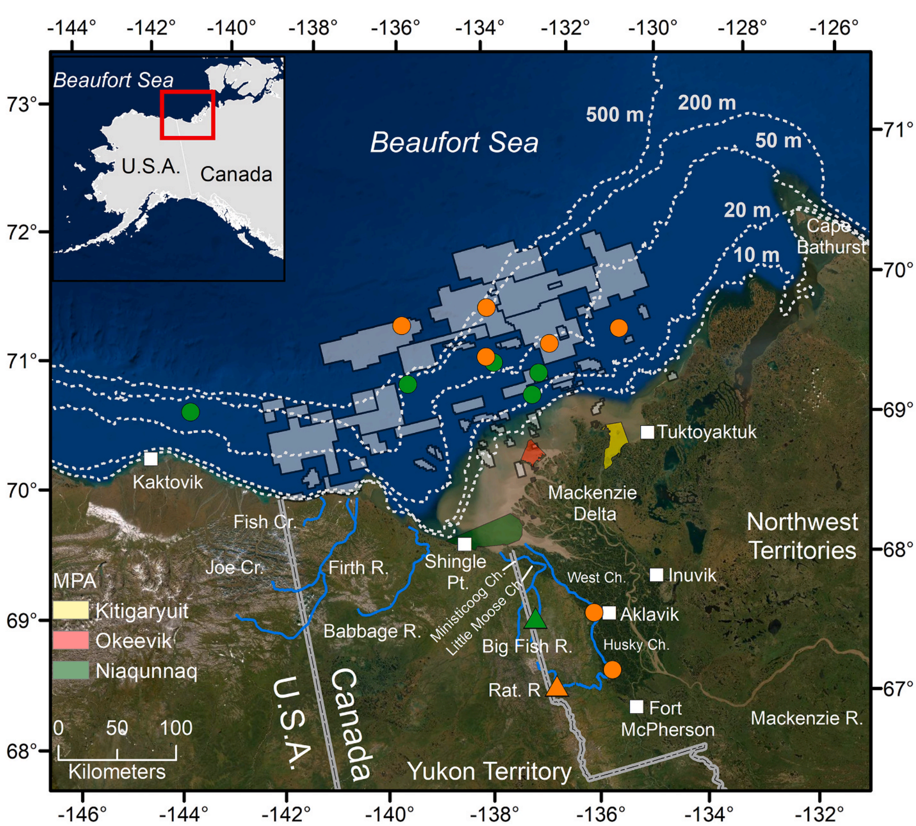

Fig. 1. Map of study area showing deployment locations (triangles) and end-locations (circles) of Dolly Varden tagged with pop-up satellite archival tags (n = 10; all in Beaufort Sea) and data storage tags recaptures (n = 2; both in Mackenzie Delta) from the Big Fish (green symbols) and Rat (orange symbols) rivers in the western Canadian Arctic. Transparent grey polygons denote hydrocarbon leases in the Canadian Beaufort Sea. Kitigaryuit (yellow polygon), Okeevik (red polygon), and Niaqunnaq (green polygon) areas of the Tarium Niryutait Marine Protected Area are noted. Dashed light-grey lines indicate 10 m, 20 m, 50 m, 200 m, and 500 m bathymetric contours. Red box in upper panel indicates extent of map. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

platforms) and their negative effects on aquatic species, including fishes and their habitats. A substantial increase in ship traffic beginning in the early 2000s in the Canadian Beaufort Sea, a strategic corridor and part of the Northwest Passage, has heightened the risk of oil spills, contaminants, and the introduction of invasive species (Dawson et al., 2018). Currently, marine traffic in the Beaufort Sea region is principally pleasure craft, cruise ships, and community supply ships; however, potential future hydrocarbon and mineral resource development, and commercial fisheries, together with ongoing sea ice reduction, could further the trend of increased shipping (Stephenson and Hartwig, 2009; Dawson et al., 2018).

Conservation tools to protect marine habitats and other valued ecosystem components in the Canadian Beaufort Sea include the Tarium Niryutait Marine Protected Area (MPA), which spans ~1,800 km^2 of the Mackenzie Delta and estuary in the Beaufort Sea (Fig. 1) (BSP , 2020). The goal of this MPA is to conserve and protect beluga whales (*Delphinapterus leucas*) and other marine species (anadromous fish, waterfowl and seabirds), their habitats, and their supporting ecosystem from activities (e.g., resource extraction and infrastructure construction) that could negatively impact the areas upon which they depend (DFO and FJMC, 2013). However, the extent to which this MPA affords protection to Dolly Varden marine and estuarine habitats, is unknown due to current knowledge gaps in marine habitat-use of this species.

In this study, our aim was to characterize Dolly Varden ocean-entry timing and marine habitat-use, their associations with environmental conditions, and investigate the geographic proximity of Dolly Varden to areas of protection and potential threats in the Canadian Beaufort Sea. Specifically, we evaluated: 1) timing of ocean-entry and associations with spring break-up of sea-ice; 2) the approximate greatest geographic extent of marine dispersal to test for occupation of offshore (>5 km) areas; 3) marine depths and temperatures occupied during the summer feeding season and their association with sea surface temperature (SST), sea-ice extent, and physical properties of the Beaufort Sea and Mackenzie River plume; and 4) the proximity of Dolly Varden summer habitat to the Tarium Niryutait MPA, hydrocarbon lease areas, and shipping routes. This study is relevant for the management and conservation of Dolly Varden and identifying how environmental conditions in relative proximity to a large river delta influence marine habitat-use of an anadromous salmonid. Furthermore, the study will improve future assessment of impacts from development activities on Dolly Varden marine habitats.

2. Materials and methods

2.1. Study area

The 13,000 km^2 Mackenzie Delta in Canada's Northwest Territories is the terminus of the Mackenzie River, which flows into the Beaufort Sea and is the largest North American river bringing freshwater to the Arctic Ocean (Macdonald et al., 1998; Ensom et al., 2012). The Mackenzie Delta is comprised of thousands of turbid lakes and a complex network of river channels that receives ~284 km^3 of water annually. It straddles the transition between subarctic boreal forest and Arctic low-shrub tundra, and is typically ice-covered between late October and late-May or early-June (Carmack and Macdonald, 2002; Ensom et al., 2012). The Mackenzie River transports approximately 127 × 10^6 tonnes of sediment each year into the Beaufort Sea (Macdonald et al., 1998). During the summer open water season the warm (~12–20 °C; Ensom et al., 2012) silt-laden water discharged from the Mackenzie River, combined with re-suspended sediments and deposits from adjacent rivers further west, produces a visible plume in the Beaufort Sea whose size, shape, and direction are strongly influenced by winds (Carmack and Macdonald, 2002; Mulligan et al., 2010; Jerosch, 2013). In certain conditions, the plume can extend hundreds of kilometers offshore (Macdonald et al., 1999). The western channels of the Mackenzie Delta (e.g., Husky, West, Little Moose, and Ministicoog channels) (Fig. 1) provide freshwater migration corridors for three known anadromous populations of Dolly Varden to enter (spring) and exit (summer/fall) the Beaufort Sea. In this study we focused on two of these populations that spawn in the Big Fish River and Rat River watersheds.

The bathymetry of the southeastern Beaufort Sea is dominated by an extensive shallow shelf that gradually slopes north to a depth of 200 m (~120 km offshore) before rapidly dropping off to several thousand meters (Carmack et al., 1989). Waters of the nearshore shelf and the shallower portion of the offshore shelf area (0–60 m isobath) are described as the Polar Mixed Layer, which is characterized as a relatively warm freshened layer produced by wind-driven mixing of water from the Mackenzie River, Pacific water mass, and ice melt (Carmack et al., 1989; Majewski et al., 2017). In summer (August), water temperature in the nearshore region of the shelf in proximity to the Mackenzie Delta and its plume can range from ~7 to 11.5 °C at the surface to ~1–7 °C at 10 m depth while temperature is nearly 0 °C at depths >20 m (Eert et al., 2012). Along the coast outside the influence of the Mackenzie Delta, freshwater inputs produce a relatively warm (~5–10 °C), and brackish (salinity = 10–25) (note, all reported salinity values in our manuscript were measured using the Practical Salinity Scale) surface water layer <0.5 km from shore adjacent to colder (~<6 °C surface temperature) nearshore marine areas ~0.5–2.0 km from shore (Craig, 1984; Harris et al., 2017). Nearshore waters are influenced by warmer freshwater run-off and landfast sea-ice that may remain in nearshore areas even when the offshore is ice-free. The extent and persistence of this warmer, freshened nearshore water mass depends on local river discharge, prevailing wind and surface currents, the prevalence of landfast ice and sea-ice floes, and presence of barrier islands and lagoon complexes (e.g., Harris et al., 2017). In contrast, offshore (~100 km) waters of the Canadian Beaufort Sea are characterized by deeper (>10 m), more stable and stratified waters (0–12 °C; salinity = 22–31 in the upper 0–15 m of the water column). In summer, the shelf area can still be mostly ice covered in July and August although it is typically clear of ice by September (Carmack and Macdonald, 2002; Howell et al., 2016).

2.2. Fish capture and tagging

Dolly Varden were captured as part of ongoing fisheries-independent population assessment studies in late September between 2014 and 2017 from spawning grounds in upper reaches of Big Fish River (68.3025°N; 136.3476°W) and Rat River (67.7558°N; 136.2935°W) watersheds, Northwest Territories (Fig. 1). Henceforth, tagged fish will be referred as belonging to the Big Fish River or Rat River populations. A long seine net was deployed to capture fish in shallow pools near perennial groundwater springs that were occupied by spawning and non-spawning (sexually immature or resting) Dolly Varden using the techniques described by Sandstrom et al. (2009) and Gallagher et al. (2013). Each fish captured in the seine net was measured for fork length (FL, nearest mm) and its current-year reproductive status (i.e., male spawner, female spawner, or non-spawner) was visually assessed and recorded (see DFO, 2017). Pop-up satellite archival tags (PSATs) (miniPAT; Wildlife Computers, USA; https://wildlifecomputers.com/our-tags/pop-up-satellite-tags-fish/minipat/) were attached to 20 Dolly Varden: 10 from the Big Fish (n = 1 in 2014; n = 9 in 2015), and 10 from the Rat River (2017) that ranged in FL between 565–645 mm and 555–693 mm, respectively. Data storage tags (DST; milli-TD and CTD; Star-Oddi, Iceland; https://www.star-oddi.com/products/data-loggers) were attached to 60 Dolly Varden from both the Big Fish (n = 30 in 2015; n = 30 in 2016) and Rat (n = 18 in 2016; n = 42 in 2017) rivers that were 430–550 mm and 420–715 mm FL, respectively. The number of PSATs deployed was mainly limited by budgetary considerations and expected reporting rates (see Musyl et al., 2011), whereas the number of DSTs deployed was based on cost and an ~10% probability of recapture after being at-large for one year estimated from previous multi-year mark-recapture studies using t-bar tags (inserted at base of dorsal fin) on Dolly Varden in the same river systems (Gallagher et al., unpublished).

2.3. Tag specifications and data acquisition

PSATs were externally attached to adult Dolly Varden >550 mm FL (Lacroix, 2014) using a "tag backpack system," previously used on salmonids (e.g., Strøm et al., 2017; Courtney et al., 2019), including Dolly Varden (Courtney et al., 2016a, 2018), following protocols described by Courtney et al. (2016b). Data storage tags (DST; milli-TD and CTD; Star-Oddi, Iceland; https://www.star-oddi.com/products/data-loggers) were externally attached to Dolly Varden >400 mm FL using methods described by Rikardsen and Thorstad (2006).

While attached to a tagged fish, PSATs were programmed to record temperature (±0.1 °C) for the entire duration of the ~9.5 month deployments and depth (±0.5 m) starting in early spring (April 1). Upon reaching the programmed pop-up date in mid-July, tags were designed to release from the fish, float to the sea surface, and transmit archived depth and temperature data (7–10 min resolution) to overhead satellites (Argos Satellite System) from which an end-location (first Argos Location Class 1–3, error <1.5 km) was determined. Mid-July was chosen as the programmed pop-up date because it was expected to represent the approximate time when tagged fish would be at their farthest geographic summer ocean feeding extent before migrating back to freshwater to spawn/overwinter (Bond and Quinn, 2013; Brown et al., 2019).

While attached to fish, milli-TD DSTs recorded temperature (±0.1 °C) and depth (±0.6% of depth range 0.1–50 m), while the CTD DSTs also recorded conductivity. DSTs were programmed to log data for one year with a 15–120 min logging rate from September to mid-June and a 4 min logging rate from mid-June to September, with the goal of collecting higher resolution data during the time when a fish would be expected to occupy marine habitats. Contact information was written on each DST for reporting purposes in case of recapture. Data from DSTs were only obtained in cases in which tagged fish were recaptured in subsistence fisheries or during the annual fisheries-independent seining program at the spawning and overwintering locations conducted in subsequent years.

2.4. Marine spatial distribution

End-locations (i.e., pop-up (PSAT) or recovery locations (DST)), dispersal distance, distance offshore, and comparisons of July tag-recorded SST and satellite-derived SST were used to provide insights into the marine spatial distribution of tagged Dolly Varden. Dispersal, considered to be the minimum (i.e., most direct path) marine displacement of each PSAT tagged fish, was determined by calculating the great arc circle distance (km) of a non-meandering route that did not pass over land between the Mackenzie Delta (approximate point of ocean-entry) and end-locations. Offshore distance was calculated as the minimum distance (km) between end-locations and the closest mainland location. In addition to known end-locations, 1–15 July tag-recorded SST (tag-temperature at depth <0.5 m) was qualitatively compared to mid-July satellite-derived SST (Table S1) to understand the likely spatial distribution and offshore extent of tagged fish. In these SST comparison analyses, satellite-derived SST isolines containing >90% of observed July tag-recorded SST were used as a metric to provide the likely mid-summer marine distribution of tagged fish in 2016, 2017, and 2018. No SST spatial analysis was conducted in 2015 because no tag data existed for the July time period (end-location date 27 June). Analyses of SST were particularly useful in discerning the likely summer distribution of Dolly Varden recaptures with archival tags (n = 2; 2017) that did not provide ocean end-locations. While these analyses did not provide fine-scale (e.g., daily) migration paths of tagged fish, they did impart information on the likely distribution in relation to shore, local sea-ice conditions and extent, the Tarium Niryutait MPA, and anthropogenic footprints (i.e., hydrocarbon lease areas and shipping lanes/areas of increasing shipping activity). Geospatial information on daily local sea-ice conditions obtained from MODIS satellite imagery (Table S1) during behaviorally-pertinent time periods (i.e., yearly median dates of ocean-entry, transitions between nearshore and offshore habitats, and extent of offshore occupation as inferred from individual tag records), were used to evaluate the relationships between sea-ice breakup characteristics and tagged fish behavior, habitat occupancy, and movement patterns. Images were also used to evaluate spatial extent of the turbid waters of the Mackenzie River plume on the day when PSATs reported. In cases where daily images for these time periods were not available due to extreme cloud cover and poor visibility, the nearest day with acceptable image quality was selected. Geospatial information for the Tarium Niryutait MPA, hydrocarbon lease areas, and shipping information was accessed from online databases (Table S1). Ship track data from the Protection of the Arctic Marine Environment's (PAME) Arctic Ship Traffic Data (ASTD) (all available Automatic Identification System locations from ASTD ship types under a Level 2 data sharing agreement) were obtained for a region encompassing the area south of the 72nd parallel (north) between the Alaska-Yukon border and Cape Bathurst between 2015 and 2018. All mapping and spatial analyses were conducted using Geographic Information System (GIS) software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California).

2.5. Marine habitat-use

Temporal patterns of depths and temperatures experienced by tagged fish were used to discern ocean-entry and periods of occupation of nearshore and offshore habitats within the Beaufort Sea following similar rationale detailed in previous telemetry studies (Teo et al., 2011; Nielsen et al., 2011; Hayes et al., 2012; Jensen and Rikardsen, 2012), including those on Dolly Varden occupying waters of the Chukchi and Beaufort seas (Courtney et al., 2016a, 2018). Ocean-entry of tagged fish was delineated as a rapid transition from the relatively warm (~12–14 °C) waters of the Mackenzie Delta (e.g., Ensom et al., 2012; Yang et al., 2014) to the cooler and more stratified waters of the Beaufort Sea (Fig. 2a; Carmack and Macdonald, 2002; Mulligan et al., 2010; Mulligan and Perrie, 2019; Harris et al., 2017). Occupancy of nearshore and offshore waters was delineated by relating depth and temperature experienced by tagged fish to known physical properties of these habitats (Carmack and Macdonald, 2002; Nghiem et al., 2014; Eert et al., 2012; Harris et al., 2017; Mulligan and Perrie, 2019). Specifically, nearshore waters of the Beaufort Sea during spring/early summer are characterized as shallow (<10 m), brackish (salinity = 10–25), and thermally dynamic (~<0–17 °C) (Harris et al., 2017). Therefore, after ocean-entry, periods when tagged fish were inferred to have occupied shallow (<5 m) depths with fluctuating surface water temperatures (~<0–17 °C) and exhibited low variability in diving behavior were considered nearshore occupancy (Fig. 2b). Inferred transitions to, and occupancy of, offshore waters was based on abrupt changes in diving behaviors and surrounding thermal environment (i.e., thermal structure and stratification of the water column), including occupancy of greater (>10 m) and more variable depths and oscillatory diving behavior in stratified waters with relatively stable daily surface temperatures (Fig. 2b). Additionally, end-locations were visually compared to imagery of the turbid waters from the Mackenzie River plume to qualitatively assess whether tagged fish inhabited areas with relatively high turbidity in mid-July.

Examination of sea-ice break-up timing and persistence of landfast ice in mid-June, and the spatial extent of the sea-ice margin and 5–10 °C SST isolines in mid-July were used to characterize each year (2015–2018) as either relatively 'cooler' or 'warmer' in open waters of the study area. Specifically, 'cooler' years were defined as those that had later sea-ice breakup, longer persistence of landfast sea-ice during spring, and 5–10 °C SST isolines with a sea-ice margin situated closer to shore during summer (mid-July), while the opposite conditions

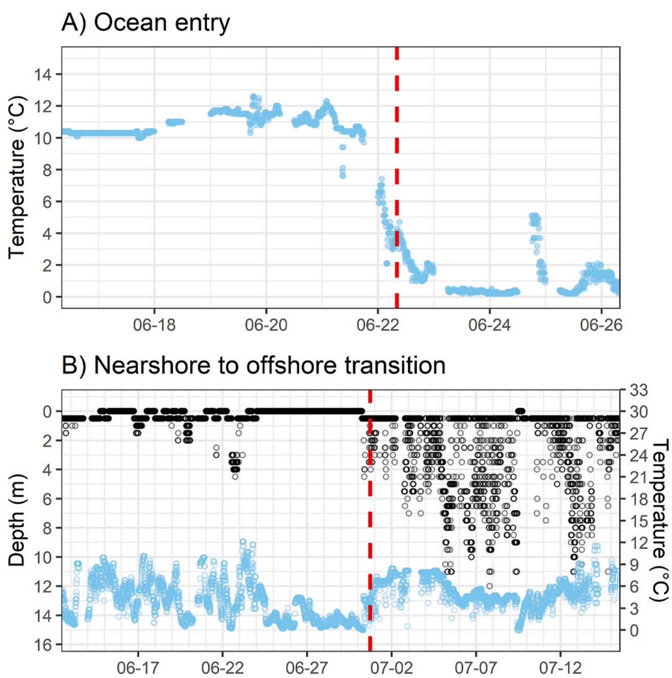

Fig. 2. Examples of A) inferred ocean entry and B) inferred transitions from nearshore to offshore habitats of the Beaufort Sea based on archival tagged Dolly Varden. Dashed red vertical lines denote A) inferred ocean-entry and B) transitions from nearshore to offshore waters in the Beaufort Sea. Blue and black circles denote temperature and depth data, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

characterized 'warmer' years. Years defined as 'cooler' included 2015 and 2018 while those defined as 'warmer' characterized years 2016 and 2017. It is noted that 2018 had a considerably heavy sea-ice cover in the Beaufort Sea compared to other years since the early 1990s (see Clarke et al., 2019).

After delineating timing of ocean-entry and inferring occupied marine habitats, the depths and temperatures of individual tagged fish were described by examining time-series plots, boxplots, descriptive statistics (range, mean ± SD), and the percentage of time spent at depth (depth bins = 0–1.9, 2–4.9, 5–9.9, 10–14.9, 15–20, >20 m). Furthermore, depth and temperature data from individual tagged fish were aggregated by marine habitat occupied (i.e., nearshore and offshore), year, and cooler and warmer years. Nonparametric Kruskal-Wallis tests were used to test for overall differences in distributions of occupied depths, temperatures, and July offshore tag-recorded SSTs among study years ($\alpha = 0.05$). If Kruskal-Wallis tests were significant, post-hoc Dunn's pairwise tests (Benjamini-Hochberg adjusted) was used to discern pairwise differences between years ($\alpha = 0.05$). A chi-square test was used to test whether the number of days spent in nearshore versus offshore habitat differed between cooler and warmer years.

3. Results

3.1. Available tag records

Of the 20 PSATs deployed, 13 reported to satellites from the Beaufort Sea on the programmed pop-up date in mid-July (n = 7 Big Fish River; n = 6 Rat River) (Table 1) while others either did not report and were considered missing (n = 3) or reported from freshwater (n = 4; Rat River) and were presumed to be attached to fish that may have died over the winter months. Of the 13 tags that reported from the Beaufort Sea, marine mortality (n = 5) was assumed if temperature and depth readings of tags indicated that the fish had suddenly sunk to the sea floor and remained at the same depth, similar to inferences of other satellite telemetry research (e.g, Lacroix, 2014; Seitz et al., 2019; Strøm et al., 2019). End-locations were excluded from dispersal analyses in three cases when tag data suggested that there was considerable drift between the location of the fish and the first reporting location of the tag (see Godfrey et al., 2015; Courtney et al., 2016b). Two DSTs (milli-TD) deployed in the Rat River in 2016 were recaptured in subsistence fisheries in fall of 2017 at locations associated with the freshwater migration corridor used by Rat River Dolly Varden (i.e., mouth of Rat River, Fig. 1) and were returned to Fisheries and Oceans Canada (Inuvik, Northwest Territories) (Table 1). In sum, tags in this study provided 421 days of depth and temperature data while fish were occupying marine waters: 18 days in 2015, 150 days in 2016, 104 days in 2017, and 150 days in 2018.

3.2. Marine spatial distribution

Of the fish with PSATs that provided accurate end-locations in the Beaufort Sea (n = 10), most (n = 9) were in offshore (37–152 km from mainland) waters mainly between the mouth of the Babbage River, Yukon Territory and Tuktoyaktuk, Northwest Territories (Fig. 1). The exception was one PSAT tagged fish from the Big Fish River (tag ID 14P0075) that performed a transboundary movement and reported from the Alaskan Beaufort Sea approximately 41 km offshore and northwest of the community of Kaktovik, USA (Fig. 1). The offshore extent (range = 37–152 km) and minimum at-sea dispersal (range = 132–298 km) of tagged fish varied by year and river system (Table 2, Fig. 1). In general, end-locations of tagged fish in mid-July were farther offshore in 2018 (60–152 km offshore where water column depth was 21–1,425 m) than in 2016 (37–104 km offshore where water column depth was 23–84 m) with minimum at-sea dispersal ranging from 157 to 217 km (median = 203 km) in 2018 as opposed to 132–298 km (median = 161 km) in 2016. The single PSAT reporting in 2015 presumably encountered a predator prior to the mid-July reporting date as the depth profile indicated the tag fell abruptly to sea floor on June 27, 2015. Therefore, the marine spatial distribution and depth/temperature information for this fish was based on and before, respectively the time when the tag fell to the sea floor.

The majority of PSAT end-locations (n = 8) were either along the edge of the sea-ice or among the floes close to the ice edge (<25 km), while some (n = 2) were found in open water south (~50–200 km) of the broken pack ice (expanse of large pieces of drifting sea-ice floating close together in a nearly continuous mass) (Fig. 3). End-locations were typically in relatively clear offshore waters adjacent to the turbid waters of the Mackenzie River plume (Fig. 3). While occupying offshore waters of the southeastern Beaufort Sea in July, significant differences in tag-recorded SSTs among the four years (Kruskal-Wallis test, $X^2 = 4636$, $p < 0.0001$) and between all pairs of years were detected (Dunn's test, all p-values <0.001) (Fig. S1). Occupied SSTs were coldest in 2018 (range of means = 4.0–7.3 °C in 2018) and warmest in 2016 (range of means = 8.3–11.5 °C) and 2017 (range of means = 8.4–8.6 °C) (Dunn's test, all p-values <0.001) (Fig. S1). Comparisons of July (1–15) tag-recorded SST and satellite-derived SSTs suggest extent of offshore occupancy by tagged fish during this period was similar to known end-locations (Fig. 3). While recaptured DSTs did not provide marine end-locations in 2017, the spatial distribution of tagged fish in mid-July 2017 was likely extended to offshore waters near the edge of the sea-ice based on comparisons of tag-recorded SST and satellite-derived SST (Fig. 3).

3.3. Marine habitat-use

Tagged Dolly Varden in the Beaufort Sea occupied depths of 0–96 m and experienced a thermal environment of −1.4–14.8 °C (Table 3; Fig. 4). The grand mean ± SD of depths and temperatures occupied by individual tagged fish were 2.5 ± 1.2 m and 5.8 ± 1.9 °C, respectively (Table 3, Fig. 4B and C). While at liberty, regardless of year, river origin, and distance from shore, Dolly Varden were highly surface oriented,

Table 1
Tag type and identification number, dates when tags were deployed and reported, biological information, date of ice break-up where ocean-entry occurred, date of ocean-entry, number of days at sea until reporting event, and estimated number of days spent inhabiting nearshore and offshore habitat (% in brackets) in the Beaufort Sea by archival tagged Dolly Varden from the Big Fish River and Rat River, Northwest Territories, Canada.

System[a]	Tag type[b]	Tag ID	Date deployed	Sex and reproductive status[c]	Fork length (mm)	Date of ice break-up[d]	Date of ocean-entry	Days at sea	Days spent nearshore	Days spent offshore	Date reported[e]
Big Fish R.	PSAT	14P0138	2014-09-26	Non-spawner	645	2015-06-06	2015-06-10	17.6	16.0 (90.9)	1.6 (9.1)	2015-07-15
	PSAT	14P0075	2015-09-23	Female spawner	615	2016-06-06	2016-06-19	26.4	3.6 (13.6)	22.8 (86.4)	2016-07-15
	PSAT	14P0129	2015-09-23	Non-spawner	620	2016-06-06	2016-06-16	20.3	0.8 (3.9)	19.5 (96.1)	2016-07-16
	PSAT	14P0130	2015-09-23	Female spawner	565	2016-06-06	2016-06-22	23.8	2.0 (8.4)	21.8 (91.6)	2016-07-16
	PSAT	14P0136[j]	2015-09-25	Female spawner	570	2016-06-06	2016-06-15	21.9	4.7 (21.5)	17.2 (78.5)	2016-07-15
	PSAT	14P0137	2015-09-23	Female spawner	590	2016-06-06	2016-06-13	32.3	2.6 (8.0)	29.7 (92.0)	2016-07-15
	PSAT	14P0139[j]	2015-09-23	Female spawner	570	2016-06-06	2016-06-15	24.2	4.8 (19.8)	19.4 (80.2)	2016-07-15
Rat R.	DST	M16097	2016-09-21	Female spawner	500	2017-06-08	2017-06-20	61.3[f]	2.3 (3.8)	59.0 (96.2)	2017-09-03[h]
	DST	M16100	2016-09-21	Female spawner	505	2017-06-08	2017-06-09	43.0[g]	9.2 (21.4)	33.8 (78.6)	2017-08-02[i]
	PSAT	17P0007	2017-09-27	Female spawner	595	2018-06-10	2018-06-26	19.1	9.3 (48.7)	9.8 (51.3)	2018-07-15
	PSAT	17P0013	2017-09-27	Female spawner	603	2018-06-10	2018-06-12	33.7	18.3 (54.3)	15.4 (45.7)	2018-07-16
	PSAT	17P0014	2017-09-27	Male spawner	607	2018-06-10	2018-06-18	27.0	7.1 (26.3)	19.9 (73.7)	2018-07-16
	PSAT	17P0015	2017-09-27	Female spawner	612	2018-06-10	2018-06-18	27.8	13.0 (46.8)	14.8 (53.2)	2018-07-15
	PSAT	17P0028	2017-09-27	Female spawner	666	2018-06-10	2018-06-22	23.7	4.3 (18.1)	19.4 (81.9)	2018-07-15
	PSAT	17P0030[j]	2017-09-27	Male spawner	693	2018-06-10	2018-06-15	18.8	14.5 (77.1)	4.3 (22.9)	2018-07-15

[a] At the spawning and overwintering area.
[b] Pop-up satellite archival tag (PSAT) and data storage tag (DST).
[c] Non-spawner (sex unknown; presumed to be sexually mature yet not spawning in current year), or female or male current-year spawner.
[d] At mouth of western channels of the Mackenzie Delta.
[e] PSAT: transmit to ARGOS satellites; DST: recaptured in fisheries.
[f] Exit Beaufort Sea on 2017-08-21.
[g] Exit Beaufort Sea on 2017-07-22.
[h] Recaptured at mouth of the Rat River (67.7595°N, 135.1389°W).
[i] Recaptured near hamlet of Aklavik (68.21293°N, 135.0977°W).
[j] No confident end-location data available for PSAT.

Table 2
Tag identification number, latitude and longitude of tag reporting location and depth of water column, minimum distance travelled in the Beaufort Sea, and distances of reporting locations from shore by pop-up satellite archival tagged (PSAT) Dolly Varden from the Big Fish River and Rat River, Northwest Territories, Canada[a].

Year	System	Tag ID	Latitude	Longitude	Depth of water column (m)	Minimum marine dispersal (km)[b]	Distance from shore (km)
2015	Big Fish R.	14P0138	N70.1190	W134.8650	33	152	48
2016	Big Fish R.	14P0075	N70.4400	W142.5860	57	298	41
2016	Big Fish R.	14P0129	N70.3010	W 137.7240	84	164	104
2016	Big Fish R.	14P0130	N70.2940	W135.7600	56	157	78
2016	Big Fish R.	14P0137	N69.9720	W135.1390	23	132	37
2018	Rat R.	17P0007	N70.7202	W135.5786	364	203	120
2018	Rat R.	17P0013	N70.3145	W134.4551	42	178	67
2018	Rat R.	17P0014	N70.3520	W135.8918	61	157	86
2018	Rat R.	17P0015	N70.7550	W137.5417	1425	210	152
2018	Rat R.	17P0028	N70.2664	W132.8793	21	217	60

[a] No confident location data available for PSAT tag ID 14P0136, 14P0139 (Big Fish R.), and 17P030 (Rat R.).
[b] Great arc circle distance travelled between reporting location and western Mackenzie Delta.

spending an average of 66% (SD = 15%) of their time within the top 2 m of the water column (Fig. 4A).

Tagged Dolly Varden were inferred to have entered the Beaufort Sea during the first three weeks of June (overall median = 16 June, range = 9–26 June) when tagged fish rapidly transitioned from the relatively warm (12–15 °C) waters of the Mackenzie Delta to cold (<0–4 °C) nearshore waters of the Beaufort Sea (Table 1; Fig. 2) adjacent to landfast sea-ice and sea-ice floes (Fig. 5). Annual median dates of ocean-entry were similar among years (within 8 days) and between river systems (within 3 days) (Table 1). Examination of satellite imagery taken in late-May and early-June revealed that median ocean-entry dates took place shortly (range of medians 5–10 days) after the channel mouths at

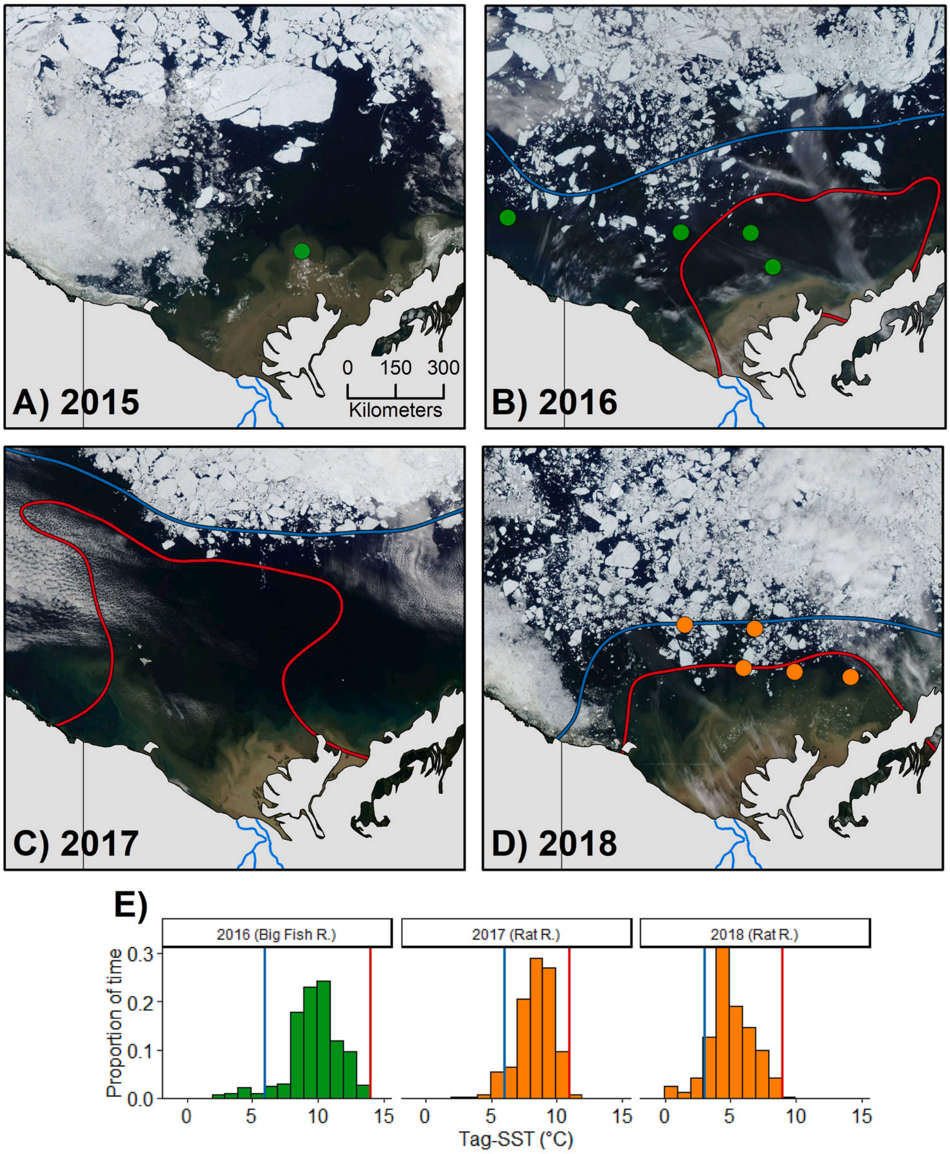

Fig. 3. Map of sea-ice conditions (MODIS satellite imagery) on A) 24 June 2015, B) 15 July 2016, C) 15 July 2017, D) 15 July 2018, and E) distributions of tag-recorded July (1–15) sea-surface temperature (SST) from archival tagged Dolly Varden from the Big Fish River (green colour) and Rat River (orange colour), Northwest Territories, Canada. Vertical blue and red lines in panel E denote intervals with >90% of July tag-recorded SST observations. Blue and red contours in panels A–D denote July 15 satellite-derived SST isolines (°C) (https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1) that correspond to dashed red lines in panel E. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the estimated point of ocean-entry (e.g., West Channel) were visibly ice-free (Table 1; Fig. 5).

After ocean-entry, tagged fish were inferred to have occupied nearshore habitats for 1–18 days in mid- to late-June before transiting to offshore habitats of the Beaufort Sea (Fig. 6, Fig. S2). While occupying nearshore waters, tagged fish spent the majority (88%) of their time in the top 2 m (grand mean ± SD = 1.4 ± 1.0 m) of the water column with occasional dives to >5 m (1.6% of observations) (Table 3). Temperatures experienced in nearshore habitats during mid-to late-June were generally cold with individual means ranging from 1.2 to 7.7 °C (grand mean ± SD = 4.4 ± 1.9 °C) in most years yet thermally dynamic in some cases (<0–15 °C) (Table 3; Fig. 4, Fig. S3). Observations of satellite imagery during times of inferred nearshore occupancy by tagged fish indicated that while some areas of the nearshore and offshore habitats within the Beaufort Sea were ice-free, large sheets of landfast sea-ice were still present adjacent to the Mackenzie Delta in all years (Fig. 5). Offshore depths inhabited by tagged Dolly Varden were, on average, slightly deeper (2.9 ± 0.9 m) compared to when nearshore (1.4 ± 1.0 m) (Table 3). While in offshore waters, tagged fish remained in the upper part of the water column (grand mean ± SD = 2.9 ± 0.9 m) where 54% of the detections were <2 m. In the offshore, vertical movements down to 5–15 m accounted for 28% of recorded depths among tagged fish while movements to depths >20 m were rare (<1% of observations) (Fig. 4). The grand mean (±SD) temperature experienced offshore was 6.3 ± 1.4 °C (Table 3).

While occupying nearshore waters, statistically significant differences in occupied temperatures were detected among (Kruskal-Wallis test, $X^2 = 1968.5$, $p < 0.0001$) and between all pairs (Dunn's test, all *p*-values <0.001) of study years (Fig. S3). Tagged fish experienced colder nearshore temperatures (grand mean ± SD) in cooler (2015 = 2.7 ± 2.9 °C; 2018 = 3.0 ± 1.6 °C) than warmer (2016 = 5.6 ± 1.2 °C; 2017 = 5.9 ± 2.1 °C) years. Occupied offshore depths were significantly different among (Kruskal-Wallis test, $X^2 = 178.8$, $p < 0.001$) and between (Dunn's test, all *p*-values <0.001) years (Fig. S3). Occupied offshore depths (mean ± SD) were deeper in warmer (2016 = 3.3 ± 4.3 m; 2017 = 4.1 ± 4.7 m) compared to cooler years (2015 = 2.9 ± 3.9 m; 2018 = 2.3 ± 3.1 m) (Table 3; Fig. 4; Fig. S3). The temperature differences detected among years appeared to influence the timing of movements from nearshore to offshore habitats. Although fish entered the ocean at similar times among all years, movement to offshore waters by tagged fish occurred earlier (median 20 June) during warmer years and later (median 30 June) during cooler years (Figs. 6 and 7). These differences

Table 3
Summary information on the depths and temperatures experienced by archival tagged Dolly Varden from the Big Fish River and Rat River, Northwest Territories, Canada while in the Beaufort Sea together with corresponding offshore sea surface temperature (SST). Mean ± SD and range in brackets of archival tag depths and temperatures were calculated based on the entire period while fish were inferred to be in the marine habitat and during each of the periods when they were inferred to be in nearshore and offshore habitats.

Year	System	Tag ID	Marine depth (m)	Marine temperature (°C)	Nearshore depth (m)	Nearshore temperature (°C)	Offshore depth (m)	Offshore temperature (°C)	July offshore SST (°C)
2015	Big Fish R.	14P0138	0.5 ± 1.4 (0–24)	3.1 ± 3.0 (−1.2–14.4)	0.2 ± 0.3 (0–6)	2.7 ± 2.9 (−0.1–14.4)	2.9 ± 3.8 (0–24)	6.4 ± 2.0 (−1.2–9.5)	NA
2016	Big Fish R.	14P0075	3.3 ± 4.5 (0–91)	7.6 ± 2.8 (−0.9–13.4)	2.0 ± 2.0 (0–8)	7.7 ± 2.3 (2.2–12.4)	3.6 ± 4.7 (0–91)	7.6 ± 2.9 (−0.9–13.4)	10 ± 2.0 (1.6–13.4)
2016	Big Fish R.	14P0129	4.5 ± 3.7 (0–22)	6.7 ± 2.6 (0.1–12.6)	2.8 ± 1.7 (0–10)	5.0 ± 1.0 (2–6.6)	4.5 ± 3.8 (0–22)	6.8 ± 2.6 (0.1–12.6)	10.7 ± 0.6 (9–12)
2016	Big Fish R.	14P0130	3.5 ± 3.5 (0–20)	8.9 ± 2.9 (−0.6–13.4)	3.7 ± 1.1 (0–6)	6.2 ± 0.1 (5.8–6.3)	3.5 ± 3.5 (0–20)	9.0 ± 2.9 (−0.6–13.4)	11.5 ± 1.1 (9.8–13)
2016	Big Fish R.	14P0136	2.5 ± 3.3 (0–39)	7.0 ± 2.8 (−1.1–11.5)	1.2 ± 1.8 (0–10)	4.2 ± 1.6 (0.3–5.9)	2.8 ± 3.5 (0–39)	7.5 ± 2.7 (−1.1–11.5)	10.3 ± 0.7 (8–11.5)
2016	Big Fish R.	14P0137	2.9 ± 4.4 (0–79)	7.0 ± 2.9 (−0.9–14.8)	2.6 ± 2.6 (0–9)	5.0 ± 0.7 (3–6.1)	2.9 ± 4.4 (0–79)	7.1 ± 2.9 (−0.9–14.8)	10.4 ± 2.4 (3.8–14.8)
2016	Big Fish R.	14P0139	2.6 ± 4.1 (0–69)	7.0 ± 2.2 (−1.1–12.1)	1.8 ± 2.4 (0–10)	5.7 ± 1.3 (1.8–10.1)	2.8 ± 4.5 (0–69)	7.4 ± 2.2 (−1.1–12.1)	8.3 ± 1.7 (2.4–10.3)
2017	Rat R.	M16097	4.5 ± 5.0 (0–32)	7.7 ± 2.2 (0–13.5)	0.8 ± 1.2 (0–10)	7.4 ± 2.6 (0.9–13.5)	4.7 ± 5.0 (0–32)	7.7 ± 2.2 (0–11.7)	8.9 ± 1.1 (5.6–11.4)
2017	Rat R.	M16100	2.9 ± 3.7 (0–34)	6.4 ± 2.2 (−0.7–11.6)	0.6 ± 1.0 (0–6)	4.4 ± 2.2 (0–9.9)	3.3 ± 3.9 (0–34)	6.7 ± 2.1 (−0.7–11.6)	8.8 ± 1.6 (1.6–11.6)
2018	Rat R.	17P0007	1.5 ± 2.0 (0–13)	3.3 ± 2.0 (−1.2–8)	1.2 ± 0.9 (0–5)	2.0 ± 2.4 (−1.2–8)	1.7 ± 2.5 (0–13)	4.2 ± 0.9 (0.6–6.3)	3.9 ± 0.6 (2–6.3)
2018	Rat R.	17P0013	1.1 ± 2.0 (0–12)	4.5 ± 2.5 (0–12.1)	0.3 ± 0.6 (0–5)	3.9 ± 2.8 (0–12.1)	2.2 ± 2.6 (0–12)	5.2 ± 1.8 (0–11.5)	5.2 ± 2.0 (0–10)
2018	Rat R.	17P0014	2.2 ± 3.9 (0–96)	4.5 ± 2.2 (−1.4–11.4)	0.8 ± 0.7 (0–6)	3.7 ± 3.5 (0.1–11.4)	2.8 ± 4.5 (0–96)	4.8 ± 1.3 (−1.4–8.2)	5.0 ± 1.3 (−0.4–8.2)
2018	Rat R.	17P0015	2.3 ± 2.2 (0–74)	2.9 ± 2.4 (−1.3–12.7)	2.0 ± 1.3 (0–7)	1.8 ± 2.7 (−0.9–12.7)	2.5 ± 2.8 (0–74)	4 ± 1.6 (−1.3–8.1)	4.2 ± 1.4 (−0.9–5.9)
2018	Rat R.	17P0028	1.9 ± 2.1 (0–13)	4.2 ± 2.1 (−0.3–8.9)	0.7 ± 0.2 (0–2)	1.2 ± 1.2 (0.2–5.1)	2.2 ± 2.2 (0–13)	5.1 ± 1.4 (−0.3–8.9)	5.2 ± 1.2 (2–8.9)
2018	Rat R.	17P0030	0.7 ± 1.1 (0–30)	5.6 ± 3.3 (−0.6–13.6)	0.3 ± 0.5 (0–7)	5.4 ± 3.7 (0–13.6)	1.7 ± 1.7 (0–30)	6.0 ± 1.6 (−0.6–8)	7.2 ± 0.7 (3.8–8)
Grand mean ± SD			2.5 ± 1.2	5.8 ± 1.9	1.4 ± 1.0	4.4 ± 1.9	2.9 ± 0.9	6.3 ± 1.4	7.8 ± 2.7

in movement timing directly affected the number of days of nearshore habitat-use between cooler and warmer years (Table 3, Fig. 6), with tagged fish spending significantly more time in nearshore versus offshore habitats in cooler (51.7% vs. 48.3%, respectively) compared to warmer years (12.6% vs. 87.5%, respectively) (Chi-square test, $X^2 = 72.5$, $p < 0.0001$).

3.4. *Spatial overlap with the marine protected area, hydrocarbon lease areas, and shipping routes*

No end-locations were found inside of the Tarium Niryutait MPA, although tagged fish presumably occupied the MPA when entering the Beaufort Sea and during transit to offshore waters. Ten PSAT end-locations were found either adjacent to (n = 6), or within (n = 4) hydrocarbon lease areas (Fig. 1). All end-locations were found within the network of known shipping routes for a variety of vessel types including tankers, cargo ships, and fishing vessels (i.e., the research fishing vessel *Frosti*; see Eert et al. 2012) (Fig. 8). Although overall levels of shipping through this region of the Arctic per year were relatively low (16, 15, 28, and 14 vessels passed through the study area in 2015, 2016, 2017, and 2018, respectively; PAME ASTD), comparison of activity levels over time (Dawson et al., 2018) show that the region of highest relative increase in shipping activity in the western Canadian Arctic coincides with Dolly Varden PSAT end-locations (Fig. 8).

4. Discussion

This is the first study to use archival tags to describe ocean-entry timing and marine feeding habitat-use and dispersal for anadromous Dolly Varden in the western Canadian Arctic, and provides a number of new findings on this species' ocean ecology and distribution. Dolly Varden migrating from the Mackenzie Delta use offshore yet shallow marine habitats during their summer feeding migrations. Furthermore, SST, sea-ice extent, and nearshore environmental factors likely influence offshore dispersal and habitat-use of Dolly Varden while feeding in the southeastern Beaufort Sea during summer. Offshore habitat-use by Dolly Varden directly overlaps with Canadian hydrocarbon lease areas and shipping activity both of which pose a previously undocumented risk to feeding habitat of this at-risk species in Canada. Although the Tarium Niryutait MPA affords no protection from resource extraction and exploration activities in offshore habitats, our findings indicate it may offer refuge to Dolly Varden during transition to offshore areas in spring.

4.1. *Ocean-entry timing*

Our study documented that timing of ocean-entry for Dolly Varden from the Rat and Big Fish rivers occurs in approximately mid-June. These findings are consistent with a four-year radio tagging study of anadromous Dolly Varden from the Canning River, Alaska, which also flows into the Beaufort Sea, approximately 425 km west of the Mackenzie Delta (Brown et al., 2019). The ocean-entry timeframe we observed was similar to the modal dates (June 7, 14, 17 in 2015, 2016 and 2017, respectively) and range of dates (predominantly June 5–21) reported by Brown et al. (2019), which coincidentally had two years of overlap with this study (2016 and 2017). Similarity in timing of both river movements and ocean-entry among anadromous populations in Canada and Alaska along the North Slope is not unexpected given that locations where river mouths drain into the Beaufort Sea are situated at similar latitudes (range ~68.8°–70.3°N; 167 km difference along ~600 km of coastline) and could experience similar timing in breakup of landfast ice even though the offshore pack ice north of the Mackenzie Delta tends to breakup 1–2 weeks earlier compared to other areas in the Beaufort Sea (Searcy et al., 1996).

While examples of studies comparing known dates of ocean-entry by anadromous salmonids with satellite imagery of sea-ice conditions in the Arctic are uncommon (see Hammer et al., 2021), our results provided

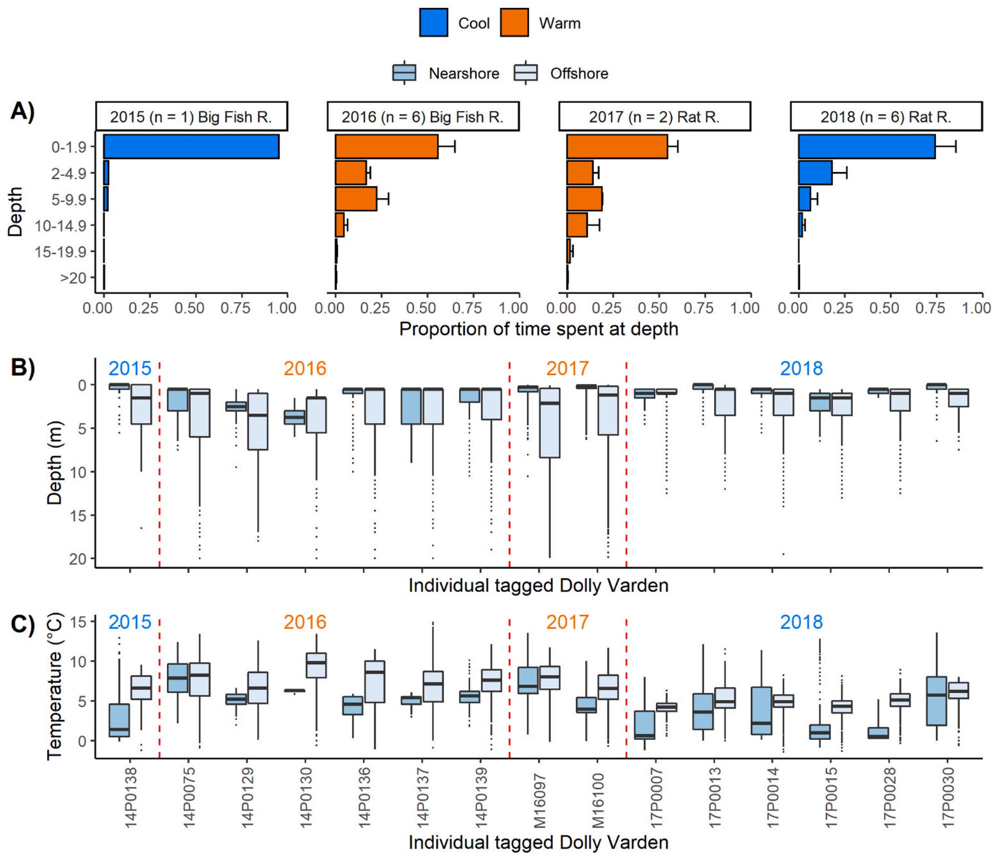

Fig. 4. Depths and temperatures in the Beaufort Sea experienced by archival tagged Dolly Varden from the Big Fish River and Rat River, Northwest Territories, Canada in the Beaufort Sea, by river system and year of deployment. Panel A) denotes the grand mean proportion of time spent at depth (m) among years. Whiskers represent the standard deviation of individual means. Panels B) and C) represent boxplots (median = thicker horizontal line, quartiles = boxes, 1.5 x interquartile range = whiskers, outliers = dots) of depth and temperature, respectively for each tagged Dolly Varden. Tag ID for B) and C) is noted on the x-axis of C).

strong evidence that timing of landfast sea-ice breakup is a key factor related to ocean-entry (e.g., Bégout Anras et al., 1999). Although the pack ice offshore of the Mackenzie Delta had already broken by early June, the presence of contiguous landfast ice just before ocean-entry in all years suggests the ice acts as a barrier (e.g., physical and/or thermal) limiting when Dolly Varden enter marine habitats for feeding. Subsequently, approximately 5–10 days before the median dates of inferred ocean-entry there were visible breaks in landfast sea-ice and open water (generally to the west of the Mackenzie Delta) near the channel mouths that was clear of ice in all years. While sea-ice breaks at the time of ocean-entry were similar among years, the extent of landfast ice adjacent to the mouth of the western Mackenzie Delta at time of ocean-entry appeared more widespread during relatively cooler (2015, 2018) than warmer (2016, 2017) years (Fig. 5). If the presence of an ice-free corridor in the landfast ice between the Mackenzie Delta and Beaufort Sea is an important determinant for the timing of ocean-entry, its development in spring and the eventual clearing likely vary annually depending on air temperature and wind conditions, and perhaps have ramifications on the ocean-entry timing of Dolly Varden. Further study of the interrelationships between the timing of both sea-ice break-up and migration timing by Dolly Varden is necessary given its effect on the bioenergetics of closely related anadromous Arctic Char (*S. alpinus*) (Harwood et al., 2013) and potential consequences associated with changing sea-ice conditions in the Arctic due to climate change (Wang and Overland, 2012; Stroeve et al., 2012).

4.2. Marine spatial extent and habitat-use

The results from this study provides the first documentation of extended offshore habitat-use of Canadian-origin Dolly Varden in the Beaufort Sea with evidence that summer offshore pack ice extent influences marine dispersal for this species. Our findings were generally consistent with those of Courtney et al. (2018) who demonstrated that PSAT tagged Dolly Varden in the Alaskan Beaufort Sea near Kaktovik (2015, 2016) occupied nearshore and offshore (up to 69 km) yet predominantly shallow (<2 m) depths in waters of typically 2–8 °C. Our results also corroborate observations from other satellite telemetry studies in the Chukchi Sea (Courtney et al. 2016a, 2016b, 2016b) suggesting Dolly Varden is not limited to nearshore waters as previously and commonly assumed (McCart, 1980; Craig, 1984; Bond and Erickson, 1989). Our results add to the large geographic extent of documented offshore habitat-use by Dolly Varden (i.e., Japan, Bering, Okhotsk, Chukchi, and Beaufort seas) (Morita et al., 2009; Courtney et al. 2016a, 2016b). However, tagged Dolly Varden in our study showed much greater northward offshore dispersal than previously shown in the Beaufort Sea with PSAT tagged fish dispersing greater than 40 km up to a maximum of 152 km offshore.

Our results suggest summer sea-ice extent influences summer marine dispersal of Dolly Varden. Specifically, the ice edge and adjacent cold waters (<0 °C; Harris et al., 2017) likely act as a barrier to offshore movements given the tendency for Dolly Varden to occupy shallow depths, even in pelagic habitat where they utilize the uppermost part of the water column, which in some instances could be shallower than the thickness (~1 m thick; see Galley et al., 2013) of floes near the pack ice edge. This contrasts with previous studies in the Beaufort (Courtney et al., 2018) that reported tagged fish with similar pop-up dates (approximately mid-July) did not show any affinity for waters near the pack ice edge. We hypothesize that the estuarine and warmer waters of the Mackenzie River plume extend the suitable habitat for Dolly Varden in proximity to Mackenzie Delta and likely allow for farther offshore dispersal in this region of the Beaufort Sea. While we do not have any direct evidence of the true marine spatial extent of two DST tagged fish (i.e., no pop-up locations), based on comparisons of tag-recorded and satellite-derived SST and the observed farther extent of the pack-ice margin (Fig. 3), these tagged fish likely dispersed much farther offshore compared to tagged fish in other years, including waters up to

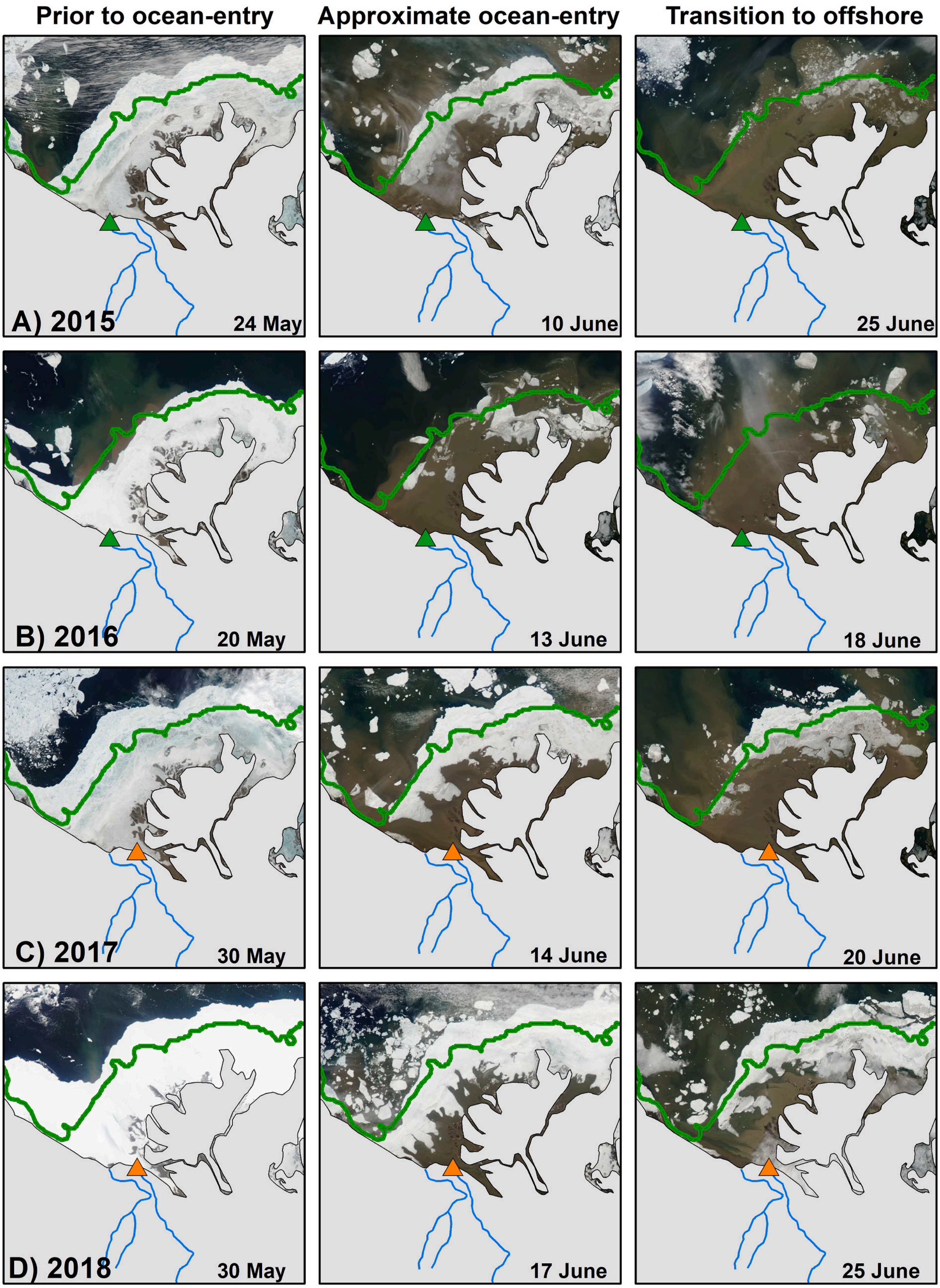

Fig. 5. Sea-ice conditions near the Mackenzie Delta during spring break-up in A) 2015, B) 2016, C) 2017, and D) 2018. Panels provide examples of observed sea-ice conditions near the Mackenzie Delta before tagged fish were inferred to have entered the ocean (left panels), near median date of ocean-entry (middle panels), and during median date tagged fish were inferred to transit from nearshore to offshore waters of the Beaufort Sea (right panels). Daily images of this data product were selected to avoid days of extreme cloud cover and poor visibility of local sea-ice conditions. Green line denotes 10 m bathymetric contour. Colored triangles indicate approximate point of ocean-entry for Big Fish River (green) and Rat River (orange) Dolly Varden. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

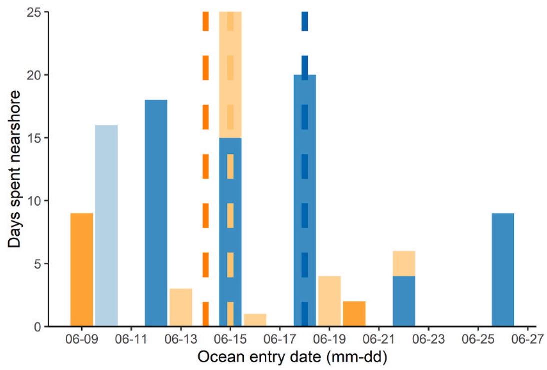

Fig. 6. Number of days spent in nearshore habitat of the Beaufort Sea by archival tagged Dolly Varden from the Big Fish River and Rat River, Canada among dates of ocean-entry and study years. Vertical dashed line is the median date of ocean-entry by tagged fish for a particular year.

>250 km offshore. The difference in the extent of distance from shore between the PSATs reporting in mid-July in 2016 (41–104 km) and 2018 (60–152 km) appears paradoxical given the lower proportion of time spent in offshore habitats during cooler (i.e., 2018) compared to warmer (i.e., 2016) years. However, this difference may be explained because the pop-up locations in 2016 may not represent the true maximum offshore extent of tagged fish. Furthermore, the differences in PSAT distances from shore between 2016 (Big Fish River) and 2018 (Rat River) suggest possible stock-specific differences in ocean-dispersal behavior. However, the low sample size along with the discrepancies in thermal conditions between 2016 and 2018 limits our ability to assess whether the stocks behave differently. More research is needed evaluate whether Big Fish River and Rat River Dolly Varden exhibit differences in the extent of their ocean dispersal, particularly given the distance of freshwater migration (i.e., distances travelled from natal streams and Mackenzie Delta) is considerably shorter for the Big Fish (~131 river km) than the Rat River (~317–345 river km).

Indigenous harvesters have long known sea-ice to influence the marine habitat-use of Dolly Varden (Benson, 2010; Harwood et al., 2012; WMAC and Aklavik HTC, 2018). Documentation of their traditional knowledge describes how Dolly Varden are more easily captured in harvesters' nets when sea-ice drifts or is blown closer to shore (Harwood et al., 2012). Furthermore, fish are reportedly more distant from shore in the absence of ice, moving in and out from shore in accordance with the sea-ice movements while feeding on pagophilic invertebrates (Benson, 2010; WMAC and Aklavik HTC, 2018). Stomach content analysis of Dolly Varden captured along the Canadian Beaufort Sea coast has detected the presence of ice-associated amphipods *Gammarus wilkitzkii* and *Onisimus glacialis* (Gallagher et al. unpublished), underscoring the link between Dolly Varden habitat-use and sea-ice. Indeed, the difference in the proportion of time spent in nearshore versus offshore habitats and its effect on mean depths occupied and temperatures experienced by Dolly Varden between generally cooler and warmer years not only reveals habitat-use plasticity in responses to marine conditions, but also raises questions regarding how climate change could affect fisheries. For example, given that years with higher SSTs resulted in Dolly Varden from both populations inhabiting warmer water temperatures, greater depths, and occupying offshore areas more often during summer, could future SST warming reduce the prevalence of nearshore habitat-use and decrease catch-rates of Dolly Varden in coastal subsistence fisheries?

Similar to sea-ice, the results of this study provides evidence that the turbid waters of the Mackenzie River plume influence the summer spatial extent of Dolly Varden. We posit that optimal offshore habitat for Dolly Varden in summer, particularly for the area north of the Mackenzie Delta, is situated between the ice margin to the north and the turbid plume to the south. Interestingly, if sea-ice and the Mackenzie River plume affect offshore movements near the Mackenzie Delta, wind patterns (e.g., speed and direction) could also be an important environmental factor regulating Dolly Varden dispersal in summer given wind is known to affect the extent and distribution of the plume (Carmack and Maconald, 2002; Mulligan et al., 2010). Easterly winds cause

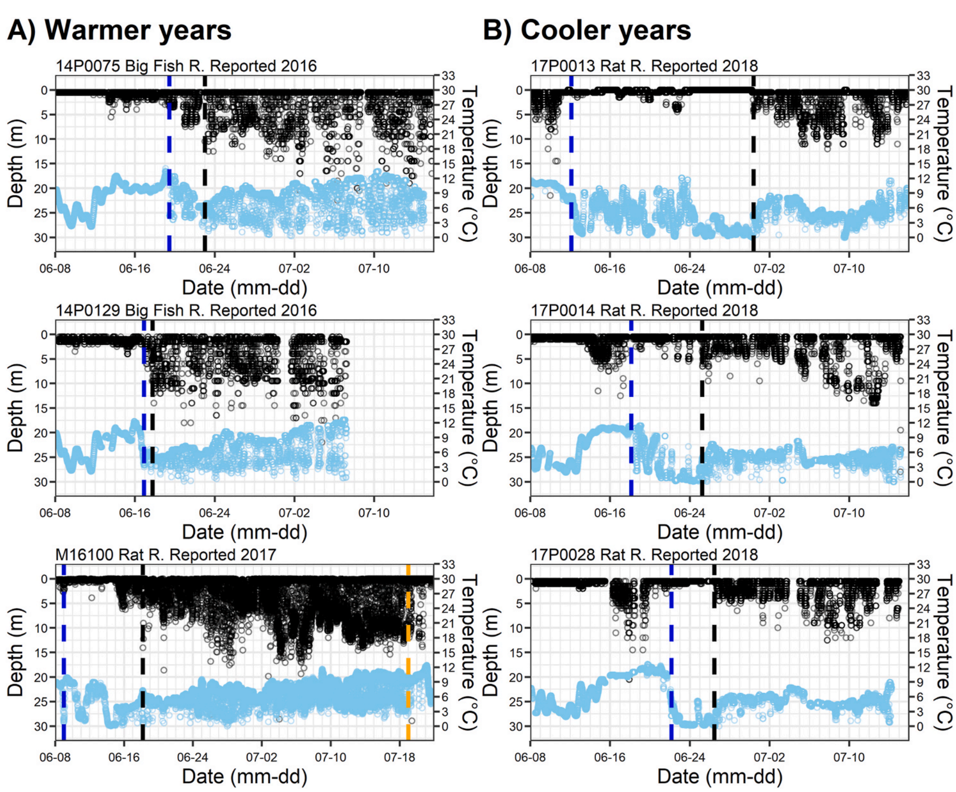

Fig. 7. Examples of temperature (blue circles) and depth (black circles) time-series data from pop-up satellite archival tags and data storage tags (DST) attached to Dolly Varden from the Big Fish River and Rat River, Northwest Territories, Canada in A) relatively warmer years (2016 and 2017) with earlier sea-ice break up (i.e., before June 16), and B) cooler years (2015 and 2018) with later sea-ice breakup in the southeastern Beaufort Sea. Dashed vertical lines indicate inferred ocean-entry (blue) (i.e., freshwater occupancy left of blue line), inferred movements between nearshore and offshore (black), and inferred movements from offshore to nearshore (orange). Tag ID, river system, and year is noted for reference purposes. Y-axis does not show depths >30 m because these accounted for <1% of observations. Note, x-axis extent differs for tag M16100, which was a recaptured DST with a greater time at liberty. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

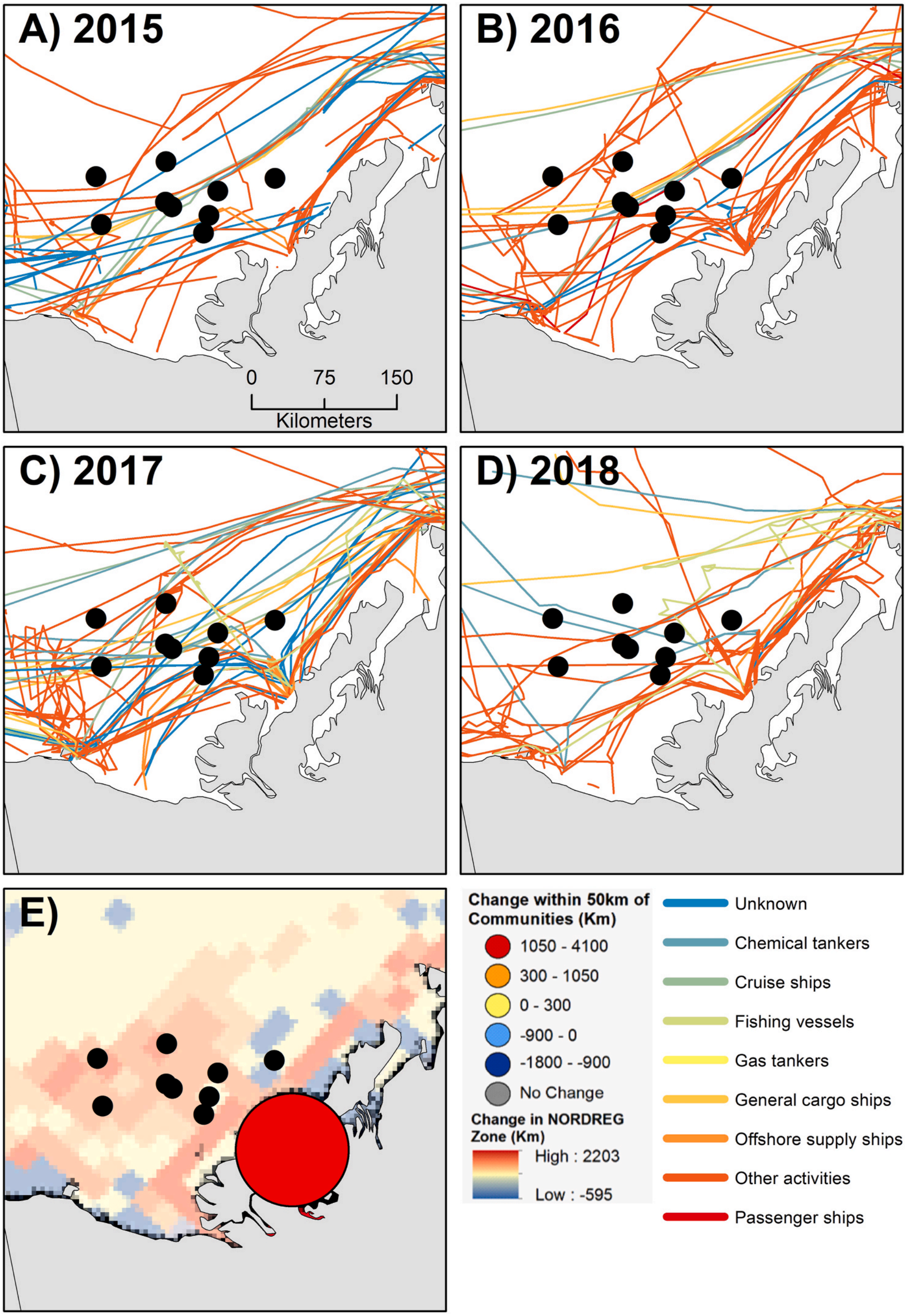

Fig. 8. Map of aggregated annual ship tracks among types of vessels that traversed the study area in the southern Canadian Beaufort Sea between the Alaska-Yukon Territory border and Cape Bathurst, Northwest Territories in A) 2015, B) 2016, C) 2017 and D) 2018 (source: Protection of the Arctic Marine Environment's (PAME) Arctic Ship Traffic Data (ASTD) database). E) denotes the change in vessel traffic within 25 × 25 km grid cells between a baseline (1990–2000) and later time period (2011–2015) in the southern Canadian Beaufort Sea illustrating changes in the sum of all voyage segment lengths within each cell over time (adapted from Dawson et al., 2018). End-locations of all pop-up satellite archival tagged Dolly Varden (black circles) reporting to satellites from the Canadian Beaufort Sea (n = 9) in mid July 2015, 2016, and 2018 are superimposed among study years to illustrate spatial overlap between fish habitat-use and shipping activity.

upwellings and extend the plume towards offshore areas (up to several hundred km) while westerly winds typically force plume waters against the coast (Carmack and Macdonald, 2002; Jerosch, 2013). Moreover, the preferred thermal habitats of Dolly Varden in the shallow depths of offshore waters would also be affected by wind given its influence on the SSTs of Polar Mixed Layer of the Beaufort Sea (Carmack et al., 1989; Majewski et al., 2017). Accordingly, this potential band of optimal offshore habitat observed in satellite imagery between 2015 and 2018 is likely highly spatio-temporally dynamic during summer and may even periodically disappear if sea-ice and turbid waters of the plume overlap. Further study is required to elucidate how the interrelationships among ice, turbidity, SST, and wind influences the marine habitat-use of Dolly Varden, which could help provide information on the movement ecology of other migratory salmonids in relative proximity to the large and complex Mackenzie Delta system.

Dolly Varden are known to be opportunistic foragers (McCart, 1980) whose patterns of occupied depths and vertical movements documented in our study likely reflect foraging behaviors shaped by the physical oceanography of the Beaufort Sea. While in the marine environment, most vertical movements were limited to the upper water column (to depth of <10 m) and those >15 m were uncommon even when occupying waters >100 m depth. Interestingly, the depth profiles of tagged Dolly Varden in this study closely followed the documented water column structure of the Mackenzie River plume (Carmack and Macdonald, 2002; Wood et al., 2013; Mulligan and Perrie, 2019). Conductivity, temperature and depth (CTD) transects of the Mackenzie River plume revealed a stratified (~<0–12 °C, salinity = 5–30) water mass with a thermocline of typically of 10–20 m in depth (depending on distance from shore) (Wood et al., 2013; Mulligan and Perrie, 2019), which is strikingly similar to the depths occupied by tagged fish in this study. Conducting short and shallow vertical movements in strongly stratified waters likely maximizes encounters with prey, which may be densely aggregated in surface waters during these time periods (Walli et al., 2009; Hedger et al., 2017) while also avoiding lethal cold (<−1 °C) (Fletcher et al., 1988) and high salinity waters (>32) found at greater depths (>~40 m; see Eert et al., 2012). While further research is needed to identify offshore diets (e.g., Volkov et al., 1996), stomach content analyses of Dolly Varden captured from coastal areas along the North Slope revealed the most frequent diet items were amphipods, mysids, and small fish (McCart, 1980; Gallagher et al., unpublished), which are common in the Canadian Beaufort Sea (Norcross et al., 2017).

Although our sample size was low, the amount of time spent feeding in the Beaufort Sea by the two Rat River Dolly Varden with DSTs (44 and 63 days at sea, Table 1) was consistent with those from the Canning River (Brown et al., 2019; range of median number of days in ocean among years = 40–51). Timing of return into freshwater and recapture of these two individuals (see Table 1) overlapped with dates when the population is harvested in fall fisheries in the Mackenzie Delta and Rat River (Gallagher et al., 2020).

4.3. Protection and threats

Our results suggest that the Niaqunnaq area of Tarium Niryutait MPA affords protection in estuarine habitat during a period of osmoregulatory stress for Dolly Varden that use the Mackenzie Delta for migration as they transition from freshwater to marine habitats in the approximately early to mid-June timeframe. The extent of nearshore habitat-use within areas of the MPA during summer requires additional study, however data from monitoring of the subsistence fishery for Dolly Varden at Shingle Point (Inuvialuktun name is Tapqaq) (see Gallagher et al., 2013) between 2011 and 2019 (~July to early-August) suggests a high amount of inter-annual variability in timing, duration, and relative abundance of catches (Gallagher et al., unpublished). Assuming the fishery in summer provides an indication of timing of nearshore occupancy by Dolly Varden at Shingle Point, the inter-annual variability could result from a combination of reasons including variation in movement among individual fish or return migration timing, and/or environmental conditions (e.g., wind, woody debris in water; Harper et al., 1988) affecting catchability of gill nets or distribution of fish (e.g., sea-ice and SST). Although there may be periodic summer-use of nearshore habitats depending on conditions, our findings clearly show the importance of offshore regions. Thus, future MPAs or Other Ecosystem Conservation Measures (Laffoley et al., 2017) in the Beaufort Sea that aim to include protection of pelagic habitats for Dolly Varden should consider areas that extend to at least 150 km from shore.

This first report of spatial overlap between Dolly Varden habitat and marine hydrocarbon lease areas and shipping corridors has implications for environmental assessment, industry regulation, and fisheries management in the Canadian Beaufort Sea, which implicates Alaskan populations that also perform transboundary movements (Krueger et al., 1999). In particular, our results help address gaps in knowledge of the distribution and habitat-use of this species required to assess impacts of anthropogenic activities in the Beaufort Sea during summer (see Kavik-Stantec, 2020). Although threats to Dolly Varden and other anadromous species from future exploration (e.g., seismic and test drilling) and possible extraction of hydrocarbons have long been recognized, these were based on the assumption that Dolly Varden marine habitats were predominantly coastal/nearshore. Direct spatial overlap with potential hydrocarbon activities places anadromous Dolly Varden in the Canadian Beaufort Sea at greater risk of cumulative effects including, but not limited to, seismic noise (Slabbekoorn et al., 2019) and bioaccumulation of contaminants such as polycyclic aromatic hydrocarbons (Pulster et al., 2020). In particular, Dolly Varden are also expected to be particularly vulnerable to offshore oil spills given their preference for inhabiting the uppermost part of the water column. Moreover, we assume that the PSATs reporting adjacent to lease areas would have likely travelled through these areas at some time during their ocean feeding, underscoring the extent of overlap between lease areas and Dolly Varden marine habitat. Given our confirmation that offshore habitat-use by Dolly Varden in the Canadian Beaufort Sea (west of Tuktoyaktuk Peninsula) overlaps with hydrocarbon exploration and shipping footprints, considerations for protecting feeding areas for this at-risk species in Canada are warranted.

Likewise direct overlap with areas of increasing shipping activities furthers the risk of exposure to additional pollutants including residuals from ballast water treatment (e.g., toxic free residual oxidants; Delacroix et al., 2013) and heavy fuel oil, a more viscous and toxic hydrocarbon used mainly by cargo vessels, tankers and cruise ships, all of which are increasing their footprint in Canadian Arctic waters, including along shipping routes through offshore feeding habitats of Dolly Varden (van Lujik et al., 2020). Shipping may also have impacts through mechanisms such as ship strikes and noise. Although studies on fish are relatively limited, strikes have been documented in some larger species (e.g., Schoeman et al., 2020) and negative effects of anthropogenic sounds on fish behavior (e.g., impedance of predator detection) and physiology are documented in a review of the impacts of rising underwater sound levels on fish by Slabbekoorn et al. (2010). Thus, potential exists for adding to the overall mortality in the marine environment. Indirect ecosystem impacts of shipping through introduction of invasive species in ballast and biofouling is well known, however these risks are expected to be relatively low under current climate and shipping levels in the Beaufort region (Goldsmit et al., 2019). Although low shipping activity should limit the above-described impacts of individual stressors, they will likely add to overall cumulative effects on mortality rates of Dolly Varden in the marine environment and be exacerbated under future scenarios of sea-ice loss and greater Arctic shipping activity (e.g., Stephenson et al., 2013).

Offshore fishing could provide a further source of mortality for Dolly Varden in the marine habitat; however, fishing activity has been relatively limited to date with no large or medium scale commercial fisheries (Ayles et al., 2016). Moreover, Dolly Varden would presumably not be vulnerable to potential offshore commercial fisheries if trawling gear is deployed in benthic habitats in the future.

4.4. Conclusions

Our study describes how the environmental conditions of SST, sea-ice extent, landfast ice and Mackenzie River plume properties in the Beaufort Sea are associated with ocean-entry timing, and marine dispersal and habitat-use of archival tagged Dolly Varden in Canada. Furthermore, we demonstrate previously undocumented offshore areas occupied by Canadian Dolly Varden overlapped spatially with the footprints of hydrocarbon exploration and shipping activities. Our study was limited by the low sample size of reported tags and the lack of information on smaller size (<500 mm) Dolly Varden, which could possibly exhibit differences in ocean-entry timing and propensity of offshore habitat-use compared to the sizes of fish we examined. Our results updating the geographical distribution of Dolly Varden in the Canadian Beaufort Sea in summer, and their proximity to Tarium Niryutait MPA and anthropogenic threats are useful for resource management and environmental regulators. Such information will improve assessment of impacts that future development activities may have on marine habitat of this at-risk and culturally important species. Given knowledge on occupation of offshore habitats gained from multiple recent studies, including ours, additional research is warranted to better understand environmental drivers influencing spatio-temporal habitat-use of Dolly Varden in marine waters. Climate change will continue to modify the extent and variability of sea-ice, among other physical and environmental conditions in the Beaufort Sea (e.g., see Park et al., 2020), which will likely alter nearshore and offshore dispersal patterns for Dolly Varden and may impact subsistence coastal fisheries. Our study characterizing ocean-entry timing and marine habitats of Dolly Varden contributes to knowledge that will support management, protection of marine habitats, and conservation measures for anadromous salmonids in Arctic marine environments.

Author contributions

CPG conceived archival tagging of Canadian Dolly Varden; CPG and KLH conceived the approach to the study; MBC and ACS provided technical guidance in application of pop-up satellite archival tags; CPG, ACS and EVL conducted the fieldwork; CPG and MBC analyzed the telemetry data, MBC analyzed the environmental data; KLH and MBC analyzed the shipping data; CPG, MBC and KLH wrote the manuscript, and all authors reviewed and edited it. CPG and KLH led proposals to secure funding for the study.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding was provided by Inuvialuit Final Agreement Implementation funds (Fisheries Joint Management Committee), Fisheries and Oceans Canada (Strategic Program for Ecosystem-based Research and Advice, and Species at Risk Funds), and Gwich'in Renewable Resources Board (Wildlife Studies Fund). In-kind support was provided by Natural Resources Canada's Polar Continental Shelf Program. We appreciate the assistance in the capture and tagging of fish by Frank Dillon, Lee John Meeyok, Danny B. Gordon, Freddie Furlong, Dennis Semple (Aklavik, NT), Kris Maier and Sarah Lord (Gwich'in Renewable Resources Board), Christie Morrison, and Shannon MacPhee (Fisheries and Oceans Canada), and safe flights provided by Great Slave Helicopters and Canadian Helicopters. We acknowledge the input, feedback and support provided by the West Side Working Group, Rat River Working Group, Aklavik Hunters and Trappers Committee, and Ehdiitat Renewable Resources Council. We thank Freddie Furlong (Aklavik) and Billy Wilson (Fort McPherson) for reporting data storage tags.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107609.

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