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Ocean migration and behavior of steelhead *Oncorhynchus mykiss* kelts from the Situk River, Alaska

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Abstract Although steelhead (*Oncorhynchus mykiss*) is an iconic species found throughout the North Pacific rim, little is known about its ocean 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 steelhead kelts in 2018 ($n=16$), 2019 ($n=12$), and 2020 ($n=35$) from the Situk River, a robust Alaskan population. PSATs recorded extensive post-spawning migrations extending to the western North Pacific Ocean, and as far north as the central 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 steelhead kelts experienced a thermal environment of 4–16 °C from June to January, after exiting the Situk River. Results from this project corroborate the limited past research suggesting that 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 important feeding grounds for steelhead kelts from the Situk River, and thus may play a critical role in the successful reconditioning of repeat spawners in this population. These results provide the first detailed insights into the ocean ecology of steelhead and may be used for a variety of applications (e.g., niche construction, and forecasting future range dynamics under climate scenarios).

Keywords Behavior · Depth · Ecology · Movement · Ocean · Steelhead

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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 southern California to Alaska and across the Bering Sea to the Kamchatka Peninsula in Russia (Burgner et al. 1992; Light et al. 1989; Myers 2018; Quinn 2005). In Alaska, steelhead are found in over 300 watersheds and are targeted in popular sport fisheries, particularly in Southeast Alaska (Harding 2008). For example, the Situk River, located near Yakutat, Alaska, sustains the largest known steelhead population and supports one of the most popular sport fisheries in the state (Marston and Power 2016).

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Steelhead spawn in freshwater, but move to the ocean to feed and are thought to make extensive ocean migrations (Burgner et al. 1992; Myers 2018; Quinn 2005). In southeast Alaska, steelhead typically rear in freshwater for 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). The majority of steelhead in southeast Alaska are referred to as spring-run fish, returning to their natal river during March–May. However, some stocks, or a subset of individuals in a stock, are referred to as fall-run fish and return during November–December. 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. 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).

While in the ocean, little is known about the ocean migration and behavior of steelhead as there has been little directed research on this species (Burgner et al. 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 ocean ecology (Myers 2018). As a result, the current understanding of steelhead ocean 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 et al. 1992; Light et al. 1988; Myers 2018; Sutherland 1973). In general, available information suggests that immature juvenile steelhead from North America quickly migrate from freshwater to offshore waters of the North Pacific Ocean. Based on the distribution of catch in the open ocean, after their first year at sea, ocean age-1 and older steelhead are distributed across the North Pacific Ocean, but are concentrated in the southeastern Gulf of Alaska in the spring and expand westward and northward in the summer (Burgner et al. 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. Even less is known about kelts while in the ocean due to differences in relative abundance between pre-spawn and post-spawn steelhead. However, in general, the migration of kelts is thought to be 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 genetic baselines exist to apportion individuals in high seas catches to individual stocks (Myers 2018).

Understanding the distribution, movement, vertical distribution, and thermal environment of steelhead in the North Pacific Ocean may provide important information to address basic and applied research questions. Therefore, the goal of this study is to provide insights into ocean distribution, movements, behavior, and thermal environment of steelhead kelts from Alaska's largest known population of steelhead, those from the Situk River.

Methods

Fish capture and tagging

The Situk River, near the town of Yakutat, Alaska, sustains the largest known steelhead population and steelhead sport fishery in Alaska. Since 1995, the Alaska Department of Fish and Game (ADF&G) has constructed a bipod and picket weir located on the Situk River, approximately 2.4 river 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). During ADF&G'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 ($n=35$). Tagged steelhead ranged from 630 to 938 mm total length (Table 1; 759 ± 60 mm, mean $\pm$ SD). Tagging only steelhead kelts larger than 60 cm ensured that the tag was <2% of the body weight of the fish, below the commonly accepted

Table 1 Deployment information for 30 pop-up satellite archival tags attached to steelhead from the Situk River in 2018, 2019, and 2020 that provided data used in analyses

Argos ID	Deploy date	Programmed attachment duration	Fork length (cm)	Ocean entry	End date	Ocean days
169144	2018-05-30	120	770	2018-05-31	2018-08-26	86
169146	2018-05-30	120	735	2018-06-01	2018-07-19	47
169154	2018-05-29	30	655	2018-06-03	2018-06-22	19
175618	2018-05-30	180	815	2018-06-03	2018-06-27	24
176929	2019-05-29	180	860	2019-06-02	2019-07-16	44
176930	2019-05-29	180	870	2019-06-03	2019-07-30	57
176932	2019-05-30	180	790	2019-06-02	2019-06-17	15
176933	2019-05-29	180	835	2019-05-31	2019-06-14	14
179508	2019-05-29	180	800	2019-06-02	2019-11-18	170
199387	2020-06-04	180	670	2020-06-09	2020-08-04	56
199389	2020-06-04	180	630	2020-06-08	2020-08-22	75
199393	2020-06-04	180	710	2020-06-09	2020-07-30	51
199398	2020-06-02	240	750	2020-06-04	2020-08-10	67
199400	2020-06-02	240	840	2020-06-05	2020-07-06	31
199401	2020-06-04	240	740	2020-06-09	2020-08-06	58
199404	2020-06-04	240	695	2020-06-08	2020-07-25	47
199406	2020-06-03	240	805	2020-06-08	2021-01-30	236
199407	2020-06-02	240	795	2020-06-07	2020-07-07	30
199489	2020-06-03	240	820	2020-06-07	2020-08-17	71
199490	2020-06-03	240	840	2020-06-09	2020-07-23	44
199491	2020-06-04	240	725	2020-06-09	2020-12-11	185
199492	2020-06-03	240	800	2020-06-07	2020-08-20	74
199497	2020-06-04	240	715	2020-06-08	2020-07-31	54
199500	2020-06-04	180	755	2020-06-08	2020-11-05	150
199501	2020-06-04	180	675	2020-06-09	2020-08-02	54
199502	2020-06-04	180	740	2020-06-08	2020-07-03	25
199504	2020-06-04	180	750	2020-06-08	2020-08-13	67
199505	2020-06-03	180	725	2020-06-09	2020-07-24	45
199506	2020-06-04	180	670	2020-06-07	2020-08-08	62
199508	2020-06-04	180	690	2020-06-08	2020-08-12	66

minimum size threshold for fish tagging (Brown et al. 2010).

Immediately after conducting ADF&G's sampling protocol, steelhead were visually assessed for health based on external appearance and vitality, and the healthiest individuals were selected for tagging. Satellite tags, described subsequently, were attached to steelhead using an attachment system, known as a "tag backpack," refined for similarly sized salmonids, including Dolly Varden char (*Salvelinus malma*) (Courtney et al. 2016a), Chinook salmon (*Oncorhynchus tshawytscha*) (Courtney et al. 2019), and Atlantic salmon (*Salmo salar*) (Strøm et al. 2017). The tag backpack was secured through the dorsal musculature and pterygiophores, anchoring it in the bony fin-ray supports (Courtney et al. 2016b). This tag attachment technique prevents muscle damage and premature rejection of the tether system caused by tearing through muscle tissue due to hydrodynamic drag of the tag. After tagging, steelhead were identified by tag number, and photographed. During the first tagging season, tagged fish were released immediately after tagging; however, 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. During the first two tagging seasons, adult female kelts were exclusively selected for tagging as they have higher post-spawn survival rates than males (Evans et al. 2008; Keefer et al. 2008, 2018). In the last year of tagging, which had a relatively large sample size ($n=35$) compared to previous years, four healthy males also were tagged to ensure all tags were deployed (Seitz et al. 2021).

Tag specifications and data acquisition

Pop-up Satellite Archival Tags (PSATs; MiniPAT model, Wildlife Computers; Redmond, WA; https://wildlifecomputers.com/our-tags/minipat/) weighed 60 g in air and were slightly buoyant. While attached to a fish, the PSATs measured and archived temperature, depth, and ambient light data at user-programmable intervals (1–3 s in this study). After releasing from the fish, the tags floated to the surface of the sea and transmitted, via satellite (Argos Satellite System), summarized temperature and depth data (resolution 1.25–10 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 of time (3–7 days in this study), or if the tag recorded depths > 1700 m to avoid extreme pressures that could damage the tag. The tag's fail-safe release mechanism detection protocol was 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 regular but varying depth and temperature data "typical" of steelhead were considered to be alive at the pop-up date. Mortality was assigned to steelhead whose tags recorded suspicious and anomalous readings that were inconsistent with those "typical" of steelhead. Specifically, unknown mortality was inferred when tag data suggested that the tagged steelhead died and sank to the sea floor (or > 1700 m), before the tag detached from the carcass, floated to the surface, and transmitted to satellites (Lacroix 2014; Seitz et al. 2019; Strøm et al. 2019). Mortality caused by 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), suggesting that the fish and PSAT had been consumed by a marine predator, similar to past research (Lacroix 2014; Seitz et al. 2019; Strøm et al. 2019).

To provide insights into the horizontal movement of tagged steelhead, tag end locations were mapped in GIS software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California). 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·day^{-1} was assumed in all individual models.

To provide insights into the behavior and thermal environment occupied by tagged steelhead, each fish's occupied depth and temperature were examined by visually inspecting all time-series data, and calculating descriptive statistics (mean, minimum, maximum, standard deviation) for data from each individual tag and for all aggregated data. Additionally, the grand mean proportion (±SD) of time that tagged steelhead spent at depth (0–5, 5–10, 10–15, 15–20, > 20 depth bins) and temperature (1 °C bins) intervals was calculated for aggregated data, and for each year of the study. To examine potential diel differences in the occupied depths of steelhead, daily periods of night (nocturnal) and day (diurnal) were determined for each tag record at the daily estimated location of each tagged fish, using the function "crepuscule" from the "maptools" R package. A Wilcoxon signed-rank test was used to test for differences in occupied depths between periods of night and day ($\alpha=0.05$). Additionally, a chi-squared test was used to test whether the number of deep (> 35 m) dives differed between periods of night and day ($\alpha=0.05$).

Results

Summary

The majority (59/63) of PSATs reported to satellites, and provided pop-up locations while the remaining tags never transmitted to satellites and were considered missing ($n=3$), or recovered from the lower Situk River before data transmission initiated ($n=1$). Of the tags that transmitted to satellites, 15 tags reported from the shore adjacent to the lower Situk River/Lagoon. The remaining tags ($n=44$) reported from the ocean. Of these 44 tags, 14 were inferred to release from live steelhead; 10 had depth, temperature, and light readings associated with predation by a marine predator; and 20 were associated with unknown mortality events. Data from these predation/mortality events were removed from all analyses and as such, only data from before mortality events were used for analyses. Additionally, only data from 30 tags with greater than 2 weeks of ocean data (i.e., ocean entry to end date) were used in data analyses. These 30 tags provided a total of 2034 days of ocean data (68 ± 52 data days per tag, mean ± SD).

Spatial distribution

End locations of tagged steelhead ($n=30$ used in analyses) were all west of the Situk River, AK, occurring throughout the northern Gulf of Alaska, the Aleutian Islands, and into the Bering Sea as far west as approximately 650 km east of the Kamchatka Peninsula, Russia (Fig. 1). Based on depth and temperature records, tagged steelhead were inferred to have exited Situk River from 31 May to 9 June, on average 3.2 (± 1.1 SD; range 0.6–5.9 days; $n=44$) days after release from tagging. After ocean entry, regardless of year, tagged steelhead quickly dispersed westward across the Gulf of Alaska in the Alaska Coastal Current and Alaska Stream, while remaining near the continental slope (Fig. 1). By the end of July, most tagged steelhead were located near 160°W longitude, south of the Alaska Peninsula. For tagged steelhead with tags attached past the month of July ($n=15$), they continued to progress in a westerly direction until approximately September–November when net-westerly movement ceased (Figs. 1 and 2). Displacement, straight-line distance between tagging and end locations of tagged steelhead ranged from 200 to 3119 km (Table 2: Fig. 2). Curvilinear track distance determined from daily location estimates ranged from 205 to 3805 km (Table 2: Fig. 2).

Depth and temperature occupancy

While occupying waters of the North Pacific Ocean from the months of June to January, tagged steelhead were largely surface oriented (2.5 ± 1.3 m, grand mean ± SD), spending the majority (> 90% of all recorded depths) of their time in the first 5 m of the water (Table 2: Fig. 3). Diving behavior varied among individual tagged fish, with dives down to 5–10 m being common (Figs. 3 and 4). Although the majority of tagged steelhead ($n=28/30$ used in analyses) recorded dives > 20 m, these dives were rare, accounting for < 1% of recorded depths. Maximum dives of tagged steelhead ranged up to 134 m, with 16 steelhead recording depths > 50 m Table (2). The deep dives were rare (< 0.1% of all records), and appeared to occur during short bouts of < 15 min (Fig. 5). Overall, depth distributions of tagged steelhead were similar among years (Fig. 3).

In addition, while occupying waters of the North Pacific Ocean 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 (Table 2; Fig. 3). Mean temperatures experienced by individual tagged fish were 8.4–12.7 °C (11.6 ± 1.1; grand mean ± SD), and when aggregated, they spent 79% of the time between 9 and 13 °C (Table 2).

While the amount of data from tagged steelhead was not equal among months, there were little observed differences in seasonal depth distributions as all monthly aggregated median occupied depths were < 3 m (Fig. 6). 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 (Fig. 6).

There were no statistical differences in occupied depths between periods of night and day (Wilcoxon signed-rank test, $V=184$, $p=0.33$) (Fig. 7). However, even though depth distributions were similar during periods of light and darkness, dives deeper than 35 m occurred significantly more often during

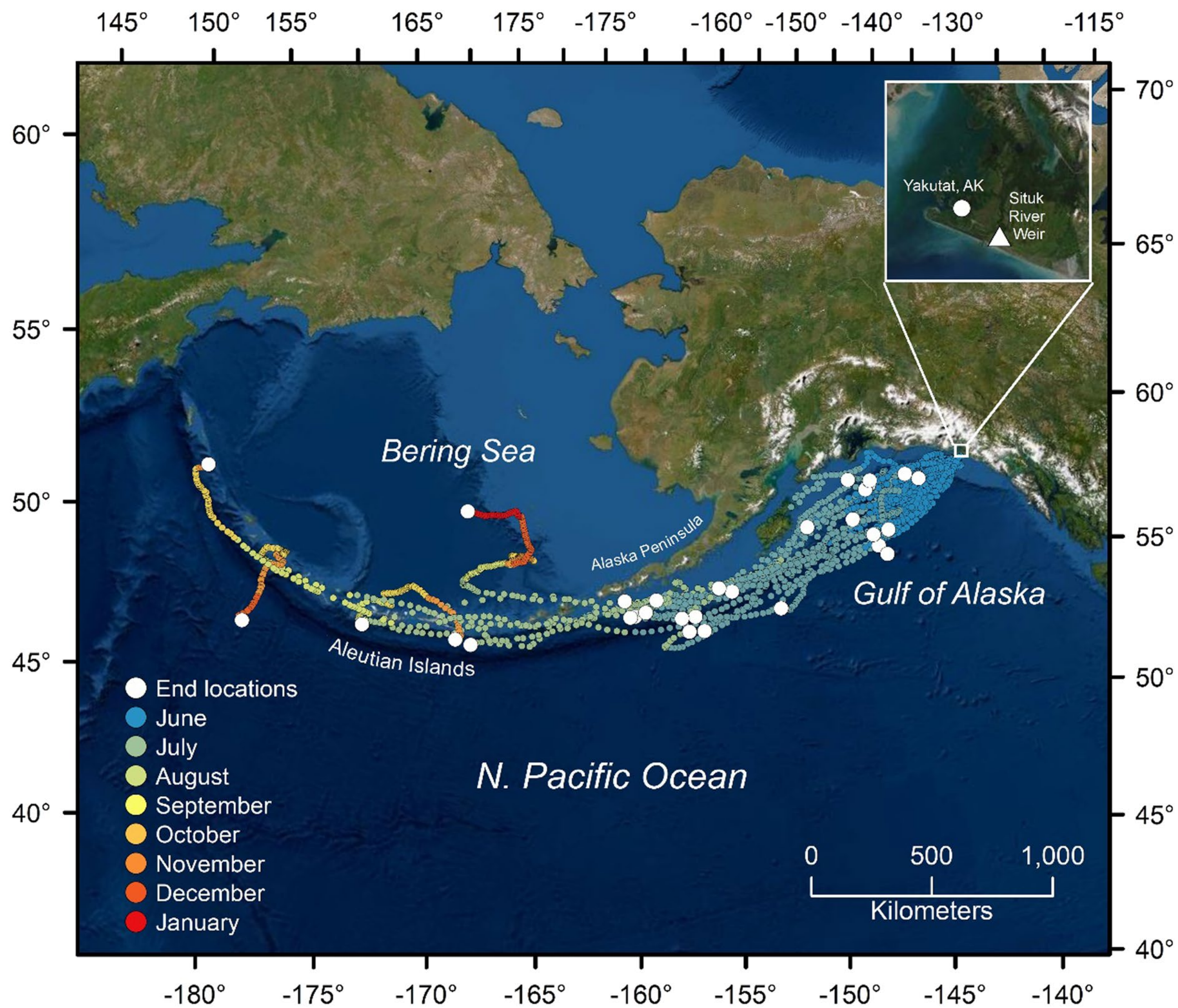

Fig. 1 End locations of the satellite tags (white dots) attached to steelhead in the Situk River, AK. Circles color-coded by month denote daily locations of tagged steelhead estimated by a hidden Markov model

periods of night compared to day (chi-square test, $X^2 = 67.7$, $p < 0.01$) (Fig. 5).

Discussion

Satellite telemetry provided some of the first detailed insights into the ocean ecology of steelhead kelts from North America. These fish participated in extensive post-spawning migrations that extended to the western North Pacific Ocean, and as far north as the central Bering Sea. While undertaking this westerly ocean migration, depth and temperature data provided information about the timing of outmigration into the ocean, depth distributions, diving behaviors, and occupied thermal environment of steelhead in the North Pacific Ocean.

PSATs 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 North American steelhead as broadly distributed in the North Pacific Ocean, particularly

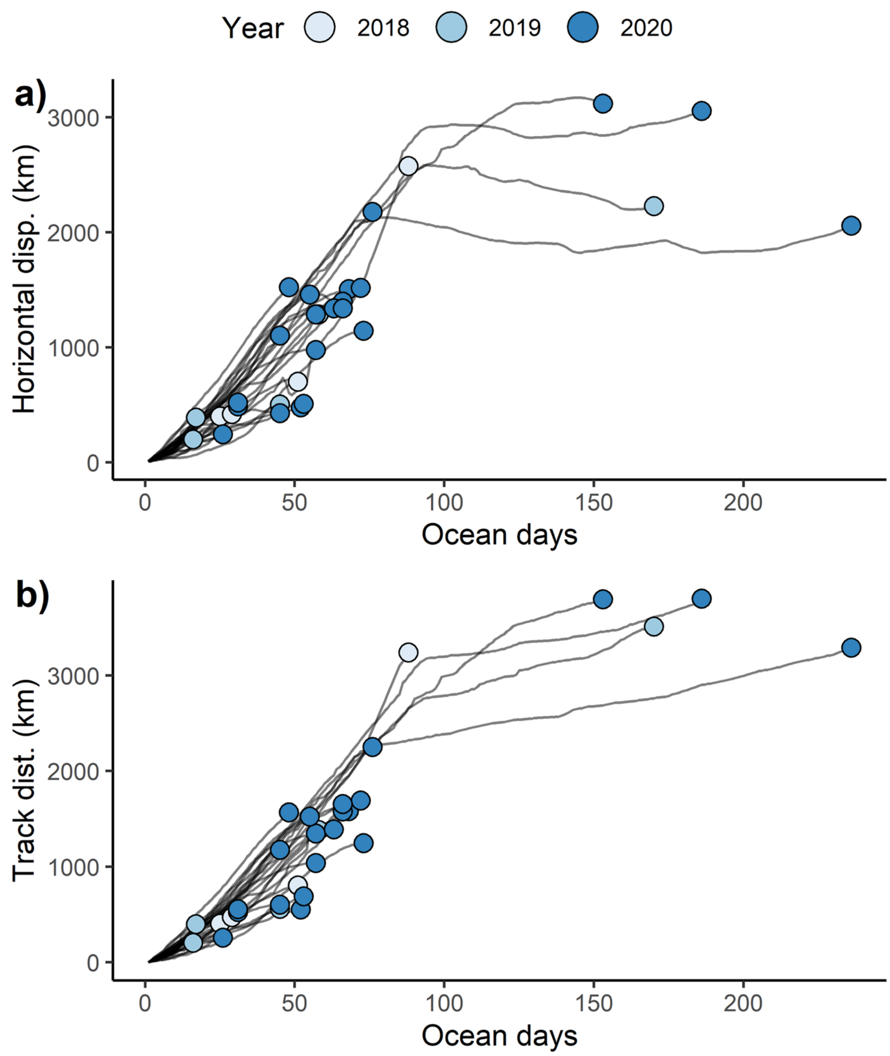

Fig. 2 Relationship between the horizontal displacement (**a**), track distance (**b**), and ocean days of tagged steelhead kelts from the Situk River, AK. Circles, color-coded by the year steelhead were tagged, indicate the last day each tag was attached to a fish. Lines portray the cumulative horizontal displacement (**a**) and track distance (**b**) for each day for tagged steelhead

near the Aleutian Islands (Burgner et al. 1992; Light et al. 1988; Myers 2018). While the ocean 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 et al. 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. The extensive migration of kelts also is consistent with past research that has suggested that those from small coastal river systems like the Situk River, AK, have more extensive migrations than those from large rivers with large estuary systems (Hayes et al. 2012; Nielsen et al. 2011; Pavlov and Savvaitova 2008; Teo et al. 2013).

Most previous research on steelhead has suggested that this species' ocean distribution is primarily governed by individuals actively avoiding temperatures outside of a specified window (Sutherland 1973; Welch et al. 1998). This suggestion is supported by bioenergetics research that suggests that steelhead have a narrow temperature window to achieve optimal growth (Atcheson et al. 2012a). In this "thermal limits" hypothesis, steelhead are thought mainly to be distributed between the 5 and 15°C sea surface temperature isotherms, which is supported by field-based research (Welch et al. 1998). To maintain this thermal environment, steelhead are thought to make seasonal movements across the North Pacific Ocean (Burgner et al. 1992; Light et al. 1988; Myers 2018), shifting north and west during the summer and south and east

Table 2 Summary of depth and temperatures occupied by steelhead kelts from the Situk River tagged with pop-up satellite archival tags in 2018, 2019, and 2020

Argos ID	Mean (±SD) depth (m)	Depth range (m)	Mean (±SD) temperature (°C)	Temperature range (°C)	Displacement (km)	Track distance (km)
169144	1.4±1.5	0–20	11.1±1.4	6.2–14.5	2577	3240
169146	1.6±2.0	0–66	11.2±1.0	6.3–13.8	704	805
169154	3.7±4.2	0–36	10.3±0.4	7.5–11.7	402	407
175618	2.0±1.7	0–25	10.9±0.9	7.7–13.0	421	472
176929	4.1±3.2	0–63	12.6±0.7	6.9–15.6	506	561
176930	3.0±1.6	0–79	12.7±1.0	6.9–15.6	1287	1385
176932	1.3±1.9	0–91	12.1±0.7	6.4–15.3	200	205
176933	1.0±1.8	0–73	11.9±0.7	7.2–13.5	392	399
179508	3.0±2.8	0–25	10.2±1.8	7.1–13.1	2228	3512
199387	6.1±7.8	0–43	12.0±1.2	6.7–14.4	978	1041
199389	3.4±2.7	0–34	11.9±0.8	7.9–14.2	2178	2252
199393	4.8±6.8	0–105	12.6±1.4	5.6–16.0	479	556
199398	2.5±1.7	0–69	12.0±0.9	4.6–15.1	1507	1583
199400	1.7±3.7	0–128	11.2±0.6	6.4–12.6	489	528
199401	2.3±1.7	0–58	12.2±1.0	6.7–15.7	1288	1347
199404	1.3±1.4	0–35	11.8±0.7	8.3–13.4	1525	1570
199406	3.0±2.5	0–38	8.4±3.1	4.3–14.0	2057	3290
199407	2.5±2.5	0–34	12.1±0.8	7.6–13.6	521	559
199489	0.9±1.9	0–134	12.0±0.9	5.8–14.8	1518	1693
199490	0.6±0.3	0–4	12.3±0.8	9.3–14.4	1103	1178
199491	1.7±2.9	0–77	9.1±2.6	5.2–14.9	3054	3805
199492	2.4±1.7	0–82	12.5±0.9	6.1–15.0	1145	1246
199497	3.0±3.1	0–56	12.7±1.2	6.1–15.1	510	691
199500	2.2±1.7	0–86	9.7±2.2	5.1–14.3	3119	3797
199501	2.0±0.5	0–24	12.3±0.8	8.1–15.2	1460	1525
199502	5.7±7.2	0–102	11.6±0.9	6.0–13.9	244	261
199504	1.6±1.6	0–36	12.1±1.0	9.0–15.1	1398	1580
199505	1.6±0.8	0–45	12.2±0.9	6.6–14.4	430	604
199506	1.7±4.1	0–74	12.1±1.1	5.9–15.1	1339	1393
199508	1.7±0.5	0–7	12.0±0.6	9.6–14.8	1341	1656

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

b) Track distance refers to curvilinear distance swam by the fish between tagging and end locations, calculated as the sum of distances between daily position estimates produced by a hidden Markov model

during autumn and winter, similar to seasonal movements displayed by other species of salmonids (Myers 2018; Myers et al. 2007). The temperature data collected by steelhead in this study provide additional evidence that this species primarily occupies surface waters in this previously described thermal range. For example, 99.9% of all recorded temperatures experienced by tagged steelhead were between 5 and 15°C. Furthermore, these results may suggest that not only the horizontal distribution but also the vertical distribution is related to these thermal limits.

Although the temperature data collected in this study generally agree with the thermal limits hypothesis (Welch et al. 1998), one exception to this is the tagged steelhead that reported 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

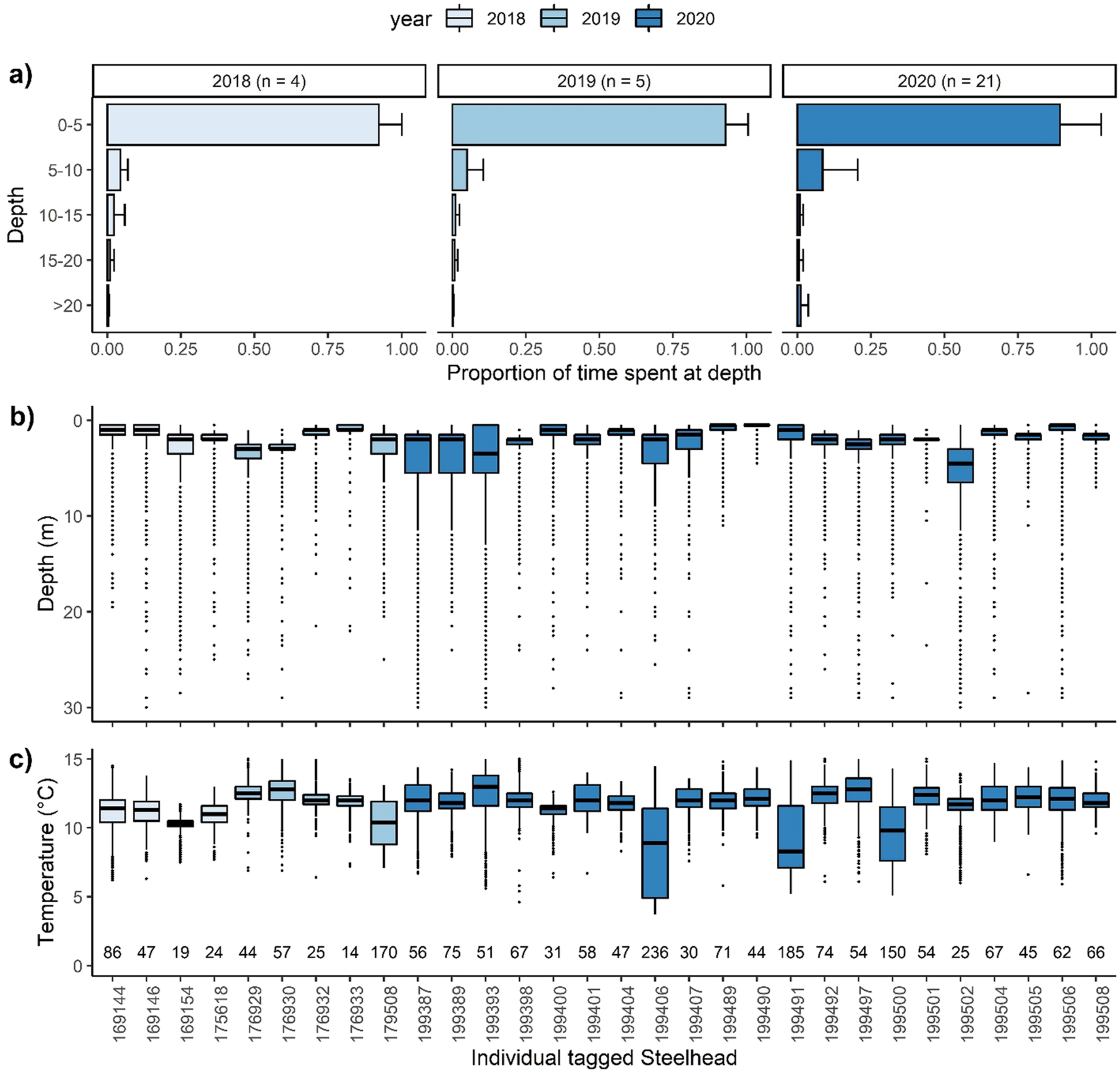

Fig. 3 Marine depth and temperatures experienced by tagged steelhead from the Situk River, AK. Panel (**a**) denotes the grand mean proportion (±SD) of time spent at depth (m) by study year. Panels (**b**) and (**c**) are boxplots of depth and temperature occupied by individual tagged steelhead. Tag identification numbers for individual steelhead in panels (**b**) and (**c**) are below the x-axis of panel (**c**). Additionally, ocean data days for each tag are noted above the x-axis of panel (**c**). For boxplots, median diving depths 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

some evidence of steelhead overwintering in a thermal environment of ~4 °C. This fish was outside of the commonly assumed winter distribution of North American steelhead that is thought to occur in the central/eastern Gulf of Alaska (Burgner et al. 1992; Light et al. 1988; Myers 2018). The discrepancy of overwintering locations is likely due to the poor understanding of true winter distribution owing to nearly non-existent research during the winter months (Myers 2018). Furthermore, wintering in the Bering Sea should not be totally unexpected, as the lower thermal limit for steelhead is not well

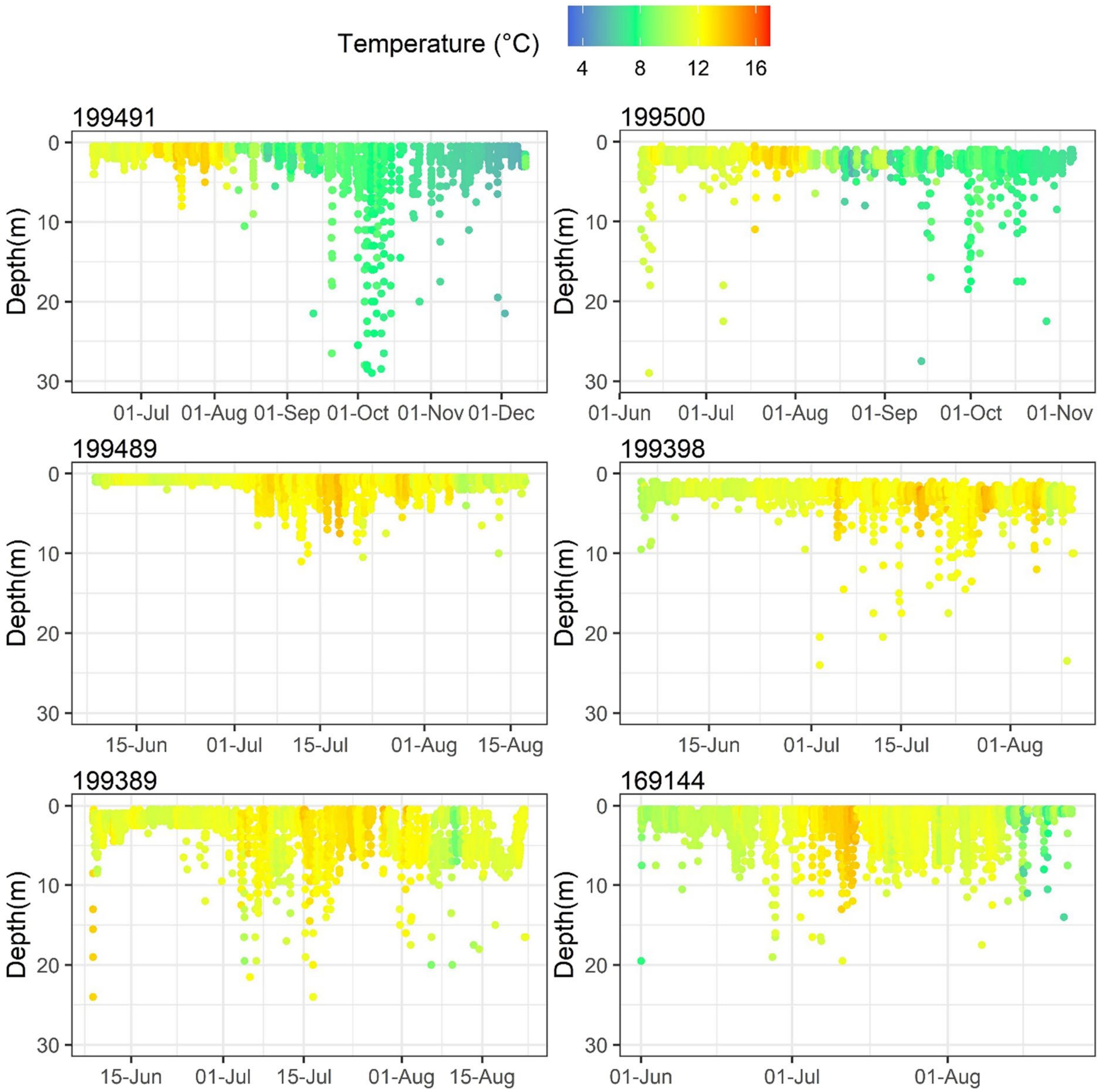

Fig. 4 Representative examples of time-series data from pop-up satellite archival tags attached to steelhead in the Situk River, AK, with > 60 ocean data days. Circles are individual depth measurements, color-coded by the corresponding temperature. Tag identification number is noted for reference purposes

defined due to a lack of catch and temperature data during the winter months (Welch et al. 1998), and due to the likelihood that older age classes of steelhead likely have lower thermal preferences than younger immature steelhead on which most assumptions are based on (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. Increases in sea surface temperatures due to anthropogenic climate change have been predicted to shift steelhead

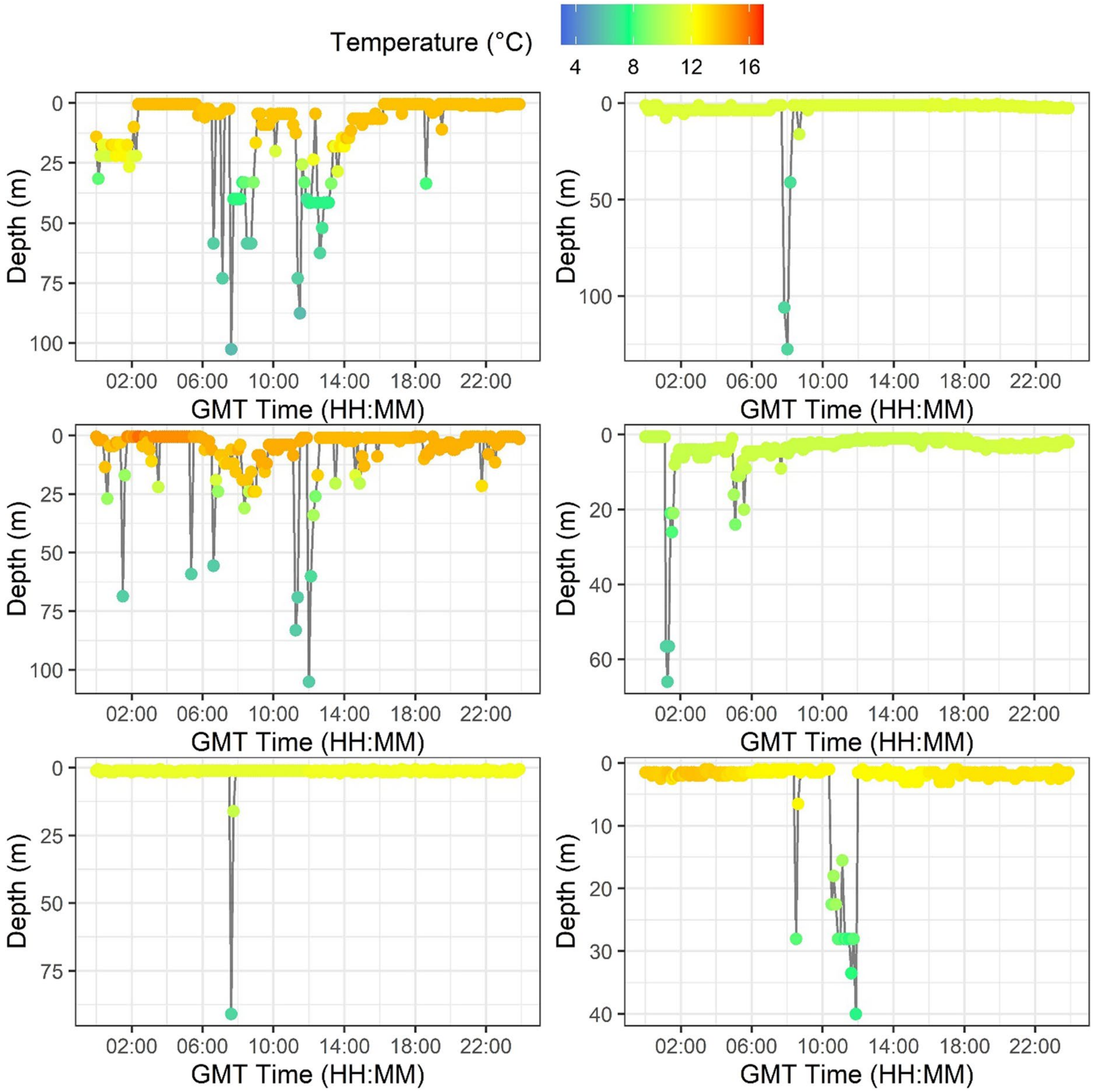

Fig. 5 Examples of deep diving activity by tagged steelhead from the Situk River, AK. Circles are individual depth measurements, color-coded by the corresponding temperature

seasonal distributions further north, including into the Bering Sea during the winter months (Abdul-Aziz et al. 2011). While it is important to acknowledge the small sample size in this study, most notably during the winter months, these results hint at a more northerly winter distribution of steelhead kelts than previously described.

While occupying offshore waters of the North Pacific Ocean, tagged steelhead were largely surface oriented, spending the majority of their time in the first 5 m of the water column. 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,

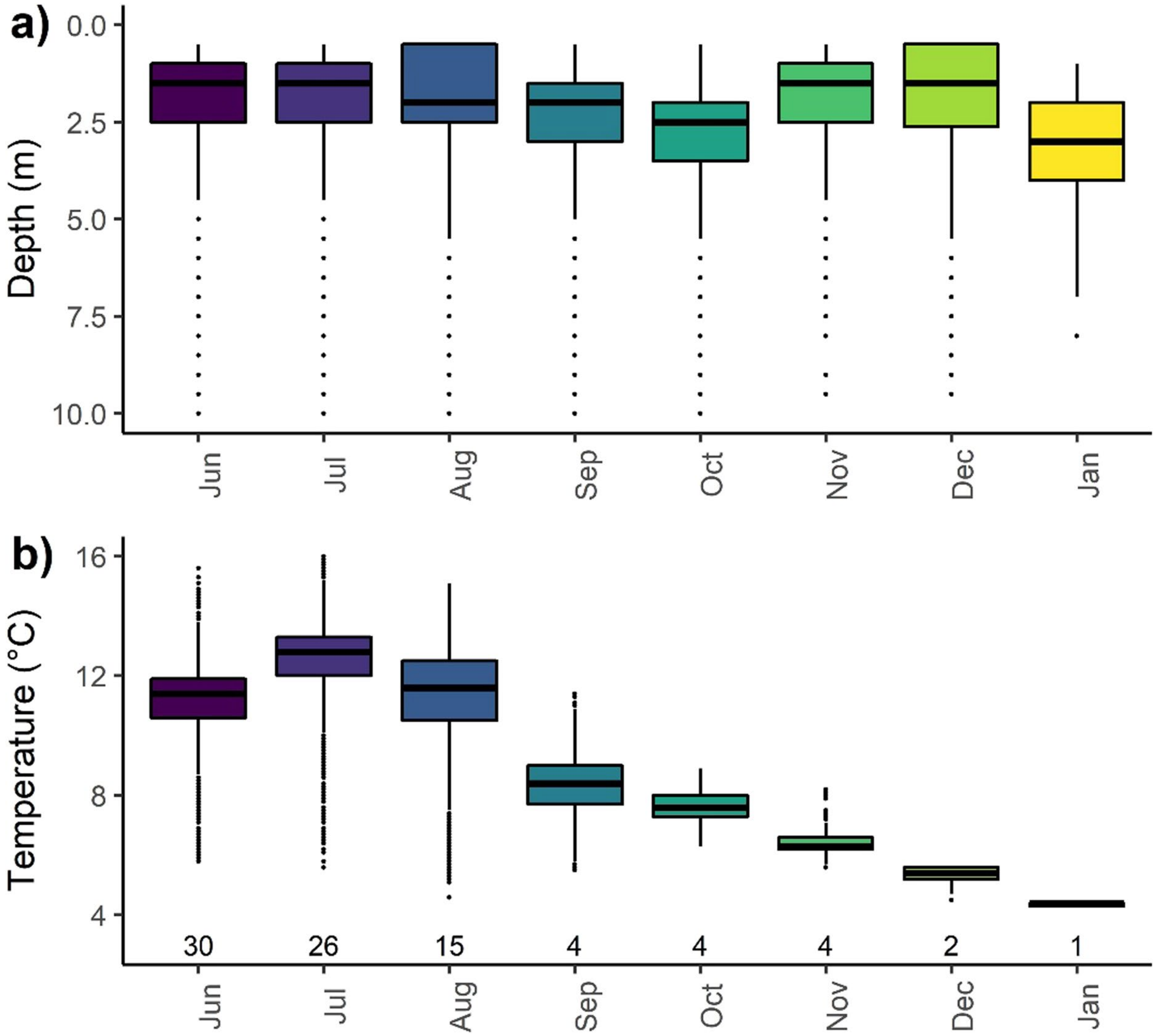

Fig. 6 Depth (**a**) and temperature (**b**) distributions of tagged steelhead ($n=30$) by month of year. Boxplots show the aggregated data for all tagged fish. Monthly sample size (satellite tags per month) is noted above x-axis. For boxplots, median diving depths are solid lines, and boxes represent 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

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). Furthermore, 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 this 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, many months, and among years of this study, supporting this claim. In contrast, other salmonids including Chinook salmon have been documented to 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

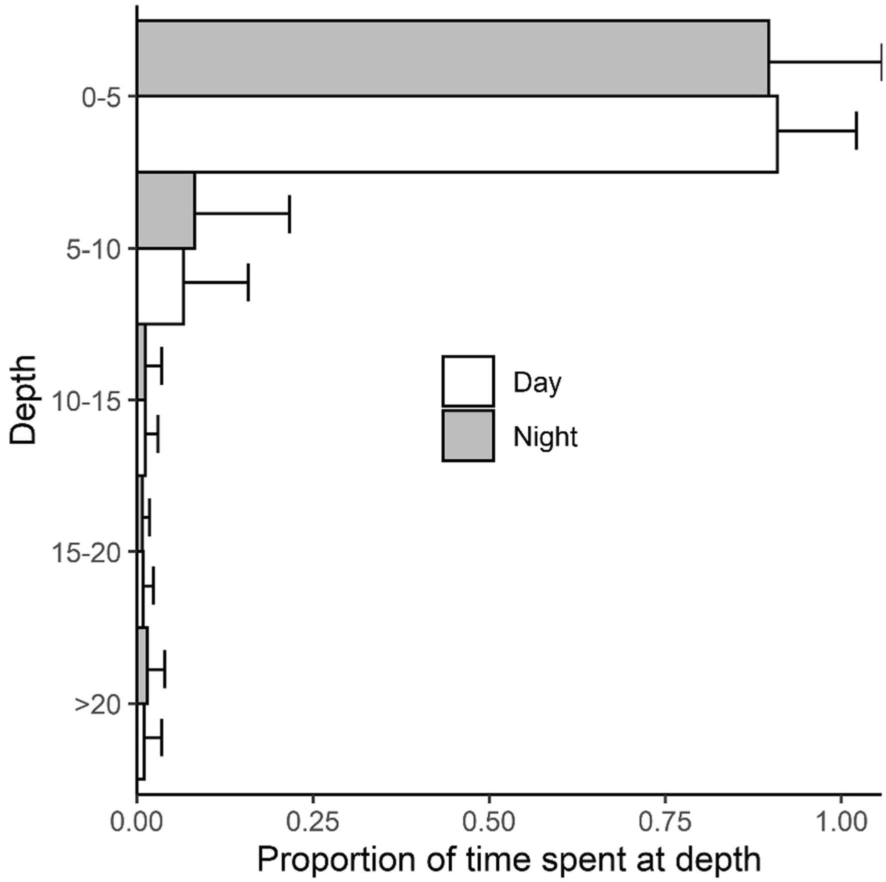

Fig. 7 Grand mean proportion (± SD) of time spent at depth (m) of tagged steelhead by periods of day and night

the water column and changes 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 past acoustically tagged steelhead in the Pacific Ocean (Ogura and Aria 1993), and that of archival tagged steelhead from the Ninilchik River, AK, which spent 16 months at sea (Nielsen et al. 2011). In contrast to these results, evidence from other research indicates that in some places at some times, steelhead kelts demonstrate diel differences in swimming behavior. Steelhead kelts from the Sacramento River tagged with archival tags occupied deeper depths during the night while occupying coastal waters near California (Teo et al. 2013). In contrast, temperature data from one archival tag attached to a steelhead in the Gulf of Alaska suggested that the tagged steelhead occupied deeper depths during the day compared to night (Walker et al. 2000). Finally, acoustic tags attached to mature homing steelhead in a fjord in British Columbia were found to occupy shallower mean depths and have faster travel rates during the day compared to night (Ruggerone et al. 1990). These reported differences in diel depth distributions of steelhead are likely influenced by many regional factors including predator avoidance behaviors, thermoregulation, or foraging tactics tailored around regional distributions and behavior of preferred prey. While no observable diel-specific behaviors were evident in this study, the overall shallow distributions of tagged steelhead may have masked subtle or periodic (e.g., scale of days) diel depth-based behaviors. Such subtle and periodic occurrence of diel diving behaviors has been documented in other salmonids (Courtney et al. 2019, 2021; 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 that this region is an important feeding ground for steelhead kelts from the Situk River, and thus may play a critical role in the successful reconditioning of repeat spawners in this population. The biological importance of the area is reinforced by many large commercial fisheries that occur in this area (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). The high biological production is thought to arise from an overall west and northward transport of well-mixed nutrient-rich waters 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).

While in this biologically productive area, the shallow depth distributions by tagged steelhead support previous research that suggests that steelhead primarily feed in the surface waters (Burgner et al. 1992; Taylor and LeBrasseur 1957). While past research has documented regional and interannual variation in steelhead diets, steelhead in the open ocean are thought to principally 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 were undertaken by several tagged steelhead in this study; however, these dives were relatively rare and occurred over short bouts of times. Given the overall high mortality rates of tagged steelhead in this study (Seitz et al. 2021), this deep diving behavior may be due to natural and/or tag-induced predator avoidance responses. However, many other factors could influence these rare deep diving events. For example, there was a tendency for these deep dives to occur during the westerly transit period in June and July to inferred feeding grounds near the Aleutian Islands and Bering Sea, even though mortality of tagged steelhead occurred over all seasons of this study. Thus, these deep dives may be orientation/navigation behaviors that are manifested as quick dives. 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).

It is important to recognize that the use of PSATs in this study may have introduced some behavioral bias to the results. While the energetic cost and behavioral effects of towing PSATs on swimming performance of fishes are poorly understood, results from recent laboratory research (Burgerhout et al. 2011; Lynch et al. 2017; McGuigan et al. 2021; Methling et al. 2011) have provided mixed results, suggesting that fish kinematics, swimming speed, and size are all factors influencing tagging effects. For example, past research has shown that externally attached PSATs can negatively affect the swimming performance and energetics of European eels (*Anguilla Anguilla*) (Burgerhout et al. 2011; Methling et al. 2011). However, research on larger fishes, including young-adult Mahi-Mahi (*Coryphaena hippurus*) and juvenile sandbar sharks (*Carcharhinus plumbeus*), has reported minimal impacts of externally attached PSATs on the metabolic cost of transport and swimming kinematics of these species (Lynch et al. 2017; McGuigan et al. 2021). While laboratory studies on the effects of salmonids towing PSATs do not currently exist, future research on this topic would be valuable to understand the possible changes in behavior or increased metabolic costs associated with this research tool.

While we studied the ocean ecology of steelhead kelts from one population in Southeast Alaska, our results may be pertinent for other populations throughout the west coast of 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), but populations further south, including those in the Pacific Northwest, have seen drastic declines since the 1980s with poor marine survival for fish from most systems (Kendall et al. 2017), highlighting 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 (i.e., kelt) is useful for understanding steelhead population dynamics and current trends in 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 important for a holistic understanding of steelhead migratory characteristics throughout their range, and assessing potential impacts of human activities, such as hydrocarbon exploration and fishing.

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Data availability The datasets used and/or analyzed during the current study are available on the Animal Telemetry Network.

Declarations

Ethics approval and consent to participate All fieldwork was conducted under 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 (Catterson and Peterson 2019; Catterson and Power 2018).

Consent for publication The authors accept the publication.

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