Ocean Migration and Behavior of Steelhead Kelts in Alaskan OCS Oil and Gas Lease Areas, Examined with Satellite Telemetry

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ABSTRACT

Although steelhead *Oncorhynchus mykiss* is an iconic species found throughout the North Pacific rim, little is known about this species' oceanic ecology. To provide insights into migratory routes and habitat occupied by steelhead in the North Pacific Ocean, we attached pop-up satellite archival tags (PSATs) to steelhead kelts (n=16 in 2018; n=12 in 2019, and n=35 in 2020) from a prominent population in the Situk River, Alaska. PSATs provided evidence of extensive post-spawning migrations extending to the western North Pacific Ocean and as far north as the central Bering Sea. Tagged steelhead mainly occupied continental shelf and slope habitats and occupied Outer Continental Shelf (OCS) planning areas throughout the Gulf of Alaska, the Aleutian Islands, and the Bering Sea. While at sea, tagged steelhead spent the majority of their time in surface waters (<5 m) and occasionally dived to 15–20 m but displayed no observable diel depth-based behaviors. Tagged kelts experienced a thermal environment of 4.3–16.0°C from June to January. Many steelhead kelts experienced mortality by predators, providing information on the timing and locations of natural mortality of this species while in the ocean. Results from this project corroborate past research that indicated steelhead predominantly occupy surface waters and that their distribution is largely influenced by sea-surface temperatures of ~5–15°C. Additionally, results from this study suggest that the waters near the Aleutian Islands are an important feeding ground for steelhead kelts from the Situk River and play a critical role in the successful reconditioning of repeat spawners in this population. The information gleaned from this study provides some of the first detailed insights into the oceanic ecology of steelhead and may be used for various applications, such as understanding interactions with human activities, including potential oil and gas exploration and extraction.

INTRODUCTION

Steelhead, the anadromous form of rainbow trout (*Oncorhynchus mykiss*), is an iconic species found across the Pacific Rim of North America and Asia from Baja California, Mexico to Alaska and across the Bering Sea to the Kamchatka Peninsula in Russia (Burgner 1992; Myers 2018; Quinn 2005). In Alaska, steelhead are found in over 300 watersheds and are targeted in recreational fisheries, particularly in Southeast Alaska (Harding 2008). The Situk River, located in southeast Alaska near Yakutat, sustains the largest steelhead population in Alaska and supports one of the most popular sport fisheries in the state. The recreational catch of steelhead in the Situk River averaged 8,495 individuals from 2015 to 2019 (Marston et al. 2012; Marston and Power 2016).

Steelhead spawn and rear in freshwater but feed in the ocean and are thought to make extensive oceanic migrations (Burgner 1992; Myers 2018; Quinn 2005). In southeast Alaska, steelhead typically rear in freshwater 2–5 years before migrating to the ocean as immature juveniles (Harding 2008; Lohr and Bryant 1999; Love et al. 2012). These immature steelhead typically spend 2–3 years feeding in the ocean before returning to their natal river to spawn (Catterson et al. 2020; Harding 2008). Most steelhead in southeast Alaska return to their natal river from March to May and are known as spring-run fish. Some stocks, or a subset of individuals in a stock, may return during November and December and are known as fall-run fish. Regardless of the timing of the return to freshwater, spawning takes place in the spring (April to early June), when water temperatures reach 6–9°C (Harding 2008). Unlike most anadromous salmonids, steelhead are iteroparous and can spawn multiple times within their lifetimes. After spawning, surviving adult steelhead (referred to as kelts) return to the sea to feed. In Alaska, the proportion of repeat spawners within a given spawning population can vary substantially year to year and by river system, but generally ranges between 11% and 38% (Harding 2008).

Little is known about the migration and behavior of steelhead while in the ocean, as there is a dearth of directed research on this species (Burgner 1992; Light et al. 1988; Myers 2018). Furthermore, because steelhead are less abundant than other Pacific salmon (*Oncorhynchus spp.*), they are infrequently encountered in the ocean, obscuring fine-scale information about their marine ecology (Myers 2018). As a result, the current understanding of steelhead oceanic migration and behavior is primarily inferred from the distribution of bycatch by commercial vessels and opportunistic capture and tagging during research on other species of Pacific salmon (Burgner 1992; Light et al. 1988; Myers 2018; Sutherland 1973). Available information suggests that immature juvenile steelhead from North America quickly migrate from freshwater to offshore waters of the North Pacific Ocean. After their first year at sea, ocean age-1 and older steelhead are distributed across the North Pacific but are concentrated in the southeastern Gulf of Alaska in the spring and expand westward and northward in the summer (Burgner 1992; Light et al. 1988; Myers 2018; Sutherland 1973). By fall and winter, steelhead distributions shift south and east into the southern Gulf of Alaska. Less information is known specific to kelts due to the differences in relative abundance between immature and mature steelhead. However, the migration of kelts is less extensive than that of immature steelhead even though adult steelhead kelts are distributed farther north than juveniles in the summer and have been documented as far north as the Bering Sea (Myers 2018). To date, population-specific migration patterns of North American steelhead remain highly speculative as they are based on a very small number of recovered tags, and insufficient genetics baselines exist to apportion individuals in high seas catches to individual stocks (Myers 2018).

Understanding the marine distribution of steelhead in the North Pacific Ocean is important for assessing the potential interactions between human activities and this fish species. Steelhead spend a large proportion of their lives at sea, making this species susceptible to marine environmental disturbances. Oil and gas exploration and development may eventually occur in offshore areas throughout the North Pacific Ocean, including the Gulf of Alaska, Aleutian Arc, and the Bering Sea. If steelhead occupy these areas, they may be exposed to habitat disturbance due to these human activities. Therefore, understanding steelhead's marine migration patterns and behavior can help identify potential anthropogenic impacts on this species to support informed resource management planning.

The goal of this study was to provide insights into the oceanic distribution, movements, behavior, survival, and thermal environment of kelts from the Situk River. Alaska's largest known population of steelhead. The objectives of this study were to examine (1) Outer Continental Shelf (OCS) planning areas occupied by steelhead kelts during their oceanic migrations; (2) timing of kelt presence, duration of occupation, and movement rate within a given planning area; (3) depths occupied by migratory steelhead to determine the potential exposure risk to a catastrophic event such as an oil spill; (4) relationships of steelhead movements to environmental correlates including temperature and current patterns; and (5) potential mortality events.

METHODS

Study site

The Situk River, near Yakutat, Alaska, sustains the largest steelhead population and steelhead sport fishery in Alaska (Figure 1). Since 1995, the Alaska Department of Fish & Game (ADFG) has constructed a bipod and picket weir located on the Situk River, approximately 2.4 km upstream from the ocean, to estimate the number of emigrating steelhead kelts and other species of Pacific salmon (Marston et al. 2012; Marston and Power 2016). The weir apparatus, erected annually, spans the entire river (~25-m width depending on discharge level) and contains upstream and downstream gates and a holding pen (~2 x 4 m). Typically, both gates are only opened during the daily period of peak steelhead emigration (0000–0400), and fish passage is quantified using underwater video cameras and artificial lights. During periods of high fish passage, ADFG intermittently traps fish by shutting the downstream and upstream gates independently. Captured steelhead are then moved to an adjacent holding pen using padded nets, and the weir gates are reopened to allow for continued fish passage. At approximately 0700 on the morning after capture (when there is sufficient ambient natural light), steelhead are retrieved from the holding pen using a smooth, knotless dipnet, and ADFG employees sample each fish for age (scales), sex (morphology), and total length (cm) (Marston et al. 2012; Marston and Power 2016).

Figure 1. Map of the study area, including the tagging site (inset) on the Situk River, AK.

Fish capture and tagging

During ADFG's annual steelhead sampling program, 63 fish were selected and satellite-tagged in late May to early June of 2018 (n=16), 2019 (n=12), and 2020 (n=35). Immediately after conducting ADFG's sampling protocol, steelhead were visually assessed for health based on external appearance and vitality, and the healthiest individuals were selected for tagging. Selected fish were placed in a custom fabricated cradle and blindfolded to reduce visual stimuli that can contribute to stress and struggle. Satellite tags were attached to steelhead using an attachment system (known as a "tag backpack") refined for similarly-sized salmonids, including Dolly Varden char (Courtney et al. 2016b), Chinook Salmon (Courtney et al. 2019), and Atlantic salmon (Strøm et al. 2017). The tag backpacks were secured through the dorsal musculature and pterygiophores, anchoring in the bony fin-ray supports. Only steelhead kelts longer than 60 cm were tagged to ensure that the trailing antenna of the tag would not interfere with the tail during swimming and to ensure that the tags were <2% of the bodyweight of the fish, a commonly accepted minimum size threshold for fish tagging (Brown et al. 2010). After tagging, steelhead were identified by tag number, photographed, and released to continue their downstream migration.

Data from a pilot study in 2018 indicated that several steelhead (n=5) suffered mortality in freshwater; therefore, in 2019 and 2020, tagged fish were temporarily held in the weir pen structure and released in the evening after dark to mimic their natural river outmigration behavior. Only female kelts were selected for tagging during the first two tagging seasons, as they have higher post-spawn survival rates than males (Evans et al. 2008; Keefer et al. 2018; Keefer et al. 2008). However, in the last year of tagging, which had a relatively large sample size (n=35) compared to previous years, four healthy males were also tagged to ensure all tags were deployed.

Ethical handling permits

All fieldwork was conducted under the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance 1536554 and Alaska Department of Fish and Game Regional Operation Plan: Situk River Steelhead Stock Assessment (ROP SF.1J.2018.04).

Tag specifications and data acquisition

Satellite tags were Pop-up Satellite Archival Tags (PSATs; MiniPAT model, Wildlife Computers; Redmond, WA; https://wildlifecomputers.com/our-tags/minipat/) that weighed 60 g in air and were slightly buoyant. While attached to a fish, the PSAT measured and archived temperature, depth, and ambient light data at user-programmable intervals, typically every 1–3 seconds. After releasing from the fish, the tags floated to the surface and transmitted, via satellite (Argos Satellite System), summarized temperature and depth data (resolution 2.5–7.5 min in this study), daily dawn and dusk times, and an end location (Keating 1995). In this study, PSATs were programmed to release at staggered intervals of 30 (n=4), 60 (n=3), 90 (n=2), 120 (n=3), 180 (n=33), and 240 (n=18) days post-deployment. Additionally, tags were programmed to release before their scheduled pop-up date if they triggered a fail-safe mechanism by remaining at a constant depth (±2.5 m) for a pre-defined period (7 days), or if the tag recorded depths >1,700 m (to avoid extreme pressures that could damage the tag). PSAT fail-safe release mechanisms activated upon dive >10 m, indicating that the tagged steelhead had left freshwater.

Data analyses

The fates of individual steelhead were classified based on visual examination of depth, temperature, and light data. Steelhead whose tags recorded consistent depth and temperature data "typical" of steelhead were considered alive at the pop-up date. Other fates were assigned to steelhead whose tags recorded suspicious and anomalous readings inconsistent with those "typical" of steelhead. Specifically, unidentified mortality was inferred when tag data suggested that the tagged fish died and sank to the seafloor or >1700 m (defined as "sinkers" in this study) before the tag detached from the carcass, floated to the surface, and transmitted data to satellites (Lacroix 2014; Seitz et al. 2019; Strøm et al. 2019). As with previous studies (Lacroix 2014;

Seitz et al. 2019; Strøm et al. 2019), predation was inferred from anomalous depth (i.e., abrupt change in depth-based behavior), temperature (abrupt increase above ambient), and/or light intensity readings (complete darkness during periods of daytime). In cases of inferred predation, it was assumed that a predator consumed both fish and tag, with the tag remaining in the predator's alimentary tract for days to months before being expelled and floating to the surface of the ocean. Likely predators were identified by qualitatively comparing known (published) species-specific visceral temperature and distribution data with stomach temperatures and diving behavior recorded by consumed tags. The depth record before inferred predation was used to determine whether a predator ate a live steelhead or scavenged a dead carcass. Depth data were visually inspected to determine whether the tag appeared to be attached to a sinker before consumption (Strøm et al. 2019).

Tag end locations (i.e., the first location reported to satellites) were mapped in GIS software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California) to assess the horizontal movement of tagged fish. Additionally, individual most likely movement paths were reconstructed using a hidden Markov model (HMM) (Wildlife Computers 2015). This state-space model was designed specifically for MiniPATs and uses observations of twilight, sea surface temperature (NOAA OI SST V2 High Resolution), and bathymetry (ETOP1-Bedrock; https://www.ngdc.noaa.gov/mgg/global/) to generate time-discrete and gridded (0.25° by 0.25°) probability surfaces to estimate the most likely daily positions of an animal (Wildlife Computers 2015). All default settings were used, and a maximum daily swim speed of 100 $km \cdot day^{-1}$ was assumed in all individual models. Estimated daily positions were assigned to Outer Continental Shelf planning areas, and the total number of fish-days in each planning area was determined.

Time-series data for occupied depth and temperature were visually inspected to provide insights into the behavior and thermal environment occupied by tagged steelhead. Only data from tags attached to live steelhead were used for depth and temperature analyses. Descriptive statistics (mean, minimum, maximum, standard deviation) were calculated for data from each tag and all aggregated data. Additionally, the grand mean proportions (±SD) of time that tagged steelhead spent at depth (0–2, 2–5, 5–10, 10–15, 15–20, >20 depth bins) and temperature (1°C bins) intervals were calculated for aggregated data and for each year of the study. Daily periods of night (nocturnal) and day (diurnal) were determined for each tag record (http://aa.usno.navy.mil/data/docs/RS_OneDay.php) at the daily estimated location of each tagged fish to examine diel differences between occupied depths. Median depths occupied during periods of night and day, and among hours of the day were examined qualitatively.

Marine survival of tagged fish was assessed using a Kaplan-Meir survival estimator to calculate survivorship rates (±95% confidence intervals). In this analysis, mortality was considered as the sum of mortality ascribed to inferred predation and unidentified mortality events. We used a time-since-release timescale in which tagged fish entered the model on the day of ocean-entry (considered day 0) as determined by identifying obvious changes in water temperature caused when each fish left the river (Courtney et al. 2016a; Hayes et al. 2012; Nielsen et al. 2011; Teo et al. 2013). Survivorship was then estimated across the monitoring period. Individual fish exited the model upon mortality (predation or unknown) or were right-censored when a tag detached from a live steelhead (Benson et al. 2018; Fieberg and DelGiudice 2009).

RESULTS

Summary

The total length of steelhead tagged ranged from 63.0 to 93.8 cm (Table 1). The majority (59/63) of PSATs reported to satellites and provided pop-up locations. One tag was recovered from the lower Situk River before data transmission was initiated, and three tags never transmitted and were never recovered. Of the 59 tags that transmitted data, 15 reported from shore adjacent to the Situk River, and 44 reported from marine waters. Of these 44 tags, 10 were inferred to have been ingested by marine predators, 20 were sinkers and suffered unknown mortality, and 13 released from live steelhead and reported to satellites before their programmed pop-up date, and 1 released from a live steelhead and reported to satellites on its programmed pop-up date. Only data from 30 tags with greater than two weeks of marine data (i.e., ocean entry to end date; Table 1) were used to analyze marine migration and behavior. These 30 tags provided a total of 2,034 days of data (mean 68±51 data days per tag).

Table 1. Deployment and reporting information for 63 pop-up satellite archival tags attached to steelhead in the Situk River in 2018, 2019, and 2020.

Year	Total length (cm) mean±SD (range)	Tags deployed (n)	# tags provided data on timing of ocean entry	# tags provided > 14 days of marine data
2018	76.1±7.3 (65.5–93.8)	16	6	4
2019	79.5±4.1 (74.0–87.0)	12	10	5
2020	74.7±5.6 (63.0–84.5)	35	28	21
Totals	75.9±6.0 (63.0–93.8)	63	44	30

Spatial distribution

The end locations of the tagged steelhead (n=30 used in marine analyses) were all west of the Situk River, AK. End locations occurred throughout the northern Gulf of Alaska, the Aleutian Islands, and into the Bering Sea as far west as ~650 km east of the Kamchatka Peninsula, Russia (Figure 2). Based on depth and temperature records, the tagged steelhead exited Situk River from 31 May to 10 June, on average 3.2 days after release (±1.1 SD; range 0.6–5.9 days). After ocean entry, the steelhead quickly dispersed westward across the Gulf of Alaska in the Alaska Current and Alaska Stream while remaining near the continental slope (Figure 2). By the end of July, most were located near 160°W longitude, south of the Alaska Peninsula. Steelhead with tags still attached past July (n=15) continued to progress in a westerly direction until fall (September–November). Movement patterns of tagged steelhead were similar among years (Figure 3). Based on daily location estimates, track lengths of tagged steelhead ranged from 205 to 3,816 km (mean 1,440±1,087 km).

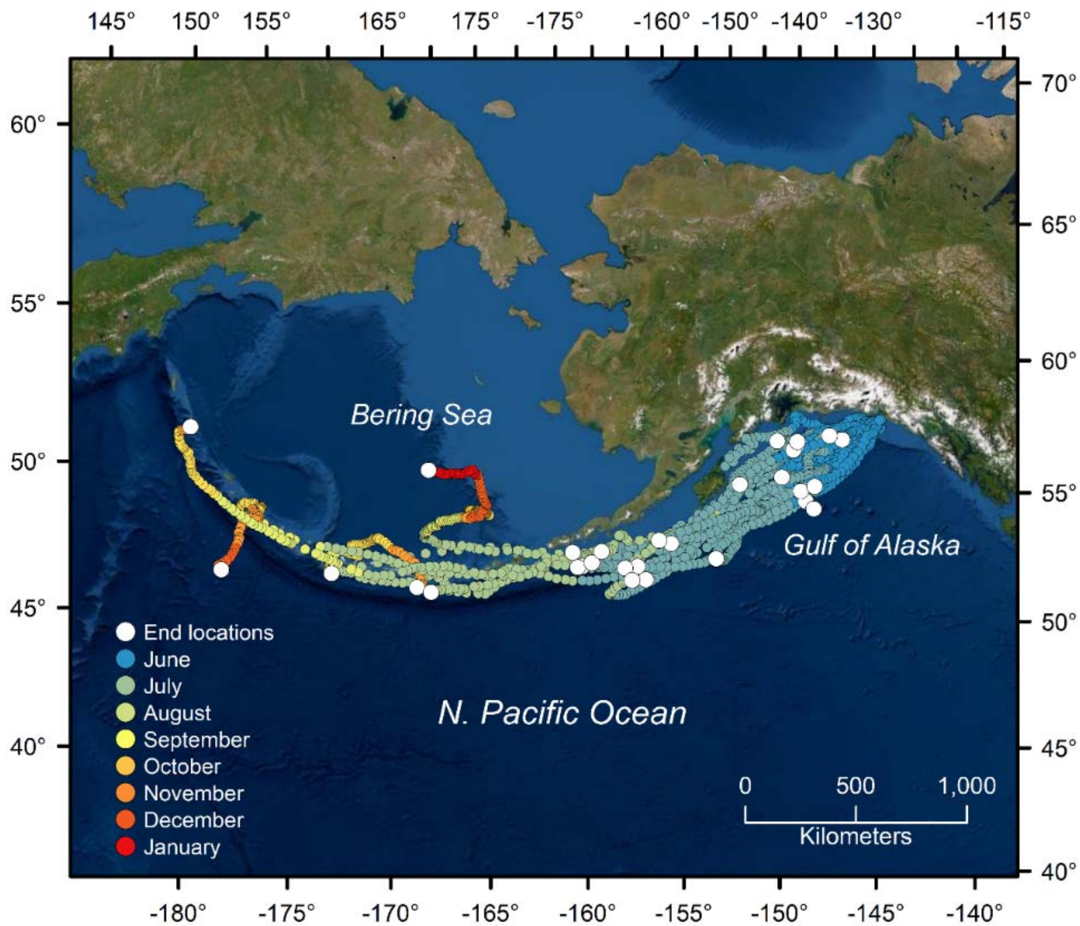

Figure 2. End locations of satellite tags (white dots) attached to steelhead from the Situk River, 2018-2020. Circles color-coded by month denote daily locations of tagged steelhead estimated from a Hidden Markov Model.

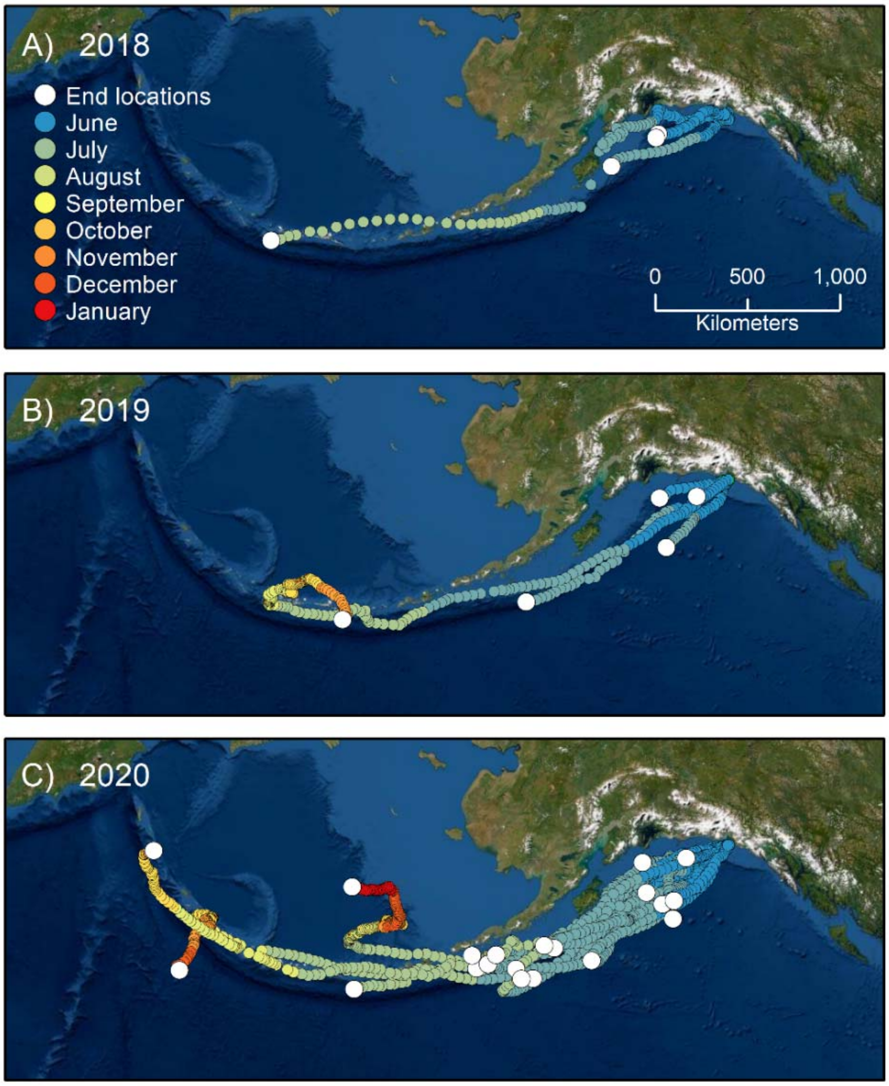

Figure 3. End locations of satellite tags (white dots) attached to steelhead from the Situk River by year: (A) 2018, (B) 2019, and (C) 2020. Circles color-coded by month denote daily locations of tagged steelhead estimated from a Hidden Markov Model.

Depth and temperature occupancy

Tagged steelhead were largely surface-oriented while occupying oceanic waters of the North Pacific Ocean from June to January, spending >80% of their time in the first 5 m of the water column (2.5±1.4 m, grand mean±SD) (Figure 4). Diving behavior varied among individual fish, and dives to 5–10 m were common (Figure 4; Figure 5). Although the majority of tagged steelhead (n= 28/30 used in analyses) recorded dives >20 m, these dives were rare, accounting for <0.01% of depths recorded. Maximum dives ranged up to 134 m, with 16 steelhead recording depths >50 m. The deep dives were very rare (<0.0001% of all records) and appeared to occur during short bouts of <15 minutes (Figure 6). Overall, depth distributions of tagged steelhead were similar among years (Figure 4).

While occupying marine waters from June to January, tagged steelhead experienced a thermal environment of 4.3–16.0°C and experienced a similar thermal environment between years of this study (Figure 4). Mean temperatures experienced by individual fish were 8.4–12.7°C (11.6°C±1.1; grand mean±SD). Aggregated data suggests they spent 67% of the time between 9 and 13°C.

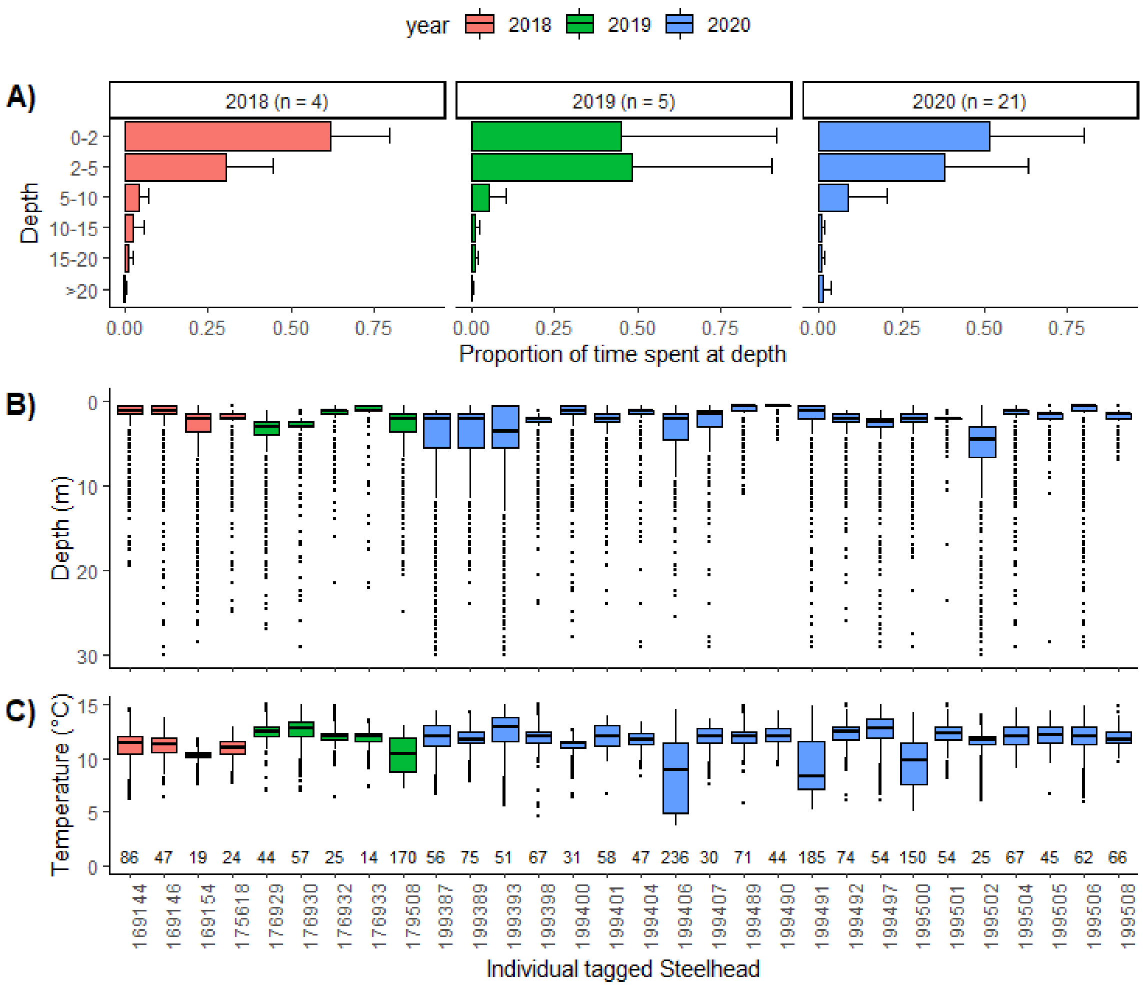

Figure 4. Marine depths and temperatures experienced by Situk River tagged steelhead. Panel A denotes the grand mean proportion (±SD) of time spent at depth (m) by study year. Panels B and C are boxplots of depth and temperature occupied by individual tagged steelhead. Tag identification numbers for individual steelhead in panels B and C are below the x-axis of panel C. Marine data days for each tag are noted above the x-axis of panel C. For boxplots, median depths and temperature are solid lines, and boxes represent the first and third quartiles. Whiskers represent the largest observation less than or equal to the box, plus or minus 1.5 times the interquartile range, and black dots represent outliers.

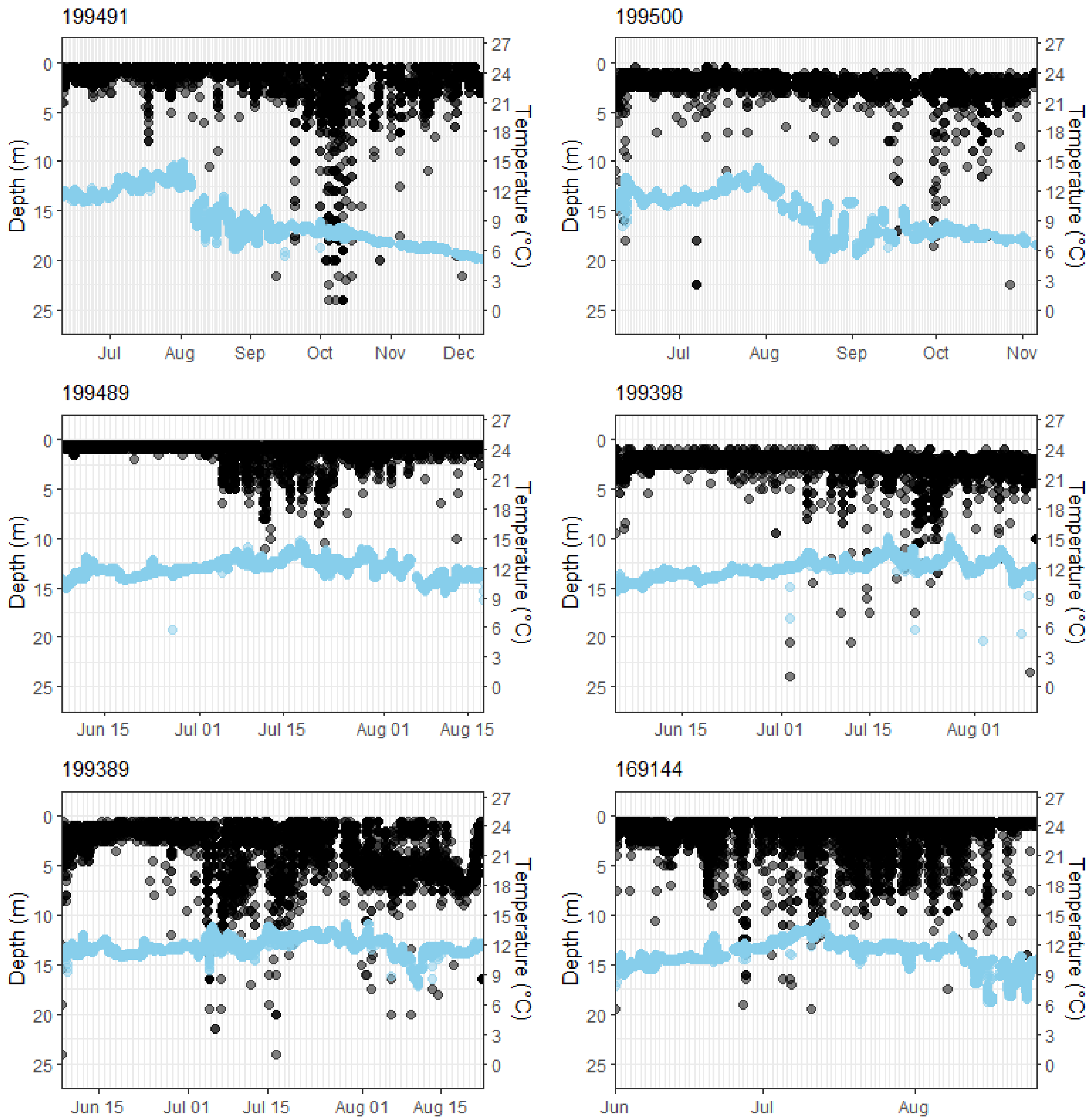

Figure 5. Examples of time-series data from pop-up satellite archival tags attached to steelhead from the Situk River. Black circles denote depth measured by the tag, and blue circles denote temperature. Tag identification numbers are noted for reference purposes.

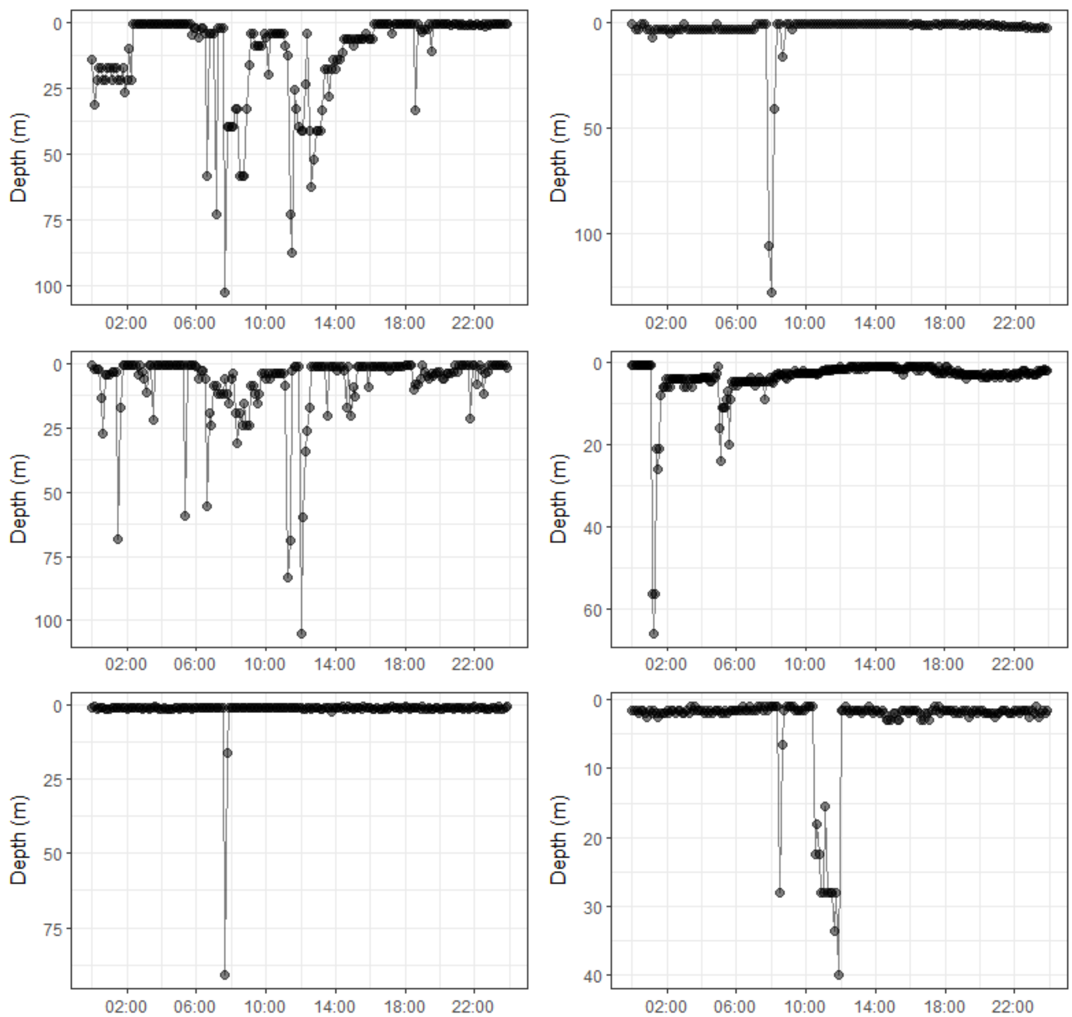

Figure 6. Examples of daily (GMT) deep diving activity by tagged steelhead from the Situk River.

While the amount of data from tagged steelhead was not equal among months, there were few observed differences in seasonal depth distributions. All monthly aggregated median occupied depths were <2.5 m (Figure 7a). In contrast, the thermal environment of steelhead varied seasonally. Generally, tagged steelhead experienced relatively warm and stratified waters from June to August, after which the thermal environment became cooler and more isothermal (Figure 7b).

There were no observable differences in diel depth occupancy of tagged fish in time series data, depth distributions between night and day, or by the hour of day (Figure 8a,b). Though median depths were similar between hours of the day, there was a tendency for deep dives (>35 m) to occur at night (Figure 8c).

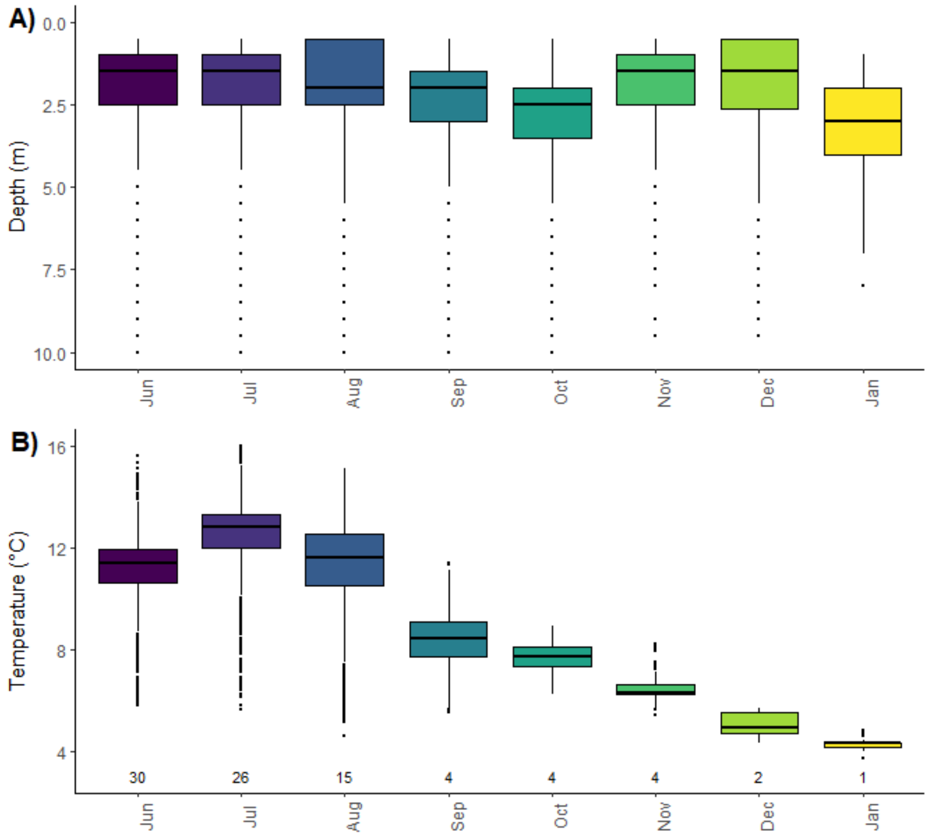

Figure 7. Depth (A) and temperature (B) distribution of tagged steelhead from the Situk River (n=30; all data aggregated) by month. Sample size (satellite tags per month) is noted above the x-axis. For boxplots, median depths and temperatures are solid lines, and boxes represent the first and third quartiles. Whiskers represent the largest observation less than or equal to the box, plus or minus 1.5 times the interquartile range, and black dots represent outliers.

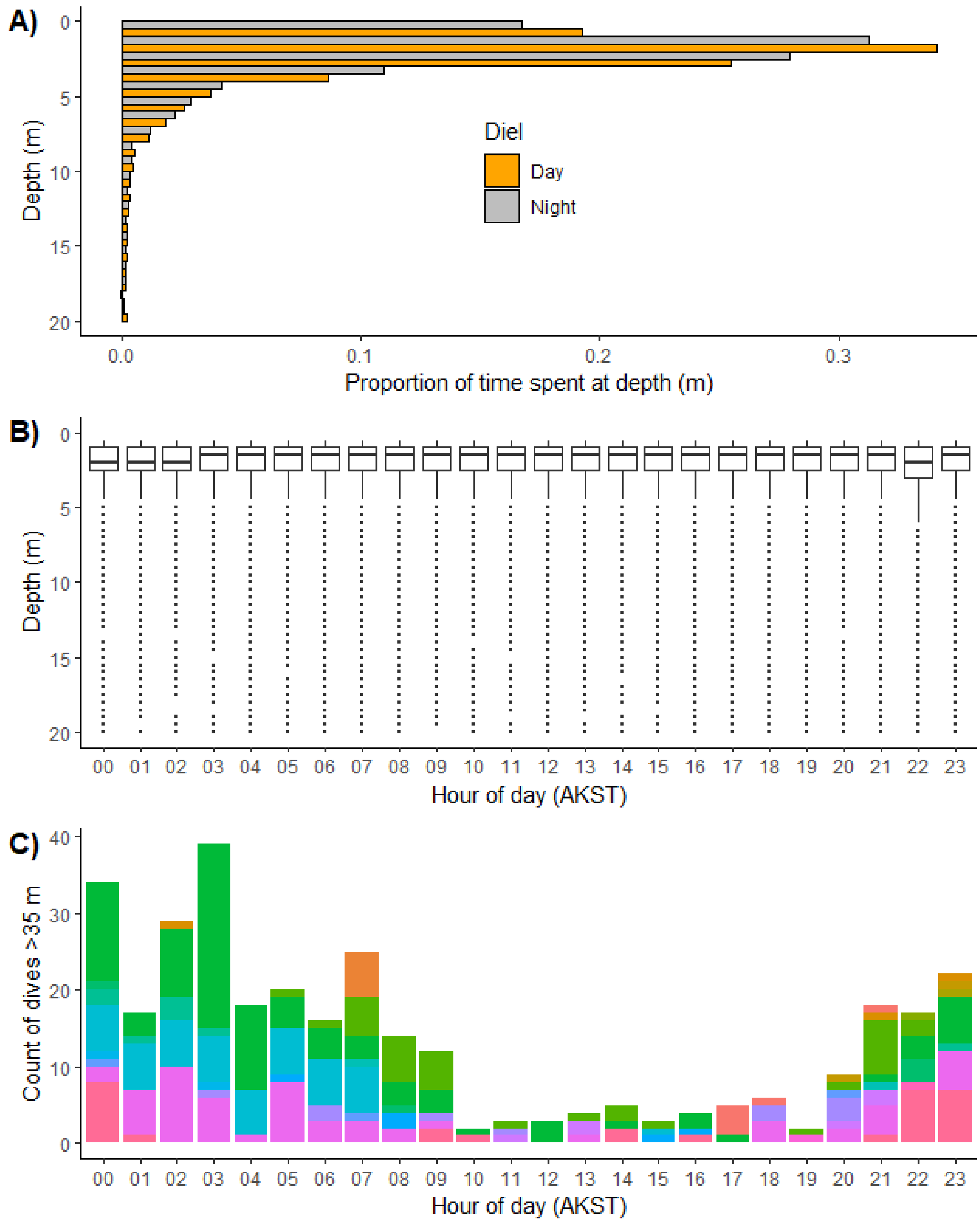

Figure 8. Depth distribution of tagged steelhead from the Situk River by periods of day and night (A) and hour of the day (B). Panel C denotes the number of depth recordings >35 m by the hour of the day (AKST). Colors in panel C denote individual tags. For boxplots, median depths and temperatures are solid lines, and boxes represent the first and third quartiles. Whiskers represent the largest observation less than or equal to the box, plus or minus 1.5 times the interquartile range, and black dots represent outliers.

Behaviors in oil and gas lease areas

Tagged steelhead (n=30, used in analyses) spent 2,016 days in seven Outer Continental Shelf planning areas, including the Gulf of Alaska (n= 865 days), Aleutian Arc (n=314 days), Aleutian Basin (n=3 days), Bowers Basin (n=60 days), Kodiak (n=388 days), Shumagin (n=252 days) and St. George Basin (n=134 days) areas (Figure 9). While in these areas, fish stayed mainly in the surface waters (2.4±3.9 m, overall mean±SD), regardless of the planning area occupied (Figure 10).

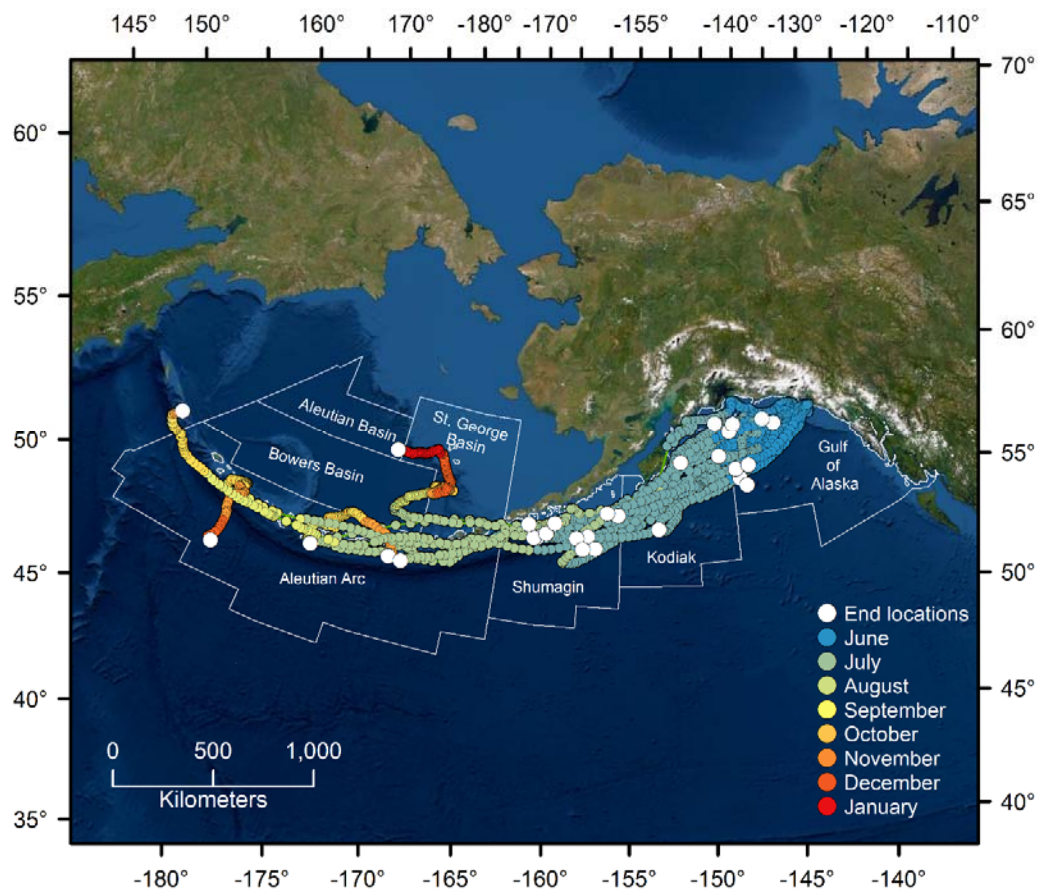

Figure 9. End locations of the satellite tags (white dots) attached to steelhead from the Situk River in relation to Outer Continental Shelf planning areas. Circles color-coded by month denote daily locations estimated from a Hidden Markov Model.

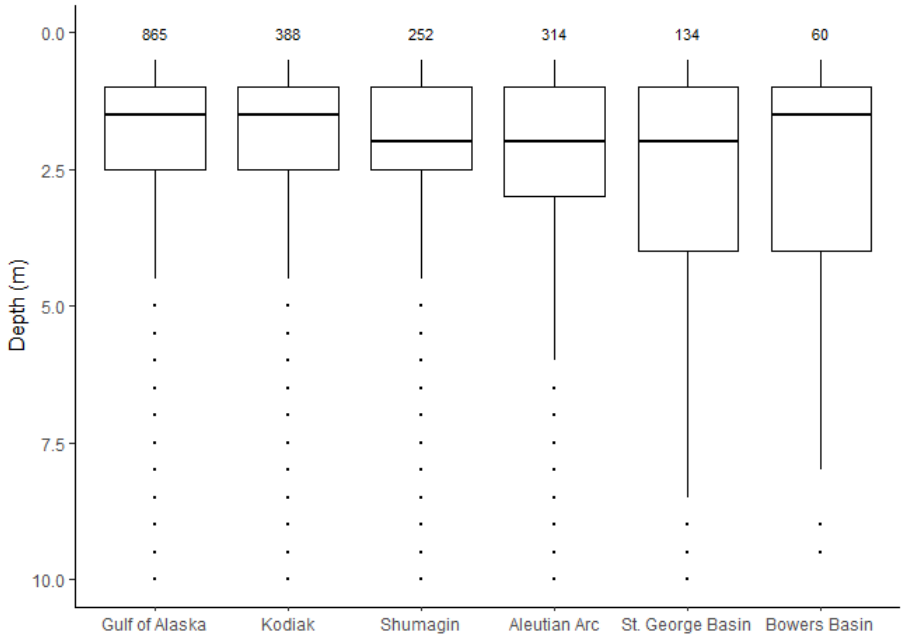

Figure 10. Depth distributions of tagged steelhead from the Situk River while occupying Outer Continental Shelf planning areas. The number of days of occupancy in each area is noted above boxplots. Boxes represent the first and third quartiles, and solid lines within each box represent median diving depths. Whiskers represent the largest observation less than or equal to the box, plus or minus 1.5 times the interquartile range, and black dots represent outliers.

Mortality

Thirty of 44 PSATs that reported to satellites from the ocean provided evidence that tagged steelhead (75.5±5.9 cm, mean±SD) experienced marine mortality (Table 2). Of these tagged fish, 10 were inferred to be consumed by predators, including endothermic fish with an internal temperature of ~25ºC 31–45 days after ocean entry (n=2; Figure 11a) and pelagic ectothermic fish approximately 0–74 days after ocean entry (n= 8; Figure 11b). In addition to predation of tagged steelhead, 20 steelhead were inferred to have succumbed to unknown causes 0–185 days after ocean entry (i.e., sinkers, (Figure 11c). End locations of tags suggested that mortality of steelhead was geographically widespread (Figure 12). The probability of survivorship of steelhead (n=44 used in survival analyses) at the end of the 236-day monitoring period was 0.07 (0.01–0.36, 95% confidence interval; Figure 13).

Table 2. Summary information for pop-up satellite archival tags attached to steelhead from the Situk River, whose tag data provided evidence of marine predation or unknown mortality.

Predator type	Sample size (n)	Total length (cm) (mean±SD, range)	Steelhead data days (mean±SD, range)
Pelagic ectothermic fish	8	75.0±5.5 (67.0–82.0)	48±29 (0–74)
Endothermic fish	2	78.3±81 (72.5–84.0)	38±10 (31–45)
Unknown (e.g., sinker)	20	75.5±60 (63.0–87.0)	44±43 (0–185)

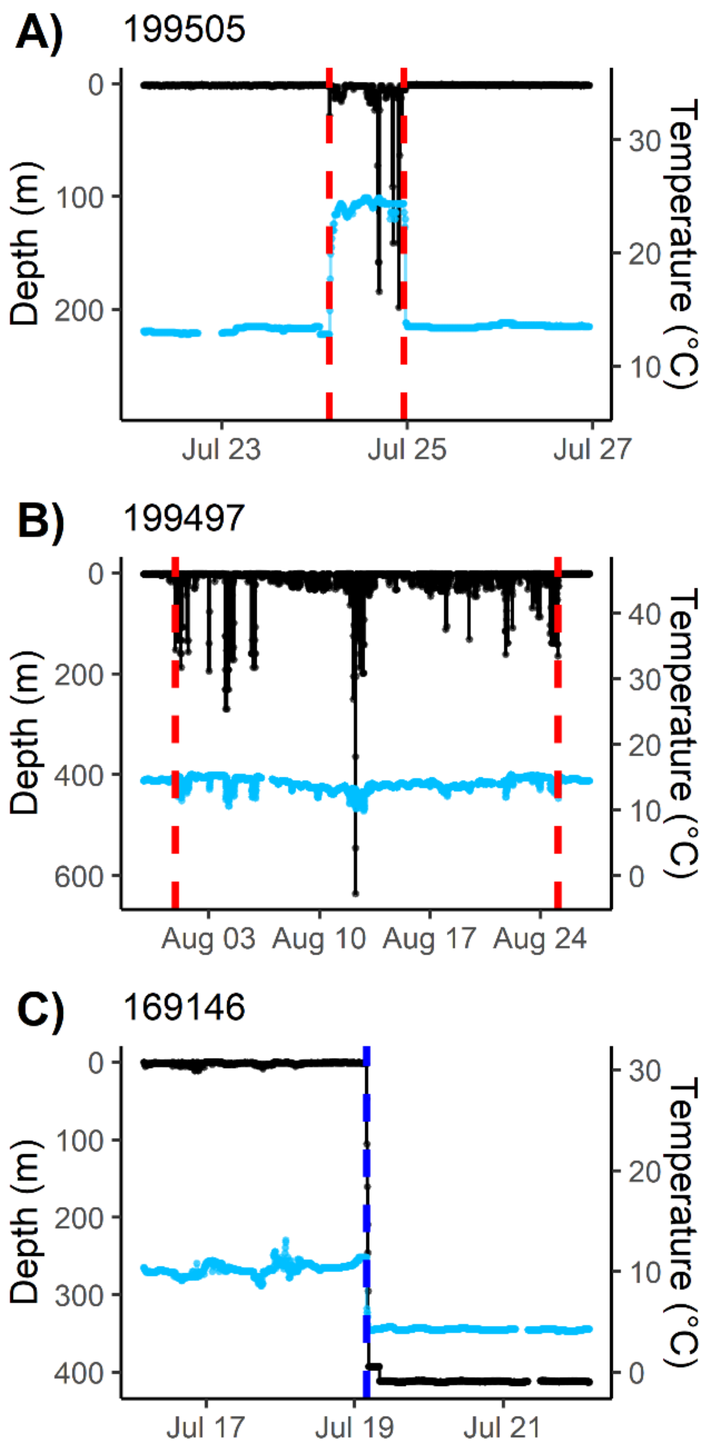

Figure 11. Examples of predation events on tagged steelhead from the Situk River by (A) an endothermic animal, (B) a pelagic ectothermic animal, and (C) an unknown cause. Red dashed lines denote estimated times of consumption of the tagged fish by the predator and subsequent expulsion of the satellite tag. The blue dashed line in panel C denotes the estimated time of unknown mortality. Tag identification numbers are noted for reference purposes.

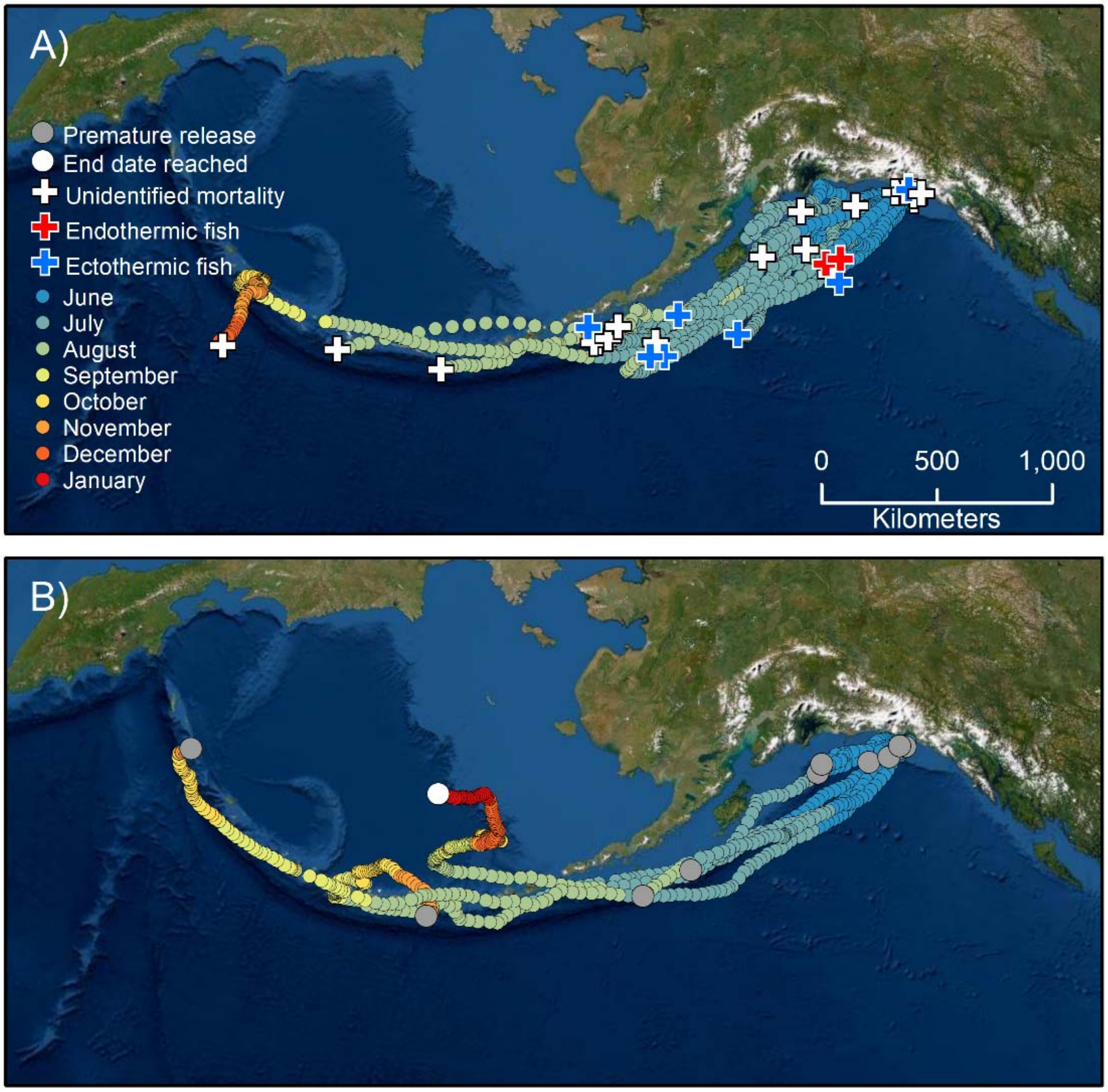

Figure 12. End locations of pop-up satellite archival tags attached to steelhead inferred to have succumbed to marine mortality (A) or assumed to be alive at the time of tag transmission (B). End locations are coded by the inferred fate of tagged fish. Circles color-coded by month denote daily locations estimated from a Hidden Markov Model.

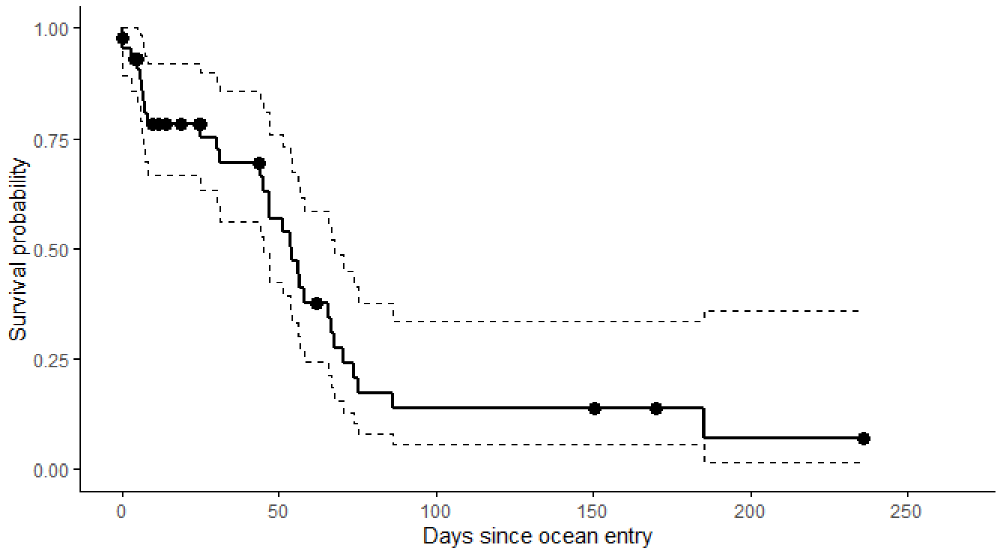

Figure 13. Kaplan-Meier survival probabilities (solid line) and 95% confidence intervals (dashed lines) of tagged steelhead (n=44; used in marine mortality estimates) from the Situk River during the period of this study. Solid circles denote tagged fish inferred to be alive when their tags transmitted (i.e., premature release for unknown reasons or reported on programmed pop-up date). Such fish are considered "censored individuals" in the model.

DISCUSSION

Satellite telemetry provided some of the first detailed insights into the marine ecology of steelhead kelts from North America. Tagged fish in this study participated in extensive post-spawning migrations that extended to the western North Pacific Ocean and as far north as the central Bering Sea. Depth and temperature data recorded during the migration provide information about the timing of outmigration into the ocean, depth distributions, diving behaviors, occupied thermal environments, and marine mortality of steelhead in the North Pacific Ocean. Furthermore, this study documented occupancy of tagged steelhead in OCS planning areas, which can inform NEPA analyses and offshore resource extraction planning to minimize potential impacts to a recreationally and culturally valuable anadromous species.

PSAT data provided evidence of a directed, surface-oriented, and extensive westerly migration of steelhead kelts following the prevailing current from the Gulf of Alaska to the waters near the Aleutian Islands and into the Bering Sea. The overall westerly movement pattern and spatial distribution of tagged fish in this study corroborate the previously described spatial distribution of steelhead inferred from past high-seas research programs that documented steelhead from North America as broadly distributed in the North Pacific Ocean, particularly near the Aleutian Islands (e.g., Burgner 1992; Light et al. 1988; Myers 2018). While the spatial distribution of North American steelhead is known to be widespread, kelt migrations are thought to be less extensive than those of immature fish (Burgner 1992; Myers 2018). The long-range migration of steelhead found in this study suggests that the ocean migration of kelts may be much more extensive than previously assumed. Our results support past research indicating that kelts from small coastal river systems like the Situk River have more extensive migrations than kelts from large rivers with large estuary systems (e.g., Hayes et al. 2012; Nielsen et al. 2011; Pavlov and Savvaitova 2008; Teo et al. 2013).

Most previous research on steelhead suggests that this species' marine distribution is primarily governed by individuals avoiding temperatures outside a specified window (Sutherland 1973; Welch et al. 1998). Similar to other salmonids (Myers 2018; Myers et al. 2007), steelhead are thought to make seasonal movements across the North Pacific Ocean to maintain their thermal environment (Burgner 1992; Light et al. 1988; Myers 2018), moving north and west during the summer and south and east during autumn and winter. Bioenergetics research suggests steelhead have a narrow temperature window to achieve optimal growth (Atcheson et al. 2012a). In this 'thermal limits' hypothesis, also supported by field observations (Welch et al. 1998), steelhead primarily reside between the 5° and 15°C sea surface temperature isotherms. The temperature data from this study support that hypothesis, with over 99.9% of temperatures recorded by tagged steelhead falling between 5° and 15°C. Furthermore, these results suggest that both horizontal and vertical distribution are related to these thermal limits.

Temperature data collected in this study aligned with the thermal limits hypothesis (Welch et al. 1998) with one exception, a tagged steelhead that reported at ~4°C from the central Bering Sea in late January. To our knowledge, this is the most northerly documented location of steelhead during the winter and provides evidence of steelhead overwintering in a thermal environment of <5°C. This fish was outside of the commonly assumed winter distribution of North American steelhead, which is thought to occur in the central/eastern GOA (Burgner 1992; Light et al. 1988; Myers 2018). This outlier highlights our poor understanding of actual winter distribution due to a lack of research during the winter months (Myers 2018). Further, the lower thermal limit for steelhead is not well defined due to a lack of catch and temperature data during the winter months (Welch et al. 1998) and the likelihood that older steelhead have colder thermal preferences than younger immature steelhead on which most assumptions are based (Atcheson et al. 2012a). Finally, the Bering Sea has undergone warming over the last several decades (Stabeno et al. 2007), potentially expanding the available overwintering habitat for North American steelhead. Increased sea surface temperatures due to anthropogenic climate change have been predicted to shift steelhead seasonal distributions further north, including into the Bering Sea during the winter months (Abdul-Aziz et al. 2011). In summary, while the sample size in this study is small, the results suggest a more northern winter distribution of steelhead than previously described.

Tagged steelhead were largely surface-oriented while occupying offshore waters of the North Pacific Ocean, spending the majority of their time in the first 5 m of the water. These results are similar to past research that suggests steelhead have a much shallower depth distribution than other species of Pacific salmon (Walker et al. 2007). For example, two archival tagged steelhead kelts from the Ninilchik River, AK, which were at liberty in the ocean for 16 months, spent over 97% of their time in the first 6 m of the water column (Nielsen et al. 2011). Electronically tagged steelhead kelts occupying coastal waters of California (Teo et al. 2013) and mature homing steelhead in British Columbia (Ruggerone et al. 1990) displayed similar surface-oriented behaviors, suggesting that an affinity for surface waters may be maintained over different geographic regions and among populations of steelhead in North America. In the current study, tagged steelhead occupied similar depths across a wide longitudinal range of the North Pacific Ocean for many months and among years of this study, supporting this claim. In contrast, other salmonids, including Chinook salmon, display seasonal and regional differences in depth distributions (Courtney et al. 2019; Hinke et al. 2005; Smith et al. 2015) which is thought to arise from seasonal changes in the stratification of the water column and differences in density or types of prey.

Tagged steelhead in this study did not show any observable diel behaviors in depth occupancy. These results are similar to data from archival-tagged steelhead from the Ninilchik River, AK, during 16 months at sea (Nielsen et al. 2011) and data from acoustically tracked steelhead in the Pacific Ocean (Ogura and Aria 1993). In contrast, evidence from other research indicated diel differences in steelhead kelt swimming behavior. Archival-tagged steelhead kelts from the Sacramento River tended to dive deeper and occupy deeper depths during the night while occupying coastal waters near California (Teo et al. 2013). Temperature data from an archival tag attached to a steelhead in the Gulf of Alaska suggested that the fish conducted dives down to 50 m during the day and remained near the ocean surface at night (Walker et al. 2000). Finally, acoustic tags attached to mature homing steelhead in a fjord in British Columbia indicated shallower mean depths and faster travel rates during the day compared to night (Ruggerone et al. 1990). These differences in diel depth distributions are likely influenced by regional factors, including predator avoidance behaviors, thermoregulation, or foraging tactics tailored to regional distributions and behavior of preferred prey. While no observable diel-specific behaviors were evident in this study, the overall shallow distributions may have masked subtle or periodic (e.g., scale of days) diel depth-based behaviors that have been documented in other salmonids (Courtney et al. 2021; Courtney et al. 2019; Walker and Myers 2009).

The overall westerly movement to the waters adjacent to the Aleutian Islands and into the Bering Sea by tagged steelhead suggests the region is an important feeding ground for steelhead kelts from the Situk River and may play a critical role in the successful reconditioning of repeat spawners in this population. The biological importance of the area is evidenced by the presence of large commercial fisheries (Fissel et al. 2016; Turner et al. 2017) and the high abundance and densities of zooplankton, forage fishes, marine mammals, and sea birds (Byrd et al. 2005; Heifetz et al. 2005; Logerwell et al. 2005). This high biological production relies on the transport of well-mixed nutrient-rich waters west and north through the many highly productive Aleutian passes into the Bering Sea (Hunt and Stabeno 2005; Ladd et al. 2005; Mordy et al. 2005; Stabeno et al. 2005).

Shallow depth distributions for tagged steelhead while in this biologically productive area support previous findings that steelhead primarily feed in the surface waters (Burgner 1992;

Taylor and LeBrasseur 1957). While in the open ocean, steelhead are thought to feed on various epipelagic fishes and invertebrates including juvenile Atka mackerel (*Pleurogrammus monopterygius*), northern lamp fish (*Stenobrachius leucopsarus*), gonatid squids (*Berryteuthis anonychus* and *B. magister*), crustaceans (euphausiids, amphipods), and polychaetes (Atcheson et al. 2012b; Kaeriyama et al. 2004; Light et al. 1988; Pearcy et al. 1988).

Deep dives (>50 m) were undertaken by several tagged steelhead in this study; however, these dives were relatively rare and occurred over short bouts of time. Given the high mortality rates of tagged steelhead in this study, deep diving behavior may be a predator avoidance response. However, many other factors could influence these rare deep diving events. For example, many of the deep dives occurred in June and July during the westerly transit period to feeding grounds near the Aleutian Arc and Bering Sea. Thus, these deep dives may be orientation/navigation behaviors that are manifested as quick dives to “measure” the earth’s magnetic field. Deep diving activity below the halocline has been suggested as orienting behavior in salmonids (Quinn et al. 1989), including maturing steelhead off the coast of British Columbia (Ruggerone et al. 1990).

Data from PSATs in this study indicated low marine survival estimates and offered a preliminary glimpse into the natural mortality of steelhead kelts from the Situk River caused by endothermic and ectothermic fishes and possibly marine mammals. Kelt survivorship and iteroparity rate are known to be low throughout this species' range, based on recaptures of tagged repeat spawning steelhead (Clemens 2015; Evans et al. 2008; Keefer et al. 2008), as well as the overall low proportion of repeat spawners in most systems (Busby et al. 1996). Little is understood about the agents and timing of adult steelhead mortality by predators, but most research has documented mortality occurring by marine mammals in marine nearshore or estuarine habitats (Naughton et al. 2011). Our results demonstrate that marine mortality occurred at a relatively constant rate for the first three months at sea and was geographically widespread. It should be noted that, as in past studies (e.g., Courtney et al. 2021; Seitz et al. 2019; Strøm et al. 2019), we assumed fish were still alive if their tags were released (for unknown reasons) before the programmed pop-up date. Half (8 of 16) of these events occurred within 24 days after ocean entry. It is possible these tags released during predation by predators that did not ingest the entire steelhead and tag, such as pinnipeds that frequently rip apart their prey (Hocking et al. 2016). If so, kelt mortality rates would be higher than reported in this study. Nevertheless, observed mortality of steelhead kelts in this study occurred >3,000 km from the mouth of the Situk River, highlighting the importance of understanding marine mortality across a bigger landscape.

Based on known visceral temperatures and species distribution, tagged steelhead were likely consumed by large marine apex fish predators. Specifically, predation by endothermic fish in this study was likely attributed to salmon sharks (*Lamna ditropis*) as indicated by their unique internal temperatures of ~25°C (Anderson and Goldman 2001; Goldman et al. 2004). Insights are much more speculative in the case of predation by pelagic ectothermic predators. Based on diving behaviors and occupancy in pelagic waters, predation was likely from blue sharks

(*Prionace glauca*), whose abundance appears to be increasing in Alaskan waters (Nakano and Stevens 2008). In the cases of unknown mortality events, pinnipeds (Hocking et al. 2016) which are not likely to ingest the entire steelhead and tag, provide a possible culprit. The role of marine kelt survival on steelhead population productivity is poorly understood; however, predation on the late-life stage of another salmonid, the Chinook salmon, highlighted in recent satellite tagging research (Seitz et al. 2019), suggests it is an essential factor in understanding the population dynamics of this species, including recent declines in size- and age-at-maturity (Manishin et al. 2021).

Tagged steelhead in this study frequently occupied OCS planning areas in the Gulf of Alaska and beyond. Natural resource extraction activities in these areas can potentially impact species at all trophic levels through habitat alteration, hydrological disturbance, biomagnification of hydrocarbon compounds and heavy metals, reduced production, and chronic and acute toxicity from leaks and spills (Holdway 2002; Olsgard and Gray 1995). The overall high frequency and duration that steelhead spent in these areas increases this species' potential for exposure to low-level chronic or higher impact acute threats from oil and gas activities (Hauser et al. 2018). Furthermore, the affinity to remain in surface waters will likely make steelhead susceptible to interactions with oil that floats at the sea surface. Recently, exposure to pollutants has been shown to affect the 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 and extensive migrations, such as steelhead in this study. Information on the occupancy of steelhead in OCS planning areas adds to the existing knowledge of this species' spatial distribution and is directly pertinent to several stakeholder groups, including biological resource managers, mineral and gas developers, and regulators for assessing the vulnerability and interactions of the species with anthropogenic activities.

While we studied the marine ecology of steelhead kelts from one population in Southeast Alaska, our results may be pertinent for other populations throughout North America. This information is important for providing a more holistic understanding of steelhead throughout its range. The stock status of steelhead in Alaska is thought to be relatively stable (Harding 2008). However, populations further south, including those in the Pacific Northwest, have seen drastic declines since the 1980s. Poor marine survival for fish from most systems (Kendall et al. 2017) highlights the importance of increasing information about this species. Given that repeat spawning has several population-level advantages, including higher fecundity and lifetime reproductive success (Seamons and Quinn 2010), understanding the marine ecology of this life stage is useful for examining steelhead population dynamics and current trends in the abundance of stocks of steelhead throughout North America. Future tagging research programs throughout the west coast of North America, including imperiled populations from British Columbia, Washington, Oregon, and California, will be necessary to develop a holistic understanding of steelhead migratory characteristics throughout their range which, in turn, can inform management strategies to mitigate the potential impacts of human activities such as fishing and hydrocarbon exploration and extraction.

STUDY PRODUCTS

Seitz, A. C., M. B. Courtney, E. A. Miller, A. Boustany, K. S. Van Houtan, M. Catterson, and J. Pawluk. 2021. Oceanic movement and behavior of steelhead, elucidated with pop-up archival satellite tags. Oral presentation at the Alaska Coastal Marine Institute 2021 Annual Research Review, Virtual meeting, January 2021.

Courtney, M. B., A. C. Seitz, E. A. Miller, M. Catterson, K. S. Van Houtan, and A. Boustany. 2021. Oceanic movement and behavior of steelhead, elucidated with pop-up archival satellite tags. Oral presentation, presented at Alaska Marine Science Symposium, Virtual meeting, January 2021.

Seitz, A. C., E. A. Miller, M. B. Courtney, M. Catterson, J. Nichols, K. D. Kiernan, J. O'Sullivan, A. Norton, K. S. Van Houtan, A. Boustany. 2020. Interpreting mortality of satellite-tagged salmonids. Oral presentation, presented at the 20th Salmon Ocean Ecology Meeting, Monterey, CA, March 2020.

Miller, E. A., A. C. Seitz, M. B. Courtney, M. Catterson, J. Nichols, K. D. Kiernan, J. O'Sullivan, A. Norton, K. S. Van Houtan, A. Boustany. 2020. Ocean movement and behavior of steelhead revealed by pop-up satellite archival tags. Oral presentation, presented at the 20th Salmon Ocean Ecology Meeting, Monterey, CA, March 2020.

Courtney, M. B., A. C. Seitz, E. A. Miller, M. Catterson, J. Nichols, K. S. Van Houtan, and A. Boustany. 2020. Oceanic movement and behavior of steelhead, elucidated with pop-up archival satellite tags. Scientific poster presented at Alaska Marine Science Symposium, Anchorage, AK, January 2020.

Seitz, A. C., M. B. Courtney, E. A. Miller, A. Boustany. K. S. Van Houtan, and M. Catterson. 2020. Ocean migration and behavior of steelhead kelts in Alaskan OCS oil and gas lease areas. Oral presentation, presented at the Alaska Coastal Marine Institute 2020 Annual Research Review. Anchorage, AK, January 2020.

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