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CASE REPORT

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Insights into the ocean migration, behavior, and ecology of steelhead kelts from Prince of Wales Island, Alaska

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Abstract

Background Although steelhead (*Oncorhynchus mykiss*) is a culturally and recreational important species throughout North America, less is known about its ocean than its freshwater ecology. To provide insights into migratory routes and habitats occupied by steelhead in the North Pacific Ocean, we attached pop-up satellite archival tags (PSATs) to female steelhead kelts from three watersheds on the east coast of Prince of Wales Island, in southern southeast Alaska.

Results PSATs successfully recorded extensive westward post-spawning migrations of nine female kelts across the Gulf of Alaska to areas near the Alaska Peninsula and Aleutian Islands. From the months of June to October, tagged steelhead occasionally dived to 10–20 m, but spent approximately 90% of their time in surface waters (< 4.5 m). During this same time period, 90% of all tag-recorded temperatures were between 8.7 and 12.8°C.

Conclusion These results corroborate past research on other North American steelhead populations, demonstrating that steelhead kelts predominantly occupy surface waters with sea-surface temperatures of 5–15 °C while transiting to and occupying purported feeding grounds in the western Gulf of Alaska and Aleutian Islands. Taken together, these results suggest that steelhead kelts originating from rivers throughout this species' North American range occupy similar habitats in the North Pacific Ocean. While we only studied the ocean ecology of a limited number of steelhead kelts from southern Southeast Alaska, our results are pertinent for other populations throughout the northern west coast of North America, and provide better understanding of this species' ocean ecology.

Keywords *Oncorhynchus mykiss*, Telemetry, Migration, Behavior, North Pacific Ocean

Introduction

Steelhead, the anadromous form of rainbow trout (*Oncorhynchus mykiss*), is an iconic fish targeted in popular sport fisheries throughout southeast Alaska. The majority of research on steelhead in southeast Alaska has occurred in freshwater and focused on providing basic information about the species' life history, abundance, and age composition of spawning adults [1]. Steelhead in southeast Alaska typically rear in freshwater for 2–5 years before migrating to the ocean as immature juveniles [1–3]. These immature steelhead typically spend 2–3 years feeding in the ocean before returning to their natal river during March–May to spawn [1, 4]. In contrast to Pacific

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Salmon, steelhead are iteroparous, and after spawning in April–June, surviving adult steelhead, referred to as kelts, return to the sea to feed.

In general, while in the ocean as juveniles and kelts, less is known about steelhead ocean migration and behavior [5–7], than about this species freshwater residency [8]. This is due to relatively little directed research on this species during its ocean residency phase and because of the low susceptibility of this species to be captured in high-seas survey methods (e.g., pelagic, midwater trawls) targeting Pacific salmon (*Oncorhynchus* spp.,) [7]. However, based on infrequent encounters in high-seas Pacific salmon research programs [5, 7, 9, 10], steelhead originating from North America are thought to make extensive migrations in the North Pacific Ocean, and be widely distributed throughout the Gulf of Alaska and the eastern North Pacific Ocean during this species' ocean phase. However, the seasonal and population-specific ocean migrations of North American stocks remain highly speculative [7].

Satellite telemetry has enabled researchers to successfully describe the ocean migration and ecology of post-spawn steelhead kelts from the Situk River, adjacent to northern southeast Alaska, the most prolific steelhead population in Alaska [11, 12]. This past research has provided unprecedented details into the diving behaviors and thermal environment experienced by steelhead in the North Pacific Ocean while conducting extensive migrations to as far as the western North Pacific Ocean. However, as this past research [11, 12] only reported on steelhead from one population in Alaska, many uncertainties on this species' ocean migration remain, including those from less abundant populations, and from other parts of the species' geographic range. Therefore, the objective of this current study is to provide preliminary insights into the ocean ecology of steelhead kelts originating from Prince of Wales Island, located in southern southeast Alaska.

Methods

Fish tagging

From 5 to 11 May 2023, 15 female steelhead kelts were captured and tagged in three watersheds, including the Thorne River ($n=5$), Harris River ($n=5$), and Eagle Creek ($n=5$) located on the eastern coast of Prince of Wales Island in southern southeast Alaska (Table 1; Fig. 1). Steelhead were captured by angling methods. Heavy-action spinning rods (60 lb test heavy braid and 20 lb monofilament leaders) and barbless hooks (size 4–8), were used to minimize fight and handling times. Pop-up satellite archival tags (PSATs) were attached to steelhead using a "tag backpack" system [13] successfully used on several salmonids [14–16], including steelhead [11]. After tagging, each fish was identified by tag number, measured in length (FL; mm), and released. All fieldwork was conducted under the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance #2021573 and State of Alaska Aquatic Resource Permit SF2023-061.

Tag specifications and data acquisition

PSATs used in this study were Wildlife Computers' Mini-PATs, which are slightly buoyant and weigh approximately 60 g in air (http://wildlifecomputers.com). While

Table 1 Deployment information and summary of ocean depth and temperatures occupied by nine female steelhead kelts from Prince of Wales Island in southern southeast Alaska

Ptt	Watershed	Fork length (mm)	Depth (m)	Temperature (°C)	Ocean days	Displacement (km)
244473*	Harris River	750	1.8 ± 1.8 (0–84)	10.9 ± 1.3 (5.0–17.5)	139	2857
244475*	Thorne River	745	1.6 ± 1.6 (0–63)	10.7 ± 1.1 (4.6–13.6)	141	2201
244477	Harris River	690	2.4 ± 4.0 (0–67)	10.6 ± 1.4 (5.8–14.3)	114	2509
244479	Harris River	777	1.5 ± 2.3 (0–38)	8.9 ± 1.0 (6.8–12.4)	14	164
244481*	Harris River	770	2.0 ± 1.0 (0–24)	9.8 ± 0.8 (6.1–13.8)	82	2263
244483	Eagle Creek	730	0.7 ± 0.8 (0–58)	10.4 ± 1.2 (5.2–13.3)	140	2635
244484*	Eagle Creek	740	1.5 ± 1.8 (0–105)	10.2 ± 1.3 (5.4–15.2)	82	1023
244485*	Eagle Creek	740	2.8 ± 3.5 (0–36)	11.4 ± 1.5 (7.2–15.5)	71	1379
244486*	Eagle Creek	780	1.3 ± 1.6 (0–90)	10.8 ± 0.9 (5.2–13.1)	87	1824

a) Ptt refers to the unique Argos Satellite System identification number for each tag

b) Depth and temperatures are represented as mean ± standard deviation (range)

c) Ocean days refers to between ocean entry and the end date

c) Displacement refers to the minimum great arc circle distance between tagging and end locations

*denotes tags which provided evidence of mortality of tagged steelhead

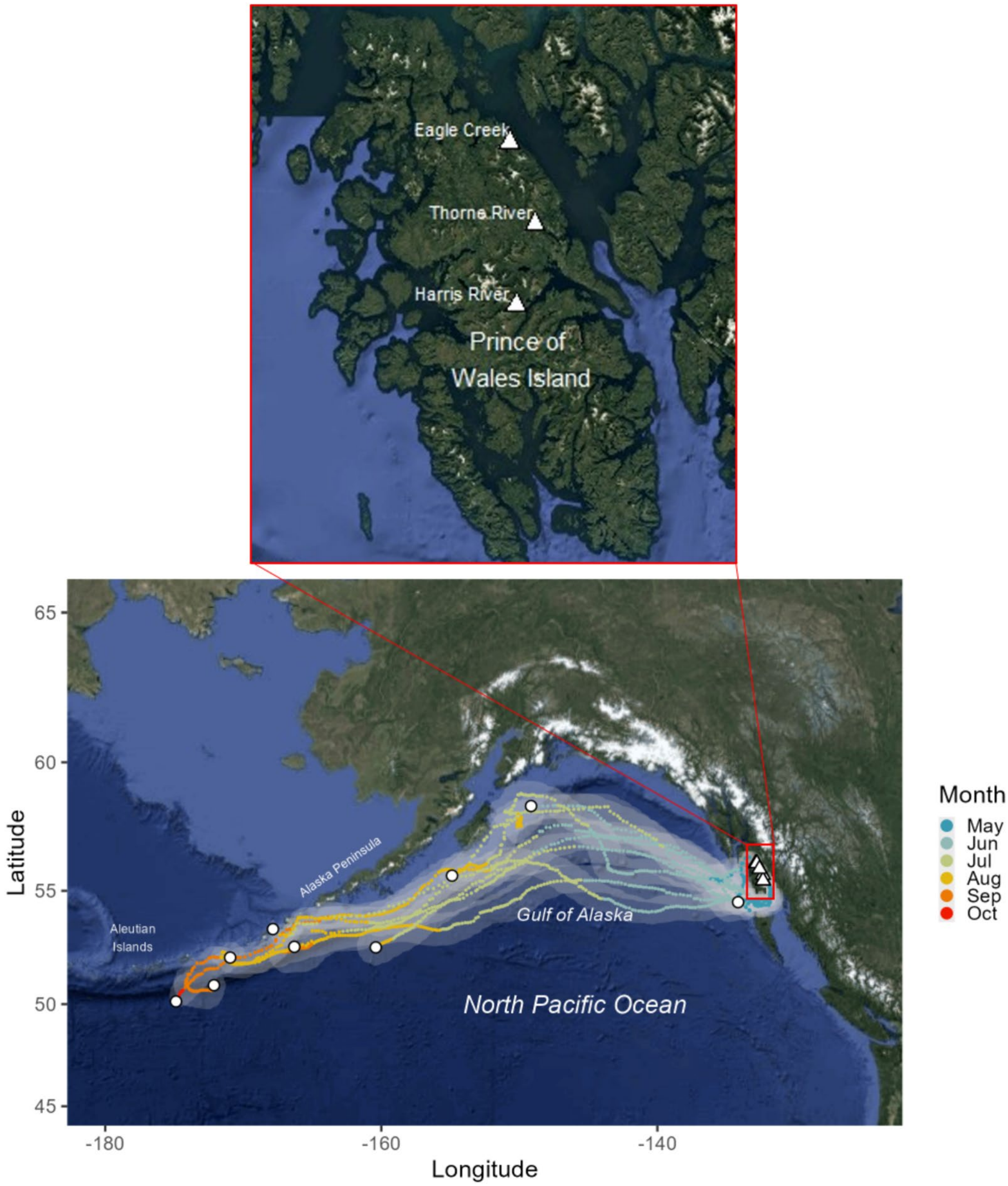

Fig. 1 Deployment locations (white triangles), most likely movement paths (smaller colored circles coded by month) and end locations (larger white circles) of tagged female steelhead kelts ($n = 9$) from Prince of Wales Island (upper panel) in southern southeast Alaska. Transparent gray polygons denote the 99% probability surfaces of individual most likely movement tracks

externally attached to the fish, the MiniPAT recorded temperature, depth and ambient light data (for daily geoposition estimates) at user-programmable intervals. On a user-programmed date, the tag released from the fish, floated to the surface of the ocean, and transmitted a subset (7.5–10 min resolution) of the archived data and an end location to the Argos Satellite System. In this study, PSATs were programmed to release from tagged steelhead at staggered intervals between 120 and 240 days post-tagging. 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 > 1700 m (to avoid extreme pressures that could damage the tag).

Data analyses

To understand the horizontal movement of tagged steelhead, the most likely movement paths of individual tagged steelhead were estimated using Wildlife

Computers' proprietary Hidden Markov Model (HMM GPE3) [17], commonly used in similar research [18–20]. Briefly, GPE3 employs observations of twilight, sea-surface temperature and bathymetry to generate time-discrete and gridded probability distributions to estimate the most likely daily positions of tagged fish [17]. The diffusion parameter was set to 100 km·day^{-1} in all individual models [15, 16, 21]. These most likely tracks and their 99% probability surfaces [22] were plotted using ggplot2 [23], in the statistical software R [24]. In addition, the daily net displacement, calculated as the great arc distance between the tagging and subsequent estimated daily locations was calculated and related to the corresponding number of days at liberty. To understand the depth and temperature occupancy of tagged steelhead, descriptive statistics (mean, minimum, maximum, standard deviation) were calculated for data from each tag. Additionally, time-weighted means of depth and temperature, and the 50% and 90% quantiles were calculated for all aggregated datasets. Furthermore, individual and seasonally occupied depths and temperatures were plotted through boxplots. Finally, mean depths occupied during periods of night and day were qualitatively examined.

Results

Summary

Tagged steelhead kelts ranged from 680 to 800 mm (746 ± 34; mean ± SD). No significant differences in size (FL) were detected between watersheds (ANOVA; p-value = 0.76). Of the 15 tags deployed, 12 transmitted to satellites. The remaining three tags never transmitted and were considered missing. Of the 12 tags that transmitted data, two reported from freshwater near their respective tagging/release sites. The remaining 10 tags transmitted from ocean waters. Of these, three were inferred to release from live steelhead and seven were associated with mortality events in which, depth data suggested that these fish died and sank to the seafloor (or > 1700 m), prior to releasing and transmitting to satellites described in [12, 25–27]. Data from these mortality events were removed from all analyses and as such, only data from before mortality events were used for analyses. Additionally, one tag transmitted little (~ 12%) of its archived data, and was not included in data analyses. In all, data from nine tags were used in analyses, providing approximately 870 data-days for steelhead kelts while in the ocean (Table 1).

Horizontal movement

Based on tag-recorded depth and temperature see [14, 28, 29], tagged steelhead were inferred to have entered the ocean from mid-to-late May, 2–16 days after tagging. After ocean entry, all tagged fish quickly dispersed westward over deep basin waters, reporting from the coast of southeast Alaska (n = 1), the Gulf of Alaska (n = 2), and near the Aleutian Islands (n = 6) (Figs. 1 and 2). By mid-July all tagged kelts at liberty (n = 8) were distributed in the central Gulf of Alaska. Movements of tagged steelhead continued westward throughout the summer, and by August, most tagged fish (n = 7 of 8) were distributed west of Kodiak to the western extent of the Alaska Peninsula. By September, the remaining tagged fish at liberty (n = 4) were south of the Aleutian Islands. In all, individual displacements ranged from 164 to 2857 km (1873 ± 873 km, mean ± SD) (Table 1; Fig. 2). Although sample sizes of available datasets differed, no

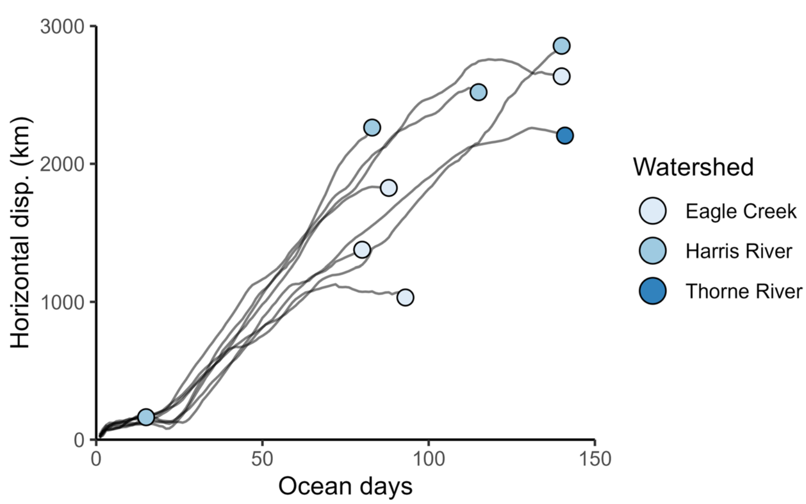

Fig. 2 Relationship between the daily horizontal displacement (i.e., displacement between tagging location and subsequent daily location estimates) of nine tagged female steelhead kelts. Colors denote the watershed where each steelhead was tagged

observable qualitative differences in migrations were observed among fish tagged in different watersheds (e.g., Eagle Creek, Thorne River, Harris River).

Depth and temperature occupancy

From May to October, tagged steelhead occupied depths of 0–105 m, and experienced a thermal environment of 4.6–17.5 °C (Table 1). Although dives up to 105 m were observed, tagged steelhead were largely surface oriented (1.7 ± 0.6 m, time-weighted mean ± SD), with 50% and 90% of all recorded depths in the top 1 m and 4.5 m water column, respectively (Fig. 3). Mean temperatures experienced by individual tagged steelhead were 8.9–11.4 °C (10.6 ± 0.4; time-weighted mean ± SD) (Table 1; Fig. 3). During this time, 50% and 90% of all recorded temperatures were between 9.7–11.5 °C and 8.7–12.8 °C, respectively. Depth occupation varied little seasonally, as all monthly median depths were < 1.6 m during all months tagged fish were at liberty (May–October) (Fig. 4). In contrast, temperatures fluctuated with changes in local seasonal sea-surface temperatures (Fig. 4). Mean depths varied little between periods of day (1.7 ± 2.4 m; mean ± SD) and night (2.0 ± 2.8 m; mean ± SD).

Discussion

Pop-up satellite archival tags provided the first insights into the ocean migration and occupied habitats of steelhead kelts originating from Prince of Wales Island, Alaska. Our results provide evidence of a directed, surface oriented, and extensive westward migration of steelhead kelts to the waters near the Aleutian Islands. The observed movements and distribution of tagged kelts in this study are similar to the conceptual migration model and distribution of North American steelhead [5, 7, 9]. By leveraging insights from historical high-seas Pacific salmon survey data collected primarily in the 1950s to the 1990s, recent research suggests that steelhead are concentrated near the western Gulf of Alaska and the Aleutian Islands during months of July and August [30]. However, it is important to note that these inferred steelhead distributions primarily consist of maiden migrants (ocean age 1–2) rather than kelts, as well as mixed life histories (e.g., run timing) and stock-origins. Furthermore, the observed movement patterns in this study are strikingly similar to those of tagged (PSAT) steelhead kelts from the Situk River, approximately 350 km north of Prince of Wales Island [11]. Even though the sample

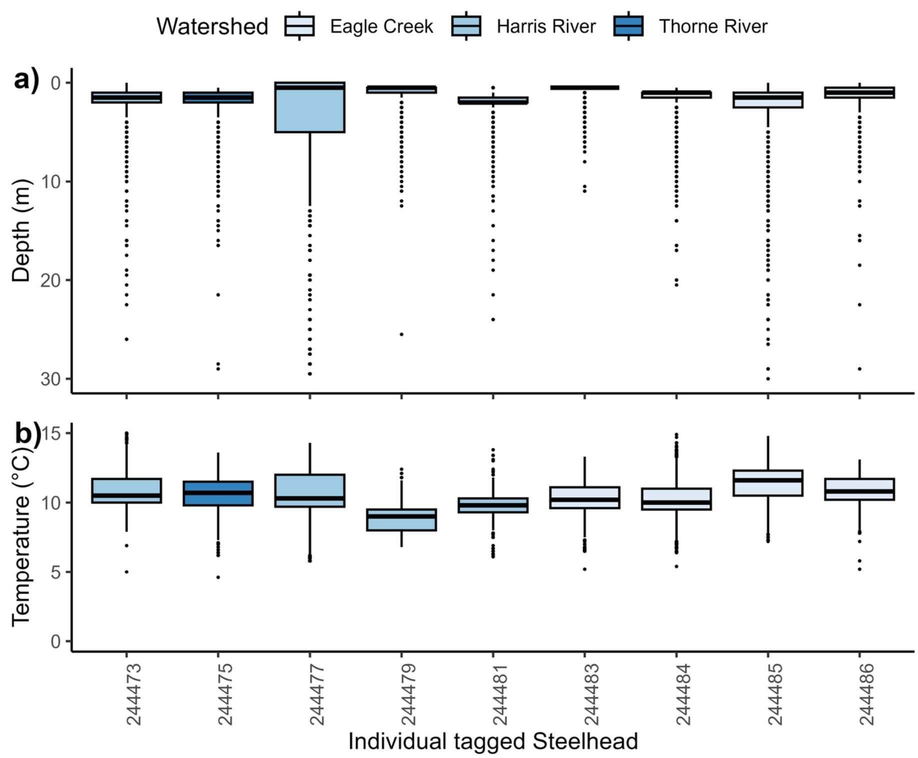

Fig. 3 Total ocean **a** depths and **b** temperatures occupied by nine female steelhead kelts from Prince of Wales Island in southern southeast Alaska. Colors denote watersheds where each steelhead was tagged. Tag identification numbers (Ptt in Table 1) for individual steelhead are below the *x*-axis. Note that panel a only portrays depths < 30 m, as this window contained 99% of all recorded depths. For boxplots, median depths/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

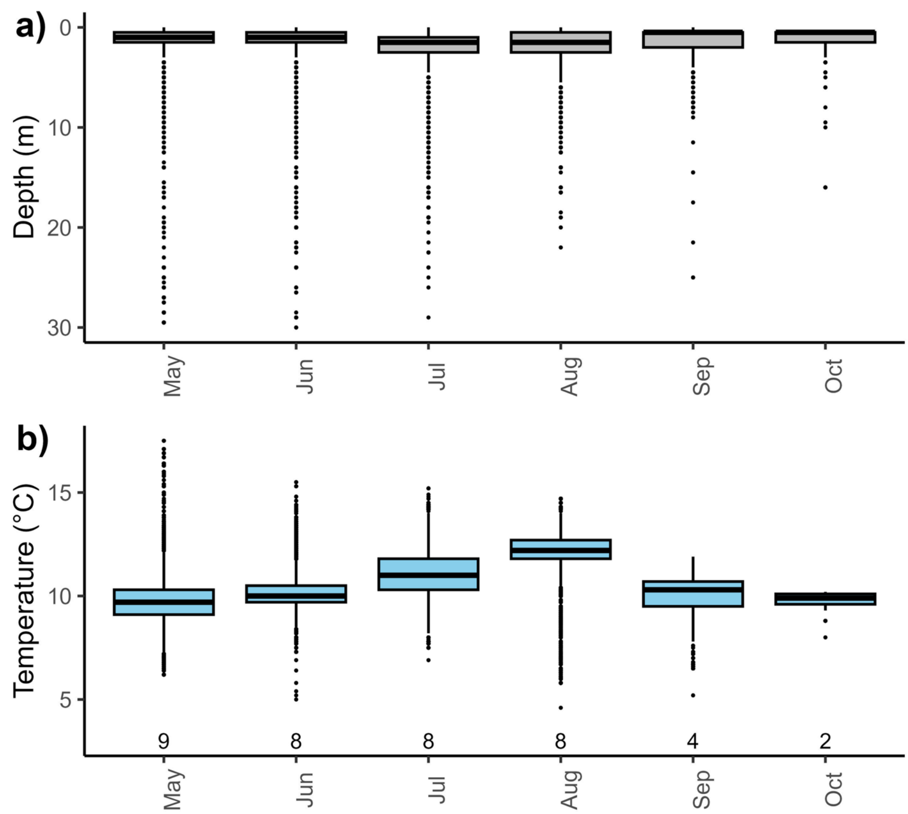

Fig. 4 Monthly **a** depth and **b** temperature distributions of tagged female steelhead kelts from Prince of Wales Island in southern southeast Alaska. Sample sizes for each month are denoted immediately above the *x*-axis of panel b. Note that panel a only portrays depths < 30 m, as this window contained 99% of all recorded depths. For boxplots, median depths/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

sizes of these recent telemetry projects are small, taken together, results from these four different populations (e.g., Thorne River, Harris River, Eagle Creek, and Situk River) suggest (1) common migratory pathways and distribution of steelhead originating throughout southeast Alaska, and (2) waters adjacent to the Aleutian Islands are an important foraging/reconditioning area for repeat spawning steelhead.

Past research has suggested that steelhead ocean distribution is primarily found between the 5–15 °C sea-surface temperature (SST) isotherms [10, 31]. Tagged steelhead in this study occupied habitats with temperatures within the previously reported range by predominantly occupying surface waters between 8 and 12 °C. Ocean temperatures recorded by our tagged steelhead kelts were similar to those reported by tags on kelts from California [$n=2$; 29], northern Southeast Alaska [$n=30$; 11], and Southcentral Alaska [$n=2$; 32], which were inferred to have migrated and occupied the northern North Pacific Ocean (i.e., Gulf of Alaska, Aleutian Islands) during the summer months. These occupied ocean temperatures by tagged steelhead all fall in the thermal range that is assumed to be preferred by steelhead during the spring and summer months [5, 10, 11, 30, 31, 33]. For example, by examining historical high-seas Pacific salmon and steelhead survey catch data, Langan, Cunningham (30) estimated the 'preferred' and 'core' spring/summer (April–August) SST range for steelhead to be 5.8–12.4 °C and 6.4–9.9 °C, respectively. In all, the commonality in occupied temperatures among several studies may suggest that similar ocean thermal preferences exist among many populations of steelhead originating from North America.

While occupying offshore waters of the North Pacific Ocean, tagged steelhead were largely surface oriented, spending the majority (~ 50%) of their time in the first 1 m of the water column, providing additional support that steelhead primarily feed in the surface layers [5, 34, 35]. This observation is strikingly similar to steelhead kelts originating from the Situk River, near northern southeast Alaska ($n=30$; 2034 ocean days) that predominantly occupied surface waters (2.5 ± 1.3 m, grand mean ± SD) and rarely dove > 20 m while occupying purported feeding grounds in the western Gulf of Alaska and Aleutian Islands from June to January [11]. Our observations are similar to those of a limited number of tagged (e.g., archival and acoustic tagged) steelhead kelts from Southcentral Alaska [32], British Columbia [36], and California [29, 37]. In all, these studies suggest that the shallow water occupancy of several populations of steelhead from North American is maintained over different geographic regions and seasons. Furthermore, these results indicate that steelhead spend significantly more time in surface waters (0–5 m) of the open ocean compared to species of Pacific Salmon [15, 38, 39].

As many wild populations of steelhead throughout North America undergo periods of depressed abundances [40–42], understanding steelhead ocean ecology is of particular interest to fisheries managers. Specifically, information on the ocean spatial distribution, seasonal movements, and temperature preferences can inform consequences of changing ocean temperature regimes and interspecific interactions, which may have important impacts on growth, survival, and migration routes [33, 35, 43, 44]. While this study contained a small number of individuals from three populations in Southeast Alaska, our results add to the limited knowledge base on the oceanic phase of steelhead, and may help contribute to better understanding of the factors affecting the abundance and distribution of this species throughout its North American range.

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Author contributions
MBC, ACS, and CJS conceived the study design. ACS secured funding. MBC and CJS arranged fieldwork logistics. MBC, ACS, BPG, JRS, and CJS participated in fieldwork. MBC conducted data analyses. MBC wrote the initial draft of the manuscript. All authors reviewed, edited and approved the final manuscript.

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Data availability
The datasets used and/or analyzed in this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
All fieldwork was conducted under the University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance #2021573 and State of Alaska Aquatic Resource Permit SF2023-061.

Competing interests
The authors declare no competing interests.

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