



Movements of anadromous coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in Puget Sound, Washington, USA

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Received: 23 October 2023 / Accepted: 3 March 2024
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Abstract Anadromous salmonid species vary in their use of open ocean, coastal, and inland marine waters. To better understand this diversity in behavior and habitat use, 120 coastal cutthroat trout, *Oncorhynchus clarkii clarkii*, were caught in southern Puget Sound, Washington, USA, tagged with acoustic transmitters, and 95 were detected by a network of receiver stations. Despite sufficient time to reach other parts of the Salish Sea where many receivers operated, none was detected beyond southern Puget Sound, indicating localized movements. Within southern Puget Sound, fish were detected at 34 of 127 receivers in marine sites throughout the year but especially in spring and fall. Most detection events (between first and last detections at a given receiver) were brief (60.5% were ≤ 2 h and 76.8% ≤ 6 h),

indicating movement along the shoreline. However, 823 events (12.8%) exceeded 12 h and 222 (3.4%) exceeded 24 h at a receiver, indicating longer occupancy at certain sites and by certain individuals. The detections also indicated that cutthroat trout were active throughout the 24-h period, but they moved more often at night and less often in other periods than would occur by chance, and they moved more often on ebbing and flooding tides and less often at slack periods. Fish with pressure-sensitive transmitters were almost always (97.3% of records) within 2.5 m of the surface and 76.8% between 1 – 2 m, despite deeper and shallower waters nearby where they could have been detected. The data provide new insights into the behavior of this species, whose marine ecology has not been extensively studied,

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and differs markedly from the region's other native salmonids.

Keywords Diel depth distribution · Home range · Movements · Salmonids · Salish Sea · Telemetry

Introduction

Anadromy is widely distributed among teleost fishes (McDowall 1988) including salmonids, and the species in this family vary greatly in the extent and patterns of anadromy, and related life history traits such as maximum size, growth rate, age at maturity, and the prevalence of repeat spawning (Rounsefell 1958; Quinn and Myers 2004; Spares et al. 2015a). Within this family, the separation between Atlantic (genus *Salmo*) and Pacific (genus *Oncorhynchus*) lineages allows comparisons of patterns (Hansen and Quinn 1998). For example, Atlantic salmon, *S. salar*, typically migrate long distances and spend one or more years at sea before returning to spawn (Jonsson and Jonsson 2011). In contrast, anadromous brown trout, *S. trutta* (known as sea trout) tend to spend less than a year at a time in marine waters (Berg and Berg 1989; Jonsson and Jonsson 2002) and stay near their natal stream (Berg and Berg 1987). Acoustic tracking has revealed movements of sea trout in estuary and marine habitats after leaving natal rivers (Middlemas et al. 2009; Davidsen et al. 2014), and variation among individuals in movement patterns (Jensen and Rikardsen 2012; Eldøy et al. 2015).

Pacific salmon in the genus *Oncorhynchus* typically migrate long distances at sea and spend one or more winters there prior to maturation (Beamish 2018). These patterns are also prevalent in steelhead, the anadromous form of rainbow trout, *O. mykiss* (Myers 2018), and this species is similar in many ways to Atlantic salmon (Hayes and Kocik 2014). The most limited migrations, in distance and duration, of anadromous *Oncorhynchus* spp. seem to occur in coastal cutthroat trout, *O. clarkii clarkii* (Pearcy et al. 2018). Like brown trout, cutthroat trout is a highly diverse species, and the coastal subspecies is the only one of many that is anadromous (Behnke 1992). Coastal cutthroat trout (henceforth, for simplicity, cutthroat trout) range from northern California to Prince William Sound, Alaska, and inland to the crests of the Coast Mountains and Cascade

Range (Behnke 1992). Their diverse life history patterns including stream resident, adfluvial, and anadromous forms (Trotter 1989; Arostegui and Quinn 2019b), and are similar in many ways to brown trout (Losee et al. 2023a). The general pattern is for anadromous cutthroat trout to rear in their natal stream for 1–4 years, migrate to marine waters and spend ca. 4–11 months there, return to fresh water, spawn in the spring, and then return to marine waters (Trotter 1989; Johnson et al. 1999; Percy et al. 2018).

Seaward migration of coastal cutthroat trout occurs primarily in April and May (Burns et al. 2021). The duration of marine residence ranges from ca. 3 months in Alaska (Armstrong 1971), to about 6 months in coastal Oregon (Sumner 1962) and 9 months or more in parts of Puget Sound, Washington (Wenburger 1998; Claiborne et al. 2020). Given 4–9 months at sea and an optimal foraging and cruising speed of about 1 body length/sec (Ware 1978), they could travel over 1000 km but tend to move less than about 70 km from natal streams in southeastern Alaska (Jones 1976) and Puget Sound (Goetz et al. 2013; Johnston 1982). Anglers' lore (Raymond 1996; Johnson 2004; Stoll 2017) is consistent with a combination of tagging and genetic research suggesting that populations in protected marine waters tend not to cross open water or move far from their natal rivers (Campton and Utter 1987; Wenburger and Bentzen 2001; Goetz et al. 2013; Losee et al. 2017). In contrast, some cutthroat trout along the Pacific Ocean coast feed in offshore waters (Percy et al. 1990, 2018), though others remain in natal estuaries (Krentz 2007), highlighting the diversity in movement patterns in the subspecies.

The Puget Sound cutthroat trout populations may differ from those along the Washington coast and elsewhere but information on them is limited (Johnson et al. 1999). The populations are wild, without long-term tagging programs typical of hatchery populations, and information on their movements is largely inferred from acoustic tracking in one region, Hood Canal (Goetz et al. 2013), and a combination of research seining efforts, genetic analyses, redd surveys, and conventional tagging in southern Puget Sound (Losee et al. 2016, 2017, 2018). Current Washington fishing regulations allow anglers to retain cutthroat trout caught in fresh water without recording their catch, and prohibit their retention in Puget Sound marine waters, and the species is not

fished commercially. Consequently, there are no catch records from which to infer seasonal movement patterns—noted in the assessment of their status (Johnson et al. 1999).

The overall objective of this study was to characterize cutthroat trout movements in southern Puget Sound marine waters by acoustic tracking. Specifically, we investigated movement patterns of tagged fish to determine 1) the extent of movement beyond southern Puget Sound, 2) the seasonal movements (including use of a stream, Skookum Creek), 3) the tendency to have home ranges or move continuously along shorelines, 4) diel and tidal patterns of movement, and 5) the depth distribution over the diel period for individuals with pressure-sensitive transmitters. These data allowed us to compare

their depth distribution with lacustrine conspecifics (Thomas et al. 2023), other salmonids in Puget Sound (Arostegui et al. 2017a; Smith et al. 2015), and with brown trout and Arctic char, *Salvelinus alpinus*, – two species showing some similarities in life history and ecology (Rikardsen et al. 2007; Mulder et al. 2020).

Materials and methods

Study sites and tagging

The study sites were selected from habitats in southern Puget Sound (Fig. 1) where anadromous cutthroat trout are commonly encountered: gravel beaches with tidal currents, woody debris, shell hash and rocks,

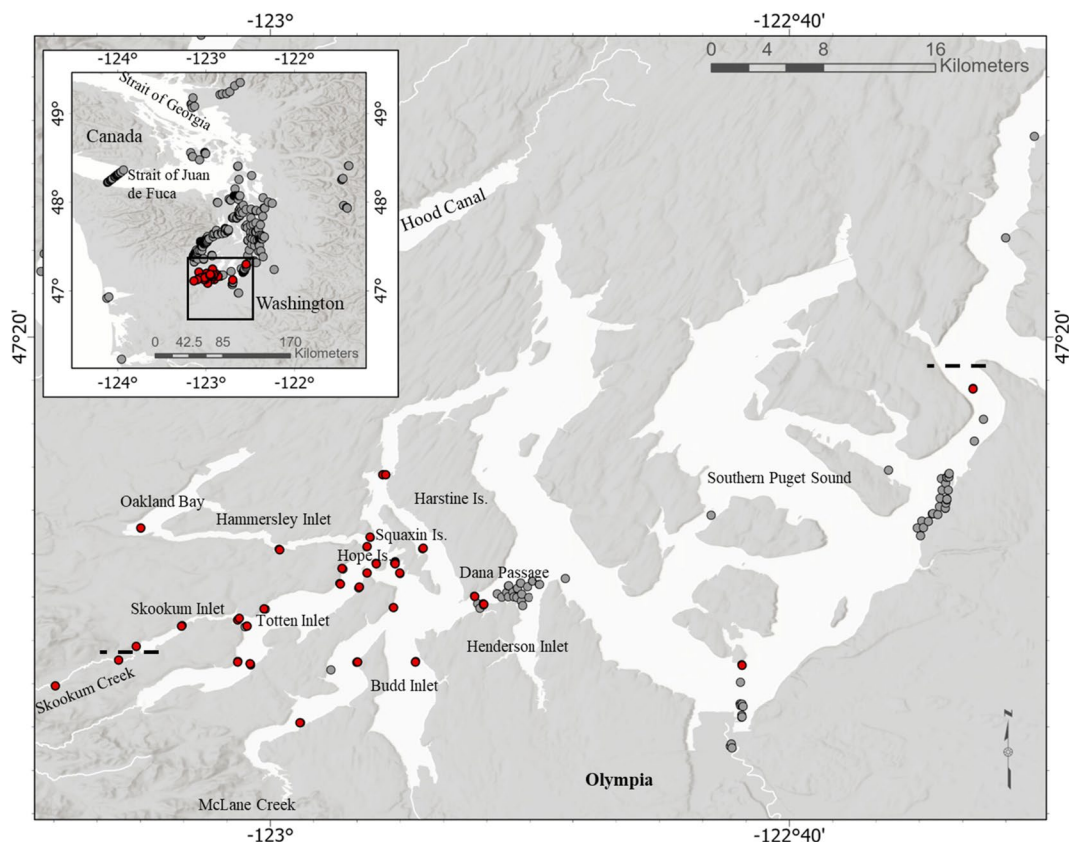


Fig. 1 Map of northwestern Washington, USA and southwestern British Columbia, Canada (inset) and more detailed map showing the distribution of 483 acoustic receivers operational during the period when coastal cutthroat trout were tagged in southern Puget Sound, Washington. Red and gray circles indicate receivers that did or did not detect tagged fish, respec-

tively, during the study. The dashed line in Skookum Creek separates the two receivers in the stream from those in marine waters, and the dashed line on the right side separates the region we designated as southern Puget Sound from regions to the north for purposes of analysis

rather than sandy or muddy habitats (Losee et al. 2017). This part of Puget Sound has many inlets fed by small streams whereas the central and northern parts of Puget Sound are much wider, less indented, and primarily fed by larger rivers (Burns 1985). All fish were captured using angling gear with barbless hooks in the spring (24 fish in April and 7 in May) and fall (40 in September, 39 in October, and 10 in November) and immediately transferred in a holding container to a surgical location nearby (Haque 2008). Fish were anesthetized in a bath of 70 mg/L MS-222 buffered to neutral pH. Fish were measured (fork length), then transferred to a foam V-block and a solution of 40 mg/L neutrally buffered MS-222 was pumped over the gills during the surgical procedure. All surgical instruments and transmitters were soaked in ethyl alcohol followed by a distilled water rinse. An incision was made anterior to the pelvic girdle and the transmitter was inserted into the peritoneal cavity. The incision was then closed with 1–2 sutures of sterile monofilament. Fish were then placed in an oxygenated recovery tank and observed for 15–30 min prior to release at or near the capture site in one of five focal areas: Hope Island ($n=22$), Oakland Bay ($n=20$), Skookum Inlet ($n=29$), Squaxin Island ($n=31$), and Totten Inlet ($n=18$). Various Vemco™ transmitters were used depending on the fish's size; > 90% were V9 (9 mm×31 mm), with a few V7 (7 mm×22.5 mm) and V13 (13 mm×45 mm), with 90 s delay and expected lifespan of 200–400 days (Haque 2008). The tag to body weight ratios used ranged from 2% for the smaller transmitters up to 7% for the largest transmitters. These ratios are within the range not expected to compromise fish performance (Chittenden et al. 2009; Smircich and Kelly 2014), but we interpret with caution the information on fish that were not detected. Field tests indicated that the V9 transmitters (> 90% of those used) had average minimum and maximum detection ranges of 269–520 m (V7: 122–292 m; V13: 311–578 m). Fourteen of the fish received pressure-sensitive transmitters. In total, 120 cutthroat trout were tagged in 2006 ($n=40$), 2007 ($n=22$), and 2008 ($n=58$).

Receiver deployment

Vemco™ VR-2 receiver-data logger units (VEMCO Ltd., Halifax, Nova Scotia, Canada) to detect tagged

fish were secured to anchor systems including buoys, existing pilings, and trees. The southern Puget Sound array in Hammersley, Totten, Budd, and Little Skookum inlets, and Dana Passage, extending through Tacoma Narrows (indicated by the dashed line in Fig. 1) between 2006 and 2009 had 127 receivers (Fig. 1). The number of receivers deployed at any time varied, as they had to be retrieved to download data and replace batteries, and some were lost, but locations that would detect entrance or exit from inlets operated throughout the study. The receivers in southern Puget Sound obtained all the detections but receivers were also deployed for other studies at many sites for a total of 483 including those for the present project, between 2006 and 2009 (Fig. 1). These receivers included ones in central Puget Sound (Andrews et al. 2009; Andrews and Quinn 2012), Hood Canal (Moore et al. 2010a, b; Goetz et al. 2013), northern Puget Sound (Rohde et al. 2013; Moore et al. 2015), the Strait of Juan de Fuca (Arostegui et al. 2017a, b; Kagley et al. 2017), and in Canadian waters. The deployment information and detection data for all networks were collected by HYDRA, a data management project focused on the collection and sharing of acoustic telemetry data. In total, we estimated that there were 5508.5 “receiver-months” of listening effort, calculated from the time receivers were active during our study.

Data analysis

The primary goal was to investigate movements within southern Puget Sound, but we also assessed the extent of movements to more distant parts of Puget Sound by searching the HYDRA database [<http://hydra3.sound-data.com/>] for tag codes corresponding to the tagged cutthroat trout. To examine patterns of movement within the southern basin, we used a series of metrics following similar telemetry studies on Puget Sound Chinook salmon, *O. tshawytscha* (Arostegui et al. 2017b; Chamberlin et al. 2011), cutthroat trout (Goetz et al. 2013), and coho salmon, *O. kisutch* (Rohde et al. 2014). We defined movement as having occurred when a fish was first detected at a receiver, and the last detection at that receiver followed by at least 1 h with no further detections there, as these would indicate movement into and from the area covered by the receiver. This 1 h rule was needed because a fish at the periphery of

a receiver's detection range might move little or not at all, and brief periods without detections would not indicate any substantial movement. Fish might also move within the receiver's detection range, but we could not distinguish such movements from a stationary fish being continuously detected. Thus, these confirmed movements were a subset of all movements, but likely unbiased because of the varied receiver locations.

We defined "residence time" as the duration of detections at a given receiver, calculated as the difference between first and last detections defined above, to indicate how long each fish spent in the vicinity of each receiver. For example, if fish moved continuously along the shoreline, we would expect many short durations whereas long durations would suggest home range behavior. Analysis of residence time was restricted to detections in marine waters because Skookum Creek was the only stream site continuously monitored (with two receivers) and therefore differed from all other receiver sites.

To examine fine scale movements, the diel period and tide stage (ebb, flood, slack) at the time of each movement event were determined. For analysis of diel activity patterns, we first tallied all detection events by hour for the entire period of record, and for each month. Then, because day length in this region varies > 8 h from winter to summer, we classified the diel period as day, night, dawn, and dusk. Diel period was determined for each day of the year using sunrise/sunset tables for Pierce County Tacoma (47.07° N, 122.13° https://sunrise.maplogs.com/pierce_county_wa_usa.902.html?year=2006). We defined dawn as the period from 1 h before to 1 h after sunrise, and dusk as 1 h before to 1 h after sunset, with day and night occupying the intervening periods. Sunrise and sunset were defined as the times when the sun's upper edge was first and last on the horizon. Thus, on an annual basis there were on average 2 h each of dawn and dusk, and 10 h each of day and night.

We conducted similar analyses to determine if movement frequency depended on the stage of the tidal cycle. Tidal stage was determined for the study period using data from the National Oceanic and Atmospheric Administration for Arcadia, Totten Inlet, in the tagging area's core (<https://tidesandcurrents.noaa.gov/map/index.html?type=TidePredictions®ion=>). Slack was defined as the period from 1 h before to 1 h after the local high or low

tide, and the ebb and flood periods as the intervals between these slacks. We used these categories of tidal exchange rather than the tidal height because the mixed semi-diurnal tides in Puget Sound result in complicated interactions between height and water movement (i.e., a given height might occur during ebbing and flooding tides: Mofjeld and Larsen 1984). Analysis of actual water movement would be virtually impossible, given the highly complex patterns of current associated with the islands and inlets of southern Puget Sound. Movement events were then pooled across all years to assess differences in frequency of movement with diel or tidal periods using chi-square tests with the expected values being generated from the distribution of tidal and diel categories when the fish were detected.

Analysis of the vertical distributions of 14 fish with pressure sensing transmitters was based on the transmitted depths (i.e., to the surface of the water), with a stated resolution of 0.2 m. The few negative readings were converted to 0.0 m (i.e., the surface). We first described the overall depth distribution of each fish but pooled them because no individual variation was seen. We then graphed them in 0.5 m depth bins by time of day (dawn, dusk, day, and night). Given the skewed distributions constrained by the surface, we calculated median and mode for each of the four diel periods. However, to some extent, the observed depth distributions might be limited by the depths available to the fish within the detection range of the receiver. For example, if the fish could only be detected in very shallow water because the deep water was beyond the range of the receiver, the observed data would be biased because fish in deeper water would go undetected. Accordingly, we used ArcGIS with clipped 200 m diameter buffers to subset a Puget Sound digital elevation model with 30 m×30 m resolution (Finlayson 2005) for the depths available within the detectable area around each receiver. The 200 m distance was chosen to be conservative; a greater stated distance would have given them access to even deeper water farther offshore. However, the heterogeneous nature of the bottom topography and shoreline at the many sites over the range of tides (ca. 4–5 m during some phases) precluded a precise determination of receiver range. This analysis allowed us to determine how much area in each depth bin was available to the fish where it could have been detected by the fixed

receiver, for comparison with the observed distribution of depths. To discern if there was a diel pattern of depth, the time of each depth detection was classified by diel period to determine if fish occupied different depths depending on diel period.

Results

Of the 120 fish tagged between 2006 and 2008, 25 were never detected, leaving 95 for analysis. There was broad overlap in the fork lengths of the fish detected (153 – 486 mm) and not detected (151 – 450 mm) but the fish detected were larger than those not detected (mean length: 308.4 vs 246.8 mm; $t=3.69$, 119 df, $P<0.001$). Moreover, fish tagged at sites with many receivers nearby were more likely to be detected than were fish tagged in areas with fewer receivers. Specifically, 86% of the fish tagged at four of the sites (Hope and Squaxin islands, and Skookum and Totten inlets, near a rich network of receivers) were detected, whereas only 45% of the fish tagged at Oakland Bay (with fewer nearby receivers) were detected ($\chi^2=23.61$, df=4, $P<0.001$). During the study, 34 of the 483 receiver locations (7%) in the inland waters collectively known as the Salish Sea detected tagged cutthroat trout, for a total of 1,468,892 detections and 6634 receiver visits (i.e., first, and last detection events as defined above). These 34 receivers included 32 on shorelines of southern Puget Sound (6493 visits with 12986 first and last detections) that were the focus of our analysis, and the 2 receivers in Skookum Creek.

To examine movement within southern Puget Sound, we pooled receivers in the three areas where the vast majority of the tagged fish were detected. The fish tagged on Hope and Squaxin islands (combined because they are so close together), Skookum Inlet and Totten Inlet, produced 5937 detection events (91.4% of those in marine waters). Those tagged in Skookum Inlet were detected primarily there (51.4%) and in Totten Inlet (45.7%), indicating movement within these adjacent water bodies (Fig. 1). Fish tagged in Totten Inlet were almost always (96.4%) detected there, and fish tagged at Hope and Squaxin Islands were there (39.0%) or Totten Inlet (45.9%) and less often in Skookum Inlet (15.1%). Thus fish tagged only tens of km apart showed very different

detection distributions, and tended to remain near the tagging area.

There was a skewed distribution of periods from tagging to last detection, with 45 fish ≤ 60 d, but 36 fish > 120 d. Two individuals, both with V-9 transmitters, had detections 406 and 416 d after tagging. Most fish ($n=53$) were detected on one or several consecutive months and then no longer detected, but 21 had a gap of a month between detections, 11 fish had gaps of 2–5 months, 3 fish were undetected for 6 months before a later detection, one was undetected for 11 months, and 6 fish had two gaps of at least a month between detections. Cutthroat trout were detected in all months in marine water, but in summer fewer different fish were detected and there were fewer detection events (Fig. 2A). The Skookum Creek receivers showed a clear seasonal pattern, with no detections in the summer and a peak from January to March (Fig. 2B) based on 141 visits and 282 first and last detections.

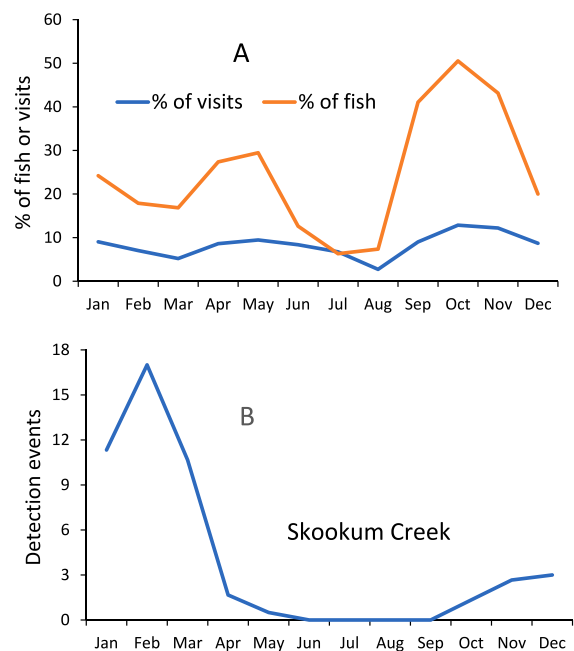


Fig. 2 Monthly movement patterns of coastal cutthroat trout with acoustic transmitters released from 2006–2008 and detected between 2006 – 2009 in southern Puget Sound. **(A)** Percent of fish indicates the % of all 95 fish ever detected that was detected in each month, and so does not sum to 100%. Percent of visits indicates the percent of all 6493 visits at receivers in each month. **(B)** Average monthly number of detections ($n=141$) of cutthroat trout in Skookum Creek

The 6493 marine detection events were examined as a whole, and with respect to each fish and each receiver. Overall, the great majority of events were brief (49.2% < 1 h, 60.5% < 2 h, 67.0% < 3 h, and 76.8% < 6 h). However, 600 events (9.2%) were 12 – 24 h, 222 (3.4%) exceeded 1 d, 116 exceeded 2 d, and there were 8 very protracted events of 403.6 – 853.5 h (almost 17 days to over a month). Similar seasonal patterns were detected in the initiation of long duration events (> 72 h) compared to ones < 72 h; in all cases the least activity was in summer (June – September). Six of the 32 receivers detecting fish (18.8%) had a maximum duration of < 1 h and 19 receivers (59.4%) had maxima < 12 h. However, the other 13 receivers had maxima > 12 h, and 9 had maxima > 1 d (Table 2). The maximum duration detected at a receiver correlated positively with the number of visits there ($r=0.49$, $n=32$).

Individual fish also varied in maximum detection duration, with a highly skewed distribution (Table 1). Specifically, 10.5% of the fish had maxima < 1 h, 24.2% < 3 h, and 38.9% < 6 h, but several individuals had maxima of days or even weeks at a receiver without a break in detections of over an hour. Subsequent detections at that or a different receiver indicated that the fish was still alive. However, as was the case with the receivers, the number of detected events for each fish and its maximum duration were positively correlated ($r=0.32$, $n=95$). Smaller fish tended to have fewer detection events and lower maximum durations, though the response was not linear. The average number of events and their average maximum duration both increased with fish size (Table 2). Thus, overall, smaller fish were less likely to be detected compared to larger fish, and those detected tended to have fewer and shorter discrete detection events than larger fish.

Movement events indicated activity throughout the 24-h period, but there were fewer movements at dawn (7.6%), during the day (34.5%), and at dusk (2.1%), and more movements at night (55.8%) than would have been expected by chance ($X^2=1388.11$, 3 df, $P<0.001$). This pattern was more pronounced in the summer compared to the winter, consistent with the longer summer days (Fig. 3) but even then, the differences were comparatively subtle. In addition, more movements occurred during ebbing (37.6%) and flooding tides (37.5%) than would be expected by chance, given the distribution of time in these periods

Table 1 Frequency distribution of maximum detection durations (in h) of 6493 separate events (time from first to last detection at a receiver) for 95 individual coastal cutthroat trout tracked in southern Puget Sound, Washington, and distribution of durations by the same fish, separated by the 32 receivers that detected them. For example, 10.5% of the fish had maxima < 1 h, as did 18.8% of the receivers

Maximum duration (h)	% of fish	% of receivers
1	10.5	18.8
2	3.2	6.3
3	10.5	0.0
4	5.3	0.0
5	5.3	3.1
6	4.2	3.1
7	2.1	9.4
8	3.2	9.4
9	1.1	3.1
10	1.1	3.1
15	8.4	6.3
20	5.3	3.1
25	1.1	6.3
30	3.2	0.0
35	1.1	0.0
40	0.0	3.1
45	1.1	0.0
50	1.1	0.0
100	11.6	3.1
200	10.5	6.3
300	2.1	0.0
400	3.2	3.1
500	2.1	3.1
600	0.0	0.0
700	1.1	3.1
800	1.1	3.1
900	1.1	3.1
1000	0.0	0.0

Table 2 The numbers of coastal cutthroat trout in fork length bins with acoustic transmitters detected, the average maximum duration of detection events, and the average number of events

Length (mm)	Sample	Maximum duration (h)	Events
< 250	21	11.9	15.5
250 to 299	17	75.9	32.5
300 to 349	35	118.1	82.9
> 350	22	123.3	82.4

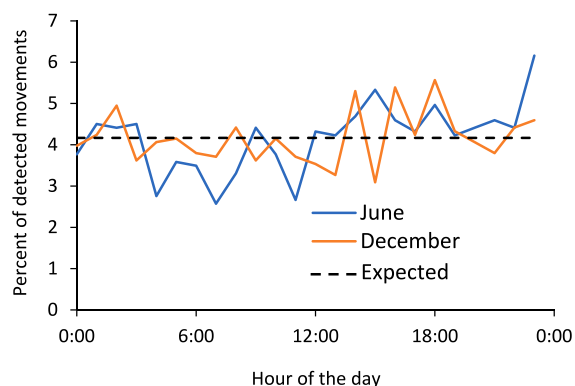


Fig. 3 Movements of coastal cutthroat trout with acoustic transmitters over the 24-h period in winter (December – orange line, $n = 1132$) and summer (June – blue line, $n = 1088$), expressed as percentages of the observations in each month. The black dashed line represents what would be expected from uniform activity throughout the 24-h period

on the days when the fish were detected (35.8% and 32.4%, respectively), and fewer movements were detected during slack periods (11.2% on high slacks and 13.7% on low slacks) compared to expected (15.9% and 15.9%, respectively; $X^2 = 341.29$, 3 df, $P < 0.001$).

The 14 cutthroat trout with pressure-sensing transmitters provided data from 129,883 depth detections on 26 receiver stations. The depth distribution was skewed to shallow water (median = 1.1 m, average = 1.06 m), with 10% of records from the surface to 1 m, and 76.8% from 1 – 2 m. The tendency to be detected in shallow water was not a consequence of the limited depths where the fish could have been detected. Rather, there was abundant habitat ≥ 10 m deep that the fish did not use (Fig. 4). For instance, the average maximum available depth within a 200 m diameter of each receiver was 14.1 m. The fish also made less use of the shallowest water than would be expected by chance (Fig. 4) and were closer to the surface at dawn and during day than dusk and night (Fig. 5).

Discussion

This study revealed patterns of cutthroat trout movements over a range of spatial and temporal scales. On the broadest scale, none of the 95 fish detected in southern Puget Sound was detected by the many

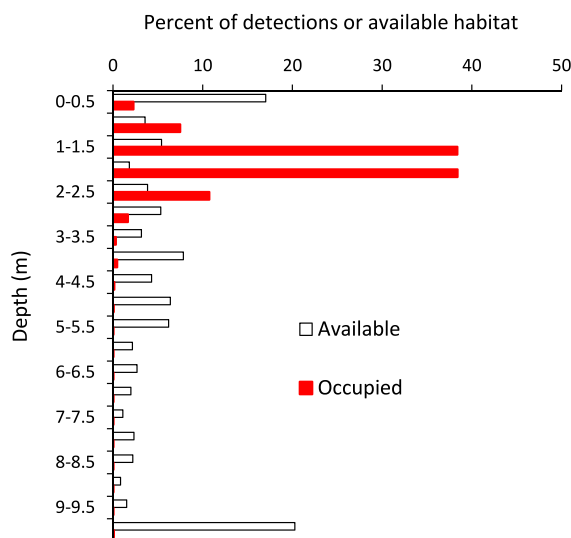


Fig. 4 Percentages of coastal cutthroat trout detections ($n = 129,883$, from 14 fish) in 0.5 m depth bins shown in red bars compared to the available habitat in each depth bin within the area where a fish could have been detected, based on the bathymetry around the receivers, shown in white bars. The last bin includes all detections and habitat > 9.5 m

operational receivers outside that region. This is noteworthy because those distant receivers detected salmonids tagged for other studies during these years including cutthroat trout (Goetz et al. 2013), steelhead (Goetz et al. 2015; Moore et al. 2015), coho and Chinook salmon (Kagley et al. 2017; Rohde et al. 2013; Smith et al. 2015), and bull trout (Goetz et al. 2021; Hayes et al. 2011). Notwithstanding detection efficiency, tag life and range, and related technical issues, the parsimonious conclusion is that cutthroat trout from southern Puget Sound seldom move to the central and northern basins and elsewhere in the Salish Sea.

The lack of observed long-distance movements did not result from brief occupancy of marine waters, as is typical of northern populations of this species (Armstrong 1971), Arctic char and brown trout (Atencio et al. 2021; Spares et al. 2015b), and bull trout (Goetz et al. 2021). Indeed, tagged cutthroat trout were detected in marine waters throughout the year and they overwinter in southern Puget Sound (Clai-borne et al. 2020). As with other salmonids, cutthroat trout vary greatly in the timing of upstream migration and spawning (Quinn et al. 2016). Some populations ascend rivers in the fall, overwinter, spawn in spring,

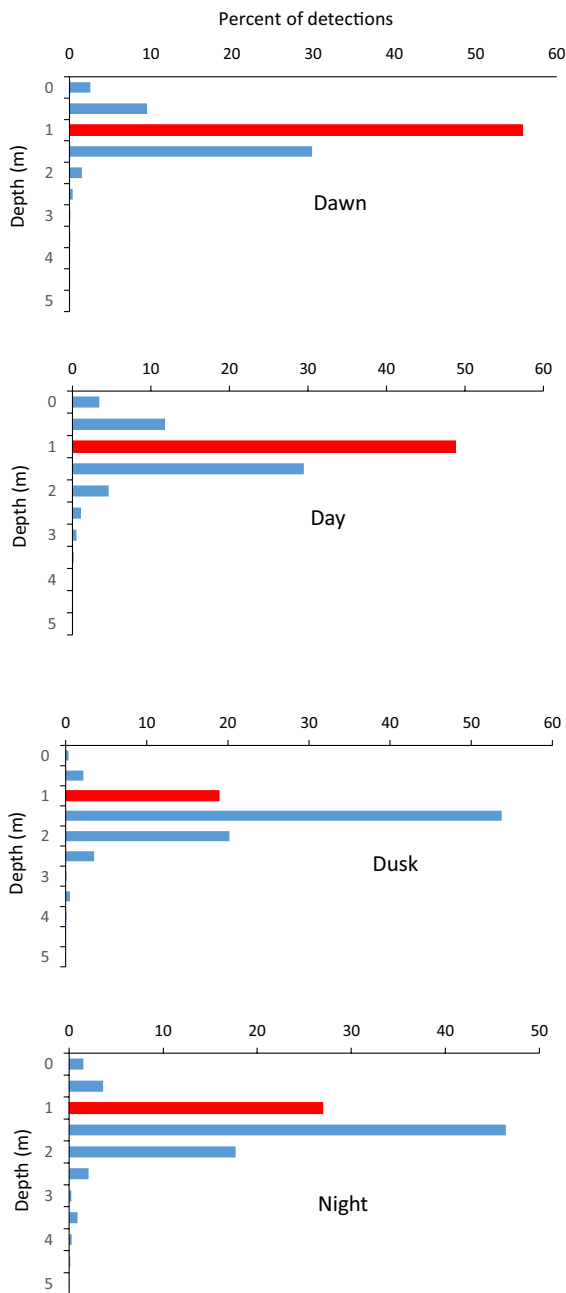


Fig. 5 Depth distributions of 14 telemetered coastal cutthroat trout at different times of the day. For ease of interpretation, the bars representing detections from 1–1.5 m are shown in red

and migrate to sea for about three months (e.g., south-eastern Alaska: Armstrong 1971) or a half-year (e.g., the larger rivers of northern Puget Sound: Johnston (1982). Populations spawning in small streams tend to enter rivers just prior to spawning and leave soon

thereafter, spending most of the year in marine waters (e.g., in Puget Sound: Royal 1972; Michael 1989; Wenburg 1998; and small coastal Oregon streams: Lowry 1965). These streams may have limited water in early fall, but rains later allow them to enter in time to feed on chum salmon, *O. keta*, eggs drifting downstream (Ellings 2003), spawn in late winter or early spring (Losee et al. 2016), migrate back to Puget Sound, and feed on chum salmon fry in the spring (Jauquet 2002).

Within southern Puget Sound, the fish tagged in areas only tens of km apart differed in detection distributions. Those tagged on Hope and Squaxin islands were primarily detected there or Totten Inlet, nearby, rather than farther away into Skookum Inlet. Conversely, those tagged in Skookum Inlet were primarily detected there and in Totten Inlet, rather than farther out around Hope and Squaxin Islands, and fish tagged and released in Totten Inlet were almost exclusively detected there. The release locations of the fish not detected in the present study were also consistent with limited movement. The highest proportion of fish tagged but not detected was in Oakland Bay, at the end of Hammersley Inlet, where the receiver coverage was most limited. If these fish had moved to the receiver-rich area around Hope and Squaxin islands, where many other fish were detected, they likely would also have been detected. As with the apparent lack of movement between basins, caution is needed when interpreting absence of detections because of tag life and power (related to fish size), details of topography and receiver sites, and variation in receiver coverage over time. However, given the longevity of the tags and the narrowness of the passage, the parsimonious conclusion is that limited movement resulted in the lack of detections, assuming comparable mortality rates to the other areas. These findings are consistent with genetic studies, that assigned 76% of the cutthroat trout sampled in Eld Inlet, in of our study area, to the nearest spawning population, in McLane Creek (Losee et al. 2018).

Limited movement within Puget Sound has important but mixed implications for cutthroat trout conservation. On the one hand, depleted or extirpated populations may not be rapidly augmented by fish from elsewhere, and thus suffer from over-fishing and severe habitat degradation. On the other hand, protective fishing regulations and conservation efforts in key spawning and rearing habitats might produce

readily detectable gains for local populations. Many small Puget Sound streams are blocked or impeded by inadequate culverts or other road-crossing structures, and considerable effort is being devoted to rectify this problem (Price et al. 2010; Till and Caudill 2023; WSDOT 2023). Small streams are habitat for coastal cutthroat trout at various life stages including spawning and rearing (Martens and Dunham 2021; Saiget et al. 2007; Zydlewski et al. 2009) and resident individuals can produce anadromous offspring (Claiborne et al. 2020). Consequently, this species might especially benefit from local habitat protection and barrier removal (Peterson et al. 2013).

The fewest detections in marine waters were in summer (Fig. 2A). We do not know where undetected trout were at this time, but the results are consistent with lower catches using beach seines during mid-late summer than in spring in southern Puget Sound (Losee et al. 2018). In general, Puget Sound is a very moderate environment with limited changes in temperature, compared to, for example, the locations in northern Norway where sea trout were studied (Berg and Berg 1987, 1989). In central Puget Sound, monthly mean temperatures from 3 m to the surface ranged from 7.9 °C in January and February to 13.6 °C in August (Smith et al. 2015). These temperatures are much milder than the fish would experience in some rivers and are adequate for year-round growth. The shallow bays of southern Puget Sound are warmer, however. For example, a Washington Department of Ecology water quality monitoring station in Henderson Inlet [<https://ecology.wa.gov/Research-Data/Monitoring-assessment/Puget-Sound-and-marine-monitoring>] accessed on September 10, 2023, indicated that average temperatures from 0 – 1.5 m depths (where cutthroat trout were most often detected) ranged from 8.3 °C in February to 16.8 °C in September. The maximum depth at this station was 23.5 m, and shallower sites might get considerably warmer in the summer, especially when low tides expose the sediment to high air temperatures and solar radiation. Salinities varied little—from a high of 29.8 PSU in October to a low of 26.7 in February, reflecting the seasonal precipitation patterns in this area. Fish may have moved out of the detection range in the summer, seeking thermal refuge in deeper marine water or freshwater systems that did not have receivers, and the summer movements and ambient temperatures should be a priority for future research.

In addition to the biological reasons why detections showed seasonal patterns, methodological factors may also have contributed to the patterns. Most fish were tagged in the fall (October – November) and fewer in April and May. Fish were detected in the months after tagging, and less so later, as expected if they moved from the area or died. Fish not surviving spawning in the spring or dying soon thereafter would not be detected in the mid-late summer. Southern Puget Sound cutthroat trout showed a low incidence of repeat spawning (seaward migration by fish having spawned twice) and a maximum age of 5 years, including typically 2 years spent in the natal stream prior to entering Puget Sound (Losee et al. 2018). The eventual depletion of the transmitter battery's power would end detections, but some fish were detected 6–12 months or more after tagging so we think battery life is a smaller issue than the seasonal patterns of tagging and mortality, and movement to cooler water offshore or possibly streams.

The period between first and last detections revealed a wide range in durations among individual fish and receivers, with many brief periods (e.g., < 3 h) and some much longer visits (Table 1). Interpretation of the data is hindered by the fact that receivers and fish with more detections tended to have higher maximum values, and smaller fish tended to have fewer and shorter detection events than larger fish. Taken as a whole, the data suggest that most of the fish moved back and forth along shorelines because so many detection events were brief, yet the fish did not leave the region, as noted above. In this regard cutthroat trout differ markedly from steelhead, a closely related congener commonly occupying the same streams with them. Steelhead smolts migrate rapidly from the Salish Sea in offshore waters (Goetz et al. 2015; Melnychuk et al. 2007) and the Columbia River (Daly et al. 2014), in contrast to the shoreline orientation and limited movements of cutthroat trout indicated here and in Hood Canal (Goetz et al. 2013). Interestingly, the movements in marine waters by naturally occurring hybrid smolts of these two species were intermediate between the species from that stream (Moore et al. 2010b).

We have limited insights into the reasons why some fish were mobile whereas others tended to stay within range of receivers for longer periods, interpreted as a form of home range behavior and consistent with mark-recapture results (Losee et al. 2018). In

contrast to other studies where cutthroat trout (Goetz et al. 2013), steelhead (Moore et al. 2015), sea trout and Arctic char (Atencio et al. 2021) were tagged as smolts, or as kelts (Eldøy et al. 2015; Kristensen et al. 2019) leaving specific streams, the fish tagged here were caught in marine waters (in spring and fall) so their population of origin was unknown. Moreover, other studies used discrete size distributions in spring to categorize the tagged fish leaving the stream as smolts or kelts. The fish in the present study ranged from 151 – 486 mm, with a unimodal distribution centered from 300 – 350 mm. This length distribution and overlap between first-time and veteran migrants are consistent with other studies in the region (Losee et al. 2018), so the fish studied here were representative of the species in this area. However, the lack of discrete size modes corresponding to life history stages made individual variation in behavior more difficult to interpret compared to studies categorizing fish as first-time and veteran migrants (Jensen et al. 2015).

Interpretation of the data showing variation in detection event duration among receivers is complicated by the fact that their spacing along the complex shoreline and islands of southern Puget Sound was neither regular (i.e., every x km) nor statistically random, and site selection was not designed to test specific hypotheses regarding habitat use. Proximity to stream mouths, bottom structure and sediment size, currents, and prey items are reported to affect angling success for cutthroat trout (Johnson 2004; Stoll 2017). These and other features might be evaluated in the future with respect to cutthroat trout density and home range. However, such analysis would be challenging because the 3 – 4 m tidal range common in the area greatly affects the accessible shallow nearshore habitat, the mixed semi-diurnal tides produce complex patterns of velocity and direction, and the biota vary as well.

At finer temporal scales, the data revealed movement throughout the day and night, though the fish moved more often at night than would occur by chance. In Hood Canal, similar telemetry techniques revealed considerable individual variation in cutthroat trout diel activity patterns, activity throughout the 24-h period, and somewhat more daytime activity than would be expected based on the day length (Goetz et al. 2013). The present study was year-round whereas the Hood Canal study was only from April

through September, which may explain the difference in specific results but in broad terms the species is clearly active throughout the 24-h period. This rather continuous activity contrasts with the shift from nocturnal migration downstream to diurnal migration in Puget Sound in steelhead smolts (Goetz et al. 2015) and diurnal activity in returning adult steelhead (Ruggerone et al. 1990). The timing of movements can vary among salmonid species in the same area (Chapman et al. 2013) and markedly affect survival (Melnichuk and Welch 2018) so we infer that selection favors the diverse movement patterns of Salish Sea salmonids.

In addition to the diel patterns, fish moved more often on ebbing and flooding tides, and less during slack periods, than would have been expected by chance. The pattern was statistically significant, given the large number of movements, but the effect was small, and fish moved at all times of the tidal cycle, or remained within range of a receiver across several tide changes. It seems clear that the fish did not use the tidal currents to facilitate rapid movement during one tidal phase (i.e., “selective tidal stream transport”) as do some fishes (Harden Jones et al. 1979; McCleave and Kleckner 1982; Parker and McCleave 1997). Rather, the movements detected here seem more like those of flatfishes that follow the rising and falling tides to remain close to shore where they feed (Gibson 1973; Raffaelli et al. 1990; Wirjoatmodjo and Pitcher 1984), as indicated by the tendency of the trout to remain near the surface (see below). The tidal amplitude in southern Puget Sound can exceed 5 m and typically 3 m. Such variation dramatically affects the gradient, substrate, and vegetation along the shoreline accessible to cutthroat trout, from steep and rocky to flat and muddy. The tides also cause complex changes in the direction and velocity of water movement, depending on the curvature of the shoreline and bathymetry of the site, proximity to islands, and other fixed features. These velocities may facilitate feeding, and in southern Puget Sound, cutthroat trout display a varied diet including a high proportion of benthic invertebrates and, when available seasonally, juvenile Pacific salmon and other small fishes (Jauquet 2002).

The fish with pressure-sensing transmitters were very close to the surface throughout the day and night, consistent with the impression among anglers that they are close to shore and in shallow water (Johnson 2004; Raymond 1996; Stoll 2017). In this regard they differ considerably from the broader and deeper distributions

of coho and Chinook salmon in Puget Sound (Smith et al. 2015; Arostegui et al. 2017a). The cutthroat trout could have been near the surface offshore, but this is unlikely because they seldom cross open water (Goetz et al. 2013). During the day cutthroat trout feed on small fishes near shore, where they are caught in beach seines (Duffy and Beauchamp 2008; Losee et al. 2018). Indeed, the daytime depths of fish with transmitters in this study were shallower than those at night. Unlike steelhead and other typical salmon smolts, whose white bellies, silvery sides, and dark dorsal coloration camouflage them in marine or lacustrine open water (Holecek et al. 2012; Arostegui and Quinn 2019a), coastal cutthroat trout in Puget Sound commonly retain the dorsal and lateral spots and colors that characterize them in rivers (see, for example, photos in Losee et al. 2020, 2023b). These colors camouflage them against the sand, gravel, shell hash, and complex colors of the shorelines that they occupy. Indeed, the fish can be very difficult to see even in shallow, clear water. Proximity to shore may afford some protection from predatory harbor seals, *Phoca vitulina* (Thomas et al. 2017) and porpoises (though they tend to eat other fishes: Nichol et al. 2013). Avoidance of the surface may afford some protection from osprey (*Pandion haliaetus*) and bald eagles (*Haliaeetus leucocephalus*), but the region has other predatory birds and river otters (*Lontra canadensis*), and the cutthroat trout are not long-lived (Losee et al. 2018).

The limited movements and shallow distribution of cutthroat trout near the Puget Sound shoreline contrasts strongly with the patterns of steelhead, which migrate rapidly in open water to the Pacific Ocean from Puget Sound (Moore et al. 2015) and the Strait of Georgia (Melnichuk et al. 2007), and experience considerable mortality in these open waters (Moore and Berejekian 2017). Other salmonid species also vary in migration patterns. Puget Sound bull trout, *Salvelinus confluentus*, migrate downstream at about the same time of year as cutthroat trout (Quinn and Losee 2022) and are similarly shoreline-oriented (Hayes et al. 2011) but stay in salt water only a few months before migrating back upriver (Goetz et al. 2021). In the Atlantic Ocean, anadromous brown trout and Arctic char were close to the surface, with > 50% of char detections between 0 and 1 m, and > 50% of sea trout detections between 1 and 2 m (Rikardsen et al. 2007), consistent with other evidence that sea trout are near the surface (Eldøy et al. 2017). In

contrast, post-smolt Atlantic salmon made frequent deep dives, often > 100 m (Einarsson et al. 2018). In general, the ecology of coastal cutthroat trout is more like that of anadromous brown trout than the congeneric *Oncorhynchus* species, though cutthroat trout seem to lack the larger-bodied and distant-migrating form seen in some anadromous brown trout populations (Losee et al. 2023b).

The Salish Sea, including Puget Sound, supports eight native anadromous salmonids. They all migrate to marine waters in spring and early summer but vary greatly in how long they remain in marine waters, how far they migrate from their natal stream (Quinn and Losee 2022), and the spatial distribution of spawning within rivers (Austin et al. 2023). These patterns affect each species' vulnerability to fisheries, predators, chemical contaminants, shoreline and riparian zone modification, and other natural and anthropogenic factors. The five Pacific salmon species and steelhead trout have been extensively studied (Losee et al. 2019) whereas bull trout and cutthroat trout lack systematic abundance assessments and basic ecological information. The data reported here contribute to a growing understanding of the ecology of anadromous cutthroat trout. The species would benefit greatly from more directed research and protective regulations because their short lifespan, coupled with nearshore distribution and limited movements in marine water, make them vulnerable to over-exploitation and shoreline degradation.

Acknowledgements Receivers were deployed by the Squaxin Island Tribe, the US Army Corps of Engineers, the Washington Department of Fish and Wildlife, NOAA-Fisheries, the Pacific Ocean Shelf Tracking program in British Columbia and other entities; our work would not have been possible without the efforts of the many people involved in those diverse programs. We thank Jennifer Scheuerell for the Hydra data management system that was essential in storing, organizing, and providing records to the many investigators, and Clayton Kinsel and Steve Corbett for helpful suggestions on a draft. We also thank the many people who assisted in field work by catching and tagging the fish in this study, including but not limited to Sayre Hodgson, Scott Steltzner, Kyle Brakensiek, Joe Jauquet, Don Freeman, and Larry Phillips, who also helped initiate and guide the research. Lastly, we acknowledge Jon Wittouck for initial data organization and preliminary analyses. MCA was supported by the Woods Hole Oceanographic Institution (WHOI) President's Innovation Fund. Data will be provided upon request after publication.

Data availability The dataset analyzed during this work is available from the corresponding author on request.

Declarations

Ethics approval This handling of fish in study was conducted and supervised by, and with the authorization of, the Washington Department of Fish and Wildlife.

Competing interests The authors declare no competing interests.

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