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REGULAR PAPER

Size, age, growth and site fidelity of anadromous cutthroat trout *Oncorhynchus clarkii clarkii* in the Salish Sea

James P. Losee | Andrew M. Claiborne | Phillip E. Dionne | Hannah S. Faulkner | Todd R. Seamons

Washington Department of Fish and Wildlife, Fish Program, Olympia, Washington

Correspondence
James P. Losee, Washington Department of Fish and Wildlife, Fish Program, Olympia, Washington 98502.
Email: james.losee@dfw.wa.gov

Pacific salmon *Oncorhynchus* spp. have been the focus of scientific research for over a century, but anadromous trout in this genus, in particular anadromous coastal cutthroat trout *Oncorhynchus clarkii clarkii*, have been neglected. *Oncorhynchus clarkii clarkii* occupy a diverse range of habitats including fresh water, brackish estuaries and marine water, but have a relatively small home range making them ideal for studies of behaviour and movements during ocean residency. In 2015, we sampled *O. c. clarkii* monthly along a small stretch of beach (47.08° N, 122.98° W) in Eld Inlet, south Puget Sound, Washington using a beach seine. We collected tissue for genetic tagging and stock identification and scales for aging from 427 *O. c. clarkii*, ranging in size from 118 to 478 mm fork length. Additionally, we enumerated redds in natal streams of those fish tagged to describe inter-habitat movement patterns and investigate site fidelity of juvenile and adult *O. c. clarkii* in the marine environment. Consistent with other anadromous salmonids, *O. c. clarkii* captured at our study beach exhibited rapid growth rates, particularly in spring following dispersal into the marine environment (mean $\pm$ SD = 0.61 $\pm$ 0.29 mm^{-d}). Genetic tag data revealed that while *O. c. clarkii* undergo inter-estuarine migrations, *O. c. clarkii* of all life stages exhibited site fidelity in the marine environment. Twenty-one percent (64/305) of sampled *O. c. clarkii* were recaptured at least once during the course of the study while multiple fish (n = 3) were recaptured up to five times. These results suggest that *O. c. clarkii* occupying south Puget Sound reside in or regularly return to a small geographic area in the nearshore environment for much of their life and therefore may be particularly vulnerable to anthropogenic disturbance (development, angling, *etc.*).

KEYWORDS

coastal cutthroat trout, marine protected areas, nearshore marine, *Oncorhynchus*, Puget Sound, site fidelity

1 | INTRODUCTION

Anadromous salmonids in the genus *Oncorhynchus* Suckley 1861 typically leave their freshwater rearing grounds as juveniles (0–3 years old) and migrate to offshore marine waters from central Oregon to the Gulf of Alaska (Fisher *et al*., 2007; Quinn and Myers, 2004). Those that survive the early marine period remain in the offshore marine environment for 1 to 5 years before returning to their natal stream to spawn (Myers *et al*., 2007). The only exception to this pattern is the anadromous form of coastal cutthroat trout *Oncorhynchus clarkii clarkii* (Richardson 1836). Recent studies in the fjord-like inlets of south Puget Sound and Hood Canal in Washington State, USA, have shed light on broad-scale migratory patterns of anadromous *O. c. clarkii* (Goetz *et al*., 2013; Losee *et al*., 2017; Moore *et al*., 2010) and demonstrated that they undergo short marine migrations relative to other *Oncorhynchus* spp. (Daly *et al*., 2014).

After entering marine water in the spring, *O. c. clarkii* exhibit one of two migration types (Goetz *et al*., 2013; Losee *et al*., 2017): those

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that remain within 5 km of their natal stream (residents) and those that travel distances > 5 km (migrants). Travel distances have been shown to be greatest among larger anadromous *O. c. clarkii* (< 400 mm; Haque, 2008), but anadromous *O. c. clarkii* of all sizes appear to exhibit a small home range and rely on nearshore marine waters (depth < 10 m) for much of their life (Goetz *et al*., 2013). Together, these and other studies concur that migration distances greater than 30 km are uncommon for anadromous *O. c. clarkii* (Pearcy *et al*., 2018). This restricted marine migration pattern allows for a unique opportunity to describe basic biological information such as size and growth of anadromous *O. c. clarkii* at various life stages and investigate specific movement patterns such as site fidelity.

Site fidelity, the tendency to return to a previously occupied location, has been observed across the Animal Kingdom including numerous taxa of freshwater fish (Lucas & Baras, 2001; Switzer, 1993). In marine waters, animals probably utilize favourable locations repeatedly, but this behaviour is difficult to detect and may be less common relative to terrestrial organisms due to the unpredictable nature of the ocean environment (Carr *et al*., 2003; Costanza *et al*., 1993). Regardless, a variety of marine fishes are known to exhibit high site fidelity (Green *et al*., 2012; Jud & Layman, 2012; Matthews, 1990). For *Oncorhynchus* spp., stock-specific migratory patterns in the marine environment have been identified (Byron and Burke, 2014; Weitkamp, 2010; Weitkamp & Neely, 2002). However, little is known regarding fine-scale movements in the marine water, due to the remote locations where they spend the majority of their marine life. Here, we sought to describe basic life-history characteristics and seasonal patterns of prevalence of *O. c. clarkii* in marine waters of Puget Sound. Specifically, this study was designed: to describe the size, age and growth rates; to describe stock specific movements; to evaluate the site fidelity of juvenile and adult life stages of *O. c. clarkii* in south Puget Sound. This work provides a new understanding of the biology and marine movements of *O. c. clarkii* and highlights the importance of the nearshore marine environment to this species. In addition, these results may provide insight into the potential for larger bodied, ocean migrating *Oncorhynchus* spp. to exhibit site fidelity in offshore marine waters.

2 | MATERIALS AND METHODS

2.1 | Overview of experiment

We sampled *O. c. clarkii* for scales (age), tissue (genetics) and length monthly at the same sampling location in 2015. Two genetic analyses were completed; first, we genetically marked individuals by collecting tissue and scales from captured trout allowing us to record patterns of recapture of individual *O. clarkii clarkii*; second, we used available genetic baseline to genetically assign a likely source population for individual *O. clarkii clarkii*. Concurrently, we conducted spawning-ground surveys in nearby streams. Taken together, this genetic mark–recapture, genetic stock assignment, scale analysis and spawning-ground surveys allowed us to describe age and growth rates and stock-specific movements of juvenile and adult anadromous *O. c. clarkii* while documenting the numbers of times individual *O. clarkii clarkii* returned to our sampling location throughout the year.

2.2 | Marine study site

Anadromous *O. c. clarkii* (Figure 1) were collected monthly in the nearshore marine environment along the southernmost end of a 0.5 km stretch of an undeveloped beach (47.08° N, 122.98° W) on the south-eastern shore of Eld Inlet (Figure 2) between January and December. This 12 month period encompasses the time when *O. c. clarkii* emigrate into the marine environment for the first time and the period when spawning occurs in the fresh water (February to May; Losee *et al*. 2016). Eld Inlet is *c*. 12 km long and oriented south-west to north-east from its origin to its mouth, *c*. 30 m deep at its deepest point near the mouth of the inlet and 2.1 km at its widest point near the middle of the inlet. Eld Inlet is near the south-west terminus of the Puget Lobe of the Cordilleran Ice Sheet glacial maximum and the beach substrata are dominated by sand and gravel eroded from glacial deposits (Burns 1985). The gradual erosion of the forested hillsides that line much of the Puget Sound add complexity to the nearshore marine habitat as sediment and fallen trees recruit to the nearshore marine environment. Puget Sound experiences mixed semidiurnal tides with the most extreme tidal range occurring in the South Basin (Lavelle *et al*., 1988), which is where our study took place. The study beach is *c*. 5.5 km from the nearest tributary that supports *O. c. clarkii* spawning (McLane Creek) and is an area well known to local anglers for its abundance of *Oncorhynchus* spp. and forage fish.

2.3 | Fish collection

Oncorhynchus clarkii clarkii were collected monthly in the nearshore marine environment during daylight hours by beach seine. Beach seining is a useful method for mark–recapture assessments because mortality rates are typically low (< 1%) across a range of fish sizes (Hahn *et al*., 2007). Sampling location and method was standardized using the same net, with one of two small outboard-propelled skiffs by one of three trained operators. We used a straight-wall configured beach seine constructed of uniform 3.2 mm knotless nylon mesh 36 m in length with an asymmetrical taper from 3.7 to 1.6 m in net depth. At its greatest depth, the net was hung with 1 kg m^{-1} lead line and tapered to 0.45 kg m^{-1} at its shallower depth. Sampling consisted of boat-deployed hauls in which the net was anchored to shore at the short end and deployed from the bow of the boat as it backed away from the beach, then pulled in reverse against the current at *c*.

FIGURE 1 Anadromous *Oncorhynchus clarkii clarkii* 478 mm fork length captured on 26 February 2015 in Eld Inlet, Puget Sound Washington

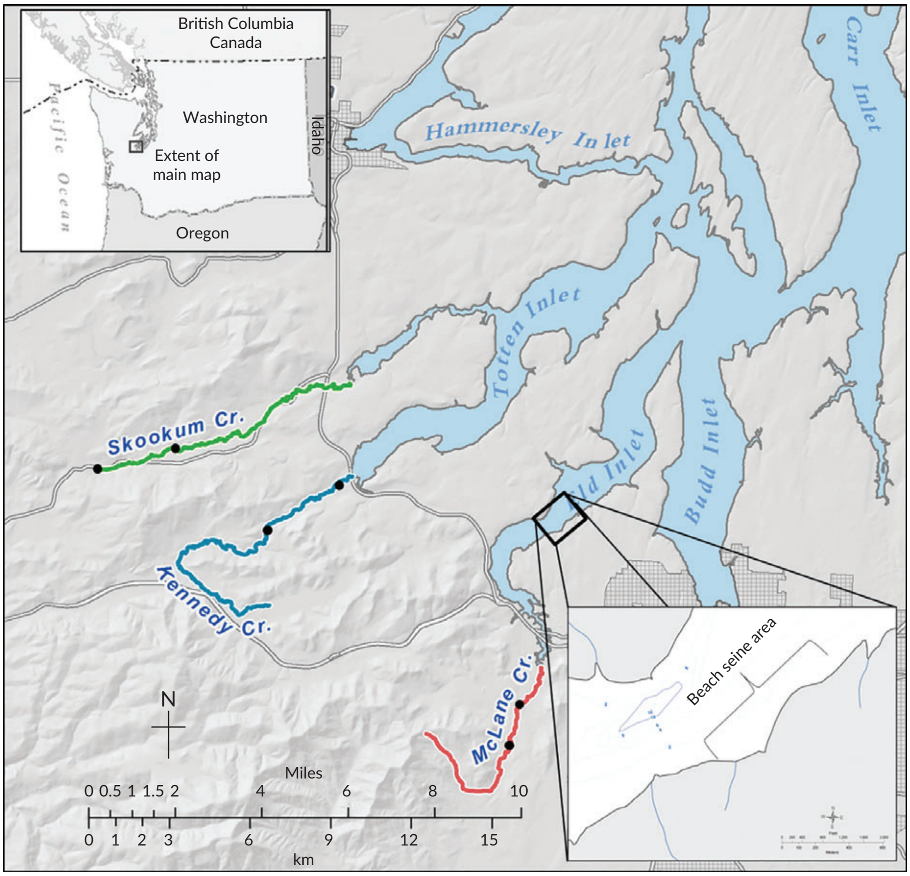

FIGURE 2 The three creeks in South Puget Sound. Colours from which anadromous *Oncorhynchus clarkii clarkii* were sampled for genetic stock assignment. ●. Location of redd surveys; □, location of marine collections

4.6 km h^{-1}. Once the net was fully deployed, a pulley system attached to a second anchor on the beach was utilized to close the net and pull the deep end of the net to the beach at a greater rate. Volume swept was *c.* 3,000 m^3 (half of the product of tow length, tow width and max depth). This netting operation was repeated for a total of five sets with each set beginning where the latter ended. Together, these five sets resulted in a total sampled area of *c.* 180 m at the southernmost end of the study beach. *Oncorhynchus clarkii clarkii* were anaesthetized with MS-222, sampled for scales, fork length (L_F, mm) and caudal fin tissue and then placed in a recovery bath for > 10 min prior to release. Fin tissue was placed in 95% ethanol in vials and stored at room temperature. Scales were collected from the preferred area above the lateral line midway between the dorsal and adipose-fins (Scarnecchia, 1979) and stored dry in envelopes.

2.4 | Scale analysis

In the laboratory, scales were cleaned in water and mounted in clear acetate sleeves. All scales were examined (×48) by one reader using a Realist Vista microfiche reader. Age was determined by counting scale annuli (Ericksen, 1999) and by determining the point of initial marine entry on each scale (Figure 3), which was identified as the first discernible and constant increase in circuli spacing. Age notation for anadromous *O. c. clarkii* typically designates freshwater annuli (*e.g.*, 2.) and annuli after marine entry as either a freshwater re-entry scar (*e.g.*, 2. + F+) or spawning scar (*e.g.*, 2. + S+). We defined fish on their first seaward migration (new migrants) as fish whose scales had no annuli after marine entry (*e.g.*, 2.+) and fish on subsequent seaward migrations (veteran migrants) as fish whose scales had at least one annulus after marine entry (*e.g.*, 2. + F+). We defined total age as the number of annuli present on the scale and age at marine entry as the number of annuli before the marine entry check. Age analysis of all fish captured resulted in multiple individuals aged at multiple points in time (recaptures) and provided an estimate of ageing precision.

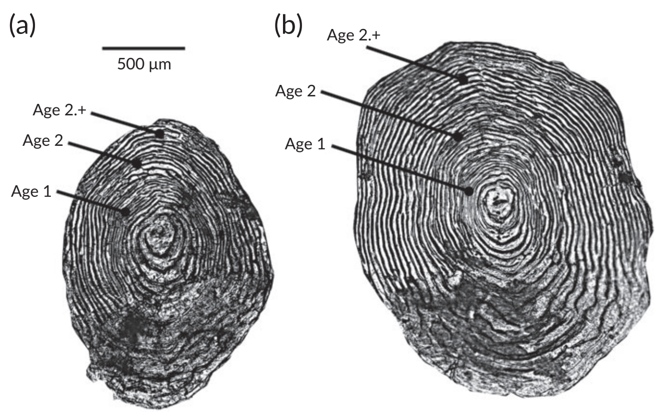

FIGURE 3 Scales from an anadromous *Oncorhynchus clarkii clarkii*, captured shortly after emigration from fresh water in (a) May 2015 then again in (b) September 2015 during which time this individual grew 86 mm in fork length. Winter annuli and age determinations (years) are shown

Estimated freshwater age (age before marine entry) agreed 70% of the time, while annuli counted after the initial marine migration agreed 89% of the time. Where ages disagreed between sample events, a resolved age was determined after further examination and used in subsequent analysis.

To describe marine growth of individual *O. c. clarkii* as juveniles and adults during their initial seaward migration we used age, L_F and the days elapsed between sampling events to estimate mean growth rates (G_R, mm d^{-1}), where for new and veteran migrants $G_R = \mu L_{Fi} - \mu L_{Fij} D_i^{-1}$; μL_{Fi} is the mean L_F at a sample event, μL_{Fij} is the mean L_F at the subsequent sampling event and D_i is the number of days elapsed between sampling events. Growth rates were calculated for months with samples of more than five individuals, which resulted in estimates of growth rate for fish on their first and second feeding migrations only. This corresponded to peak catches April–November of new migrants and January–April for veteran migrants on their second migration. We used the observed change in L_F of genetically identified recaptures with scale age determinations (n = 35) to corroborate monthly mean growth rates.

2.5 | Genetic stock identification

Oncorhynchus clarkii clarkii were genotyped at seven microsatellite loci and 96 single-nucleotide polymorphisms (SNP). To extract and isolate DNA from fin tissue, we used Qiagen DNEasy kits (Qiagen Inc.; www.qiagen.com) and followed recommended protocol for animal tissues. Three SNP loci were designed to distinguish *O. mykiss*, *O. clarkii* and their F1 hybrids. Hybrid individuals were identified as heterozygous at two or three of the three loci. Further details of the DNA extraction, PCR amplification and visualization steps can be found in the supplementary materials of Losee *et al*. (2017).

The genetic stock was estimated for each fish using the partial Bayesian algorithms employed by the software ONCOR (Anderson *et al*., 2008; Rannala & Mountain, 1997). Population assignments were finalized with a threshold assignment posterior probability of > 0.85 resulting in a subset of individuals designated unassigned when the probability was < 0.85. An assumption of individual assignment tests is that all source populations were sampled. A commonly used hatchery stock and three local populations (McLane, Kennedy and Skookum Creeks) were included in baseline collections; however, based on previous analysis, some *O. c. clarkii* caught at the marine study site may have originated from nearby un-sampled populations (Losee *et al*. 2017). To test this assumption, the probability of inclusion was calculated for all individuals of unknown source population using the algorithms employed by the software GENECLASS2 (Piry, 2004) using the methods of Paetkau *et al*. (2004). Ten thousand individuals were simulated with α = 0.001.

2.6 | Mark and recapture

Recaptures were identified using genetic tags; samples with matching genotypes were assumed to be the same individual. Genotyping errors may cause mismatches in repeated samples from the same individual. To account for genotyping errors, matching genotypes were identified using the maximum likelihood algorithms in COLONY 2.0.6.1 (Wang, 2016).

2.7 | Timing of *O. c. clarkii* spawning

To improve clarity of seasonal patterns of movements of *O. c. clarkii* and to characterize the time of spawning, spawning-ground surveys were conducted in nearby freshwater habitats. Specifically, we surveyed previously identified spawning index areas on McLane (river kilometre, RKM 5.6 to 7.7), Kennedy (RKM 2.4 to 3.7) and Skookum Creeks (RKM 8.9 to 12.1) weekly from January to June in 2015. These streams represent the numerically dominant *O. c. clarkii* populations captured in marine waters during this study. No surveys were conducted in July due to low water and absence of spawning *Oncorhynchus* spp. observations in previous years (Washington Department of Fish and Wildlife, unpubl. data). We used standardized redd survey methodology and distinguished anadromous *O. c. clarkii* redds from those of resident *O. c. clarkii* and lamprey (*Lampetra* sp.) based on published descriptions (Brumo *et al*., 2009; Gallagher and Gallagher, 2005; Losee *et al*., 2016).

3 | RESULTS

3.1 | Age, growth and life history

Oncorhynchus clarkii clarkii ranged in size from 118 to 478 mm (mean ± SD = 285 ± 68.7; Figure 4). We completed scale analysis of 326 fish captured from January to December 2015. Of those, 18% had scales that were regenerated resulting in a total age that was undetermined. Scale analysis revealed that *O. c. clarkii* captured in the marine environment ranged in age from 1 to 5 years old. Seventy-five percent of fish entered marine waters for the first time at age 2 years (range 1–3 years; Figure 5). Similarly, 71% of veteran migrants entered marine waters for the first time at age 2 year (range 1–3 years; Figure 5). Overall, new migrants made up 52% of fish captured while veteran migrants on their second and third seaward migration made up 43 and 5% respectively. New migrants made up a small proportion of the total catch in winter months (2.5% January–March) but accounted for 50–84% of the monthly catch from April–December. Fish that had previously migrated to the marine environment made up 60–97% of the monthly catch January–March but were captured less frequently in the spring, corresponding to peak redd counts in Skookum, McLane and Kennedy Creeks (Figure 6). Peak catch of new migrants occurred in May (n = 41) *v.* the peak catch of veteran migrants, which occurred in February for all three source populations (n = 73), 2 months prior to the peak of redd counts in all three study streams (Figure 6).

Mean ± SD L_F of new migrant *O. c. clarkii* increased from 178.2 mm (±36.5 mm) in April to 290.1 mm (±28.7 mm) in November of 2015. Overall, monthly mean growth rates from April to November ranged from 0.30 to 0.72 mm day^{-1} (Figure 7). There was seasonal variation in marine growth rates, such that growth increased throughout spring and early summer and decreased August to November (Figure 7). Mean ± SD L_F of fish in their second seaward migration

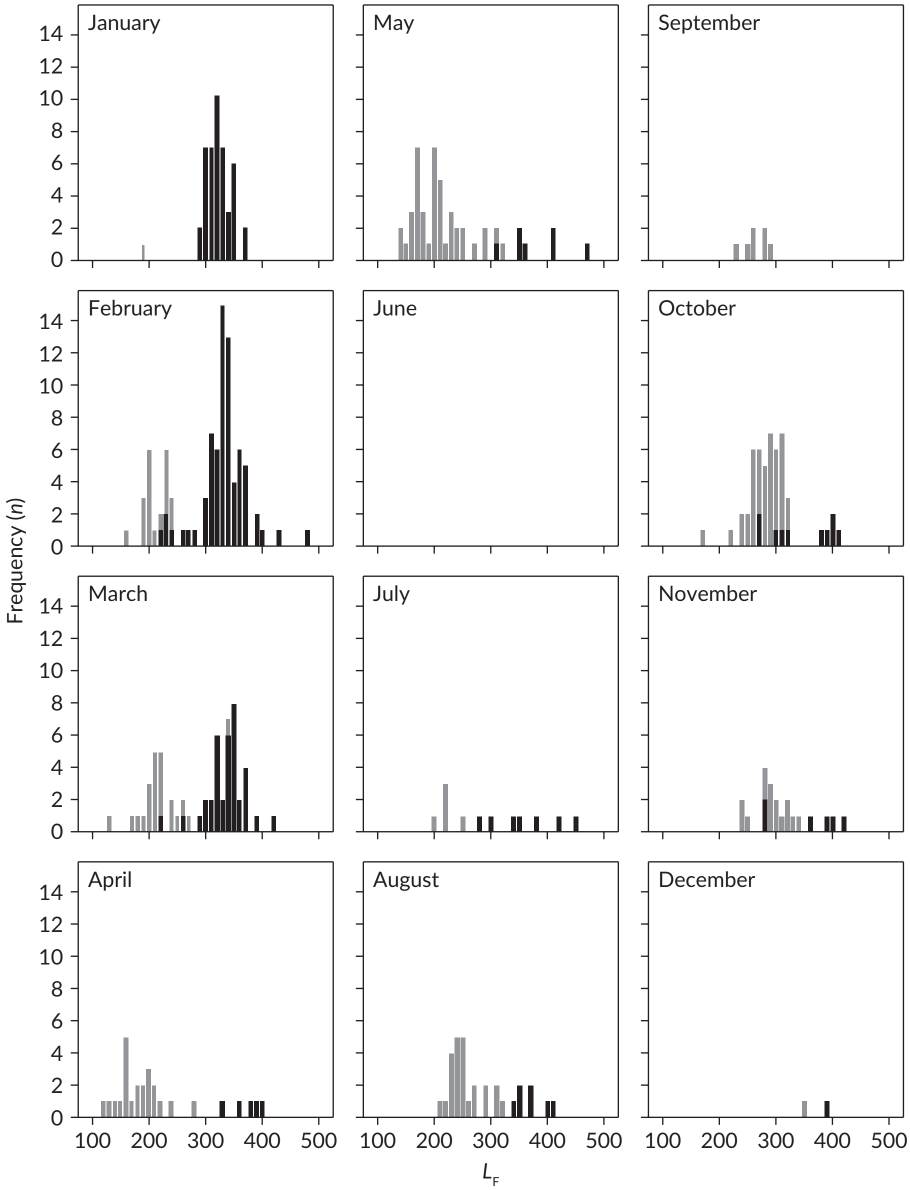

FIGURE 4 Fork length (L_F)-frequency distribution by month of new migrant (■) and veteran migrant (■) anadromous *Oncorhynchus clarkii clarkii*, captured in Eld inlet, South Puget Sound Washington in 2015

increased from 319.6 mm (±19.7 mm) in January to 351.3 mm (±22.1 mm) in April (Figure 7). Mean growth of veteran migrants in January (0.16 mm d^{-1}) was the lowest observed in the study, but rapidly increased (0.59 mm d^{-1}) by March of 2015 (Figure 7). Growth rates of genetically identified recaptured individuals was 0.61 mm d^{-1} (SD ± 0.36 mm d^{-1}) and 0.35 mm day^{-1} (SD ± 0.24 mm d^{-1}) for fish on their first and second feeding migrations respectively.

3.2 | Stock composition

Most (76%, 142/186) of the *O. c. clarkii* sampled in Eld Inlet assigned to the stream closest in proximity to the marine study area, McLane Creek. *Oncorhynchus clarkii clarkii* assigned to McLane Creek were captured in marine water in all months except June when no *O. c. clarkii* were captured (Figure 6). Kennedy and Skookum Creeks *O. c. clarkii* were encountered less frequently, accounting for 12.4% (23/186) and 4.8% (9/186) of the total assignments, respectively. These proportions are consistent with their geographic proximity to the study beach, with lower contribution of those fish assigned to streams further away. *Oncorhynchus clarkii clarkii* from more than one population were captured in all months of the year (Figure 6). No individuals had probabilities of inclusion less than 0.10 for all three putative source populations, including those with posterior assignment probabilities < 0.85, suggesting all sampled fish originated from populations included in the genetic baseline.

3.3 | Mark and recapture

A total of 427 *O. c. clarkii* were sampled in Eld Inlet in 2015 (Table 1) comprising 305 unique individuals. Following the initial sampling event in January 2015, we identified recaptures (genetic matches) in every month of the study except for June, when no *O. c. clarkii* were captured (Table 1 and Figure 8). Overall, 21% (64/305) of *O. c. clarkii* sampled in this study were encountered during subsequent sampling

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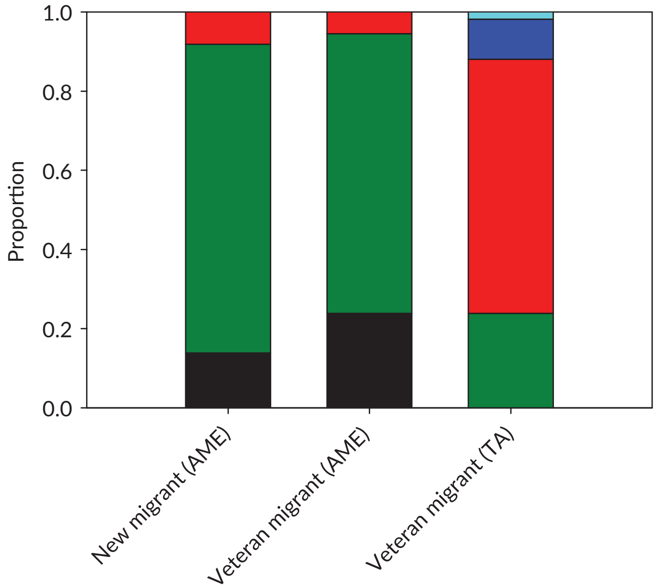

FIGURE 5 Proportion of age at marine entry (AME), and total age (TA) for new and veteran migrating anadromous *Oncorhynchus clarkii clarkii*, in Eld Inlet, South Puget Sound Washington in 2015. Age: ■, 1 year; ■, 2 years; ■, 3 years; ■, 4 years; ■, age 5 years

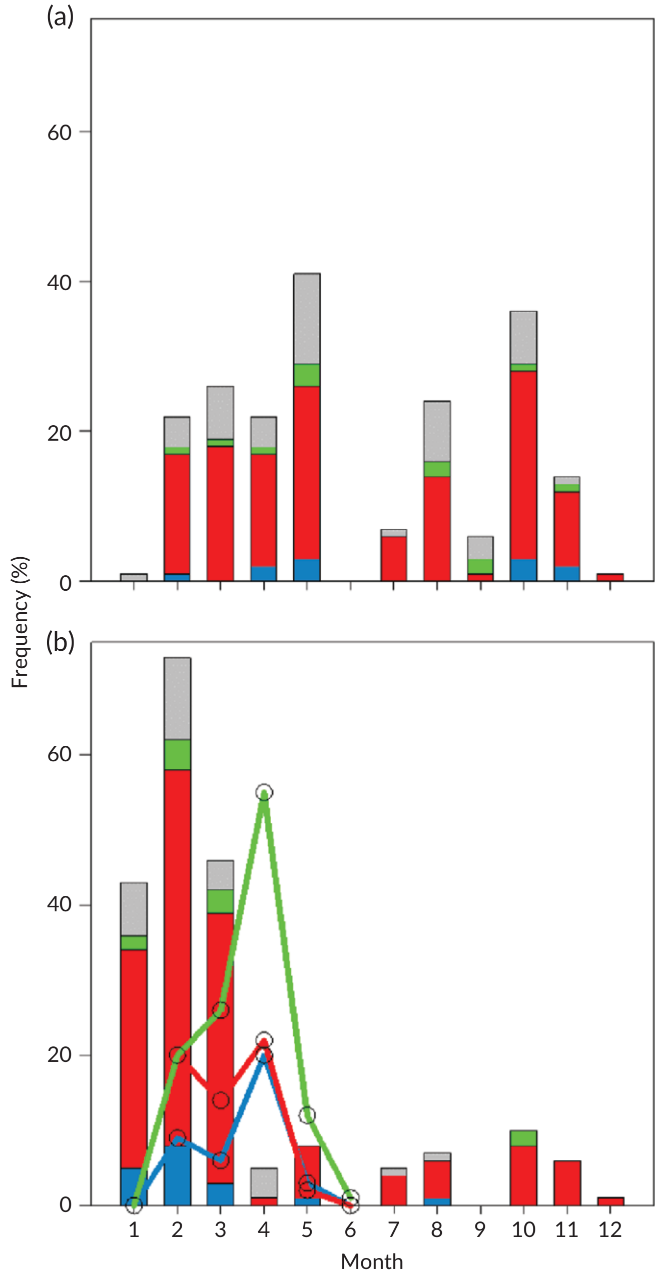

FIGURE 6 Frequency distribution of genetic assignment of anadromous *Oncorhynchus clarkii clarkii*, (stacked bars) and redd counts in associated streams (lines) in South Puget Sound Washington in 2015 of (a) new migrants and (b) veteran migrants. Streams of origin are: ■, ——, Kennedy Creek; ■, ——, McLane Creek; ■, ——, Skookum Creek; ■, undetermined

events. Highest recapture rates occurred on 26 March (Table 1) when 86% of the total catch had been captured previously (25/29) and 100% of adults captured had been sampled previously (*n* = 24). During the study, 13.1% (21/160) of new migrant *O. c. clarkii* captured at the study site were captured more than once and 30.8% (37/120) of veteran migrant *O. c. clarkii* were captured more than once. Thirty-one percent (20/64) of recaptured individuals were caught more than twice and 35% (22/64) of the recaptured fish were caught two or more months later. Among the three baseline populations, all demonstrated site fidelity (Figure 8). Veteran migrants from Kennedy and Skookum Creeks, however, were not recaptured following the end of spawning season (June; Figure 8).

4 | DISCUSSION

Recent work by Washington Department of Fish and Wildlife has identified challenges in management of anadromous *O. c. clarkii* due to their mixed-stock composition in marine water (Losee *et al*., 2017), unpredictable migratory patterns (Moore *et al*., 2010), variability in spawning time (Losee *et al.* 2016) and increased angling effort (Gresswell & Harding, 1997; J.J. DeShazo, unpublished data). Because of the uncertainty surrounding the biology of anadromous *O. c. clarkii*, management actions by the Washington Department of Fish and Wildlife are intentionally conservative utilizing catch-and-release regulations in marine water to maximize recreational opportunity and limit mortality associated with fishing. Results of the current research clarify the age composition, stock structure and movement patterns of this species and suggest that today, anadromous *O. c. clarkii* populations comprise short-lived individuals that rely on relatively small sections of nearshore habitat. This information combined with the mixed-stock nature of sampled populations provides support for conservative regulations, which aim to minimize the effects of harvesting on *O. c. clarkii* while providing the greatest economic benefit by maximizing catch rates over the long term for what appears to be small population sizes (Gresswell & Harding, 1997).

Growth rates results suggest that availability of prey is probably one factor driving the high site fidelity we observed. Growth rates of *O. c. clarkii* in south Puget Sound were comparable with that of other salmonids in estuarine environments (Campbell, 2010; Goertler *et al*., 2016), but were lower than other *Oncorhynchus* spp. in coastal marine waters (Claiborne *et al*., 2014; Orsi *et al*., 2000). In addition, multiple

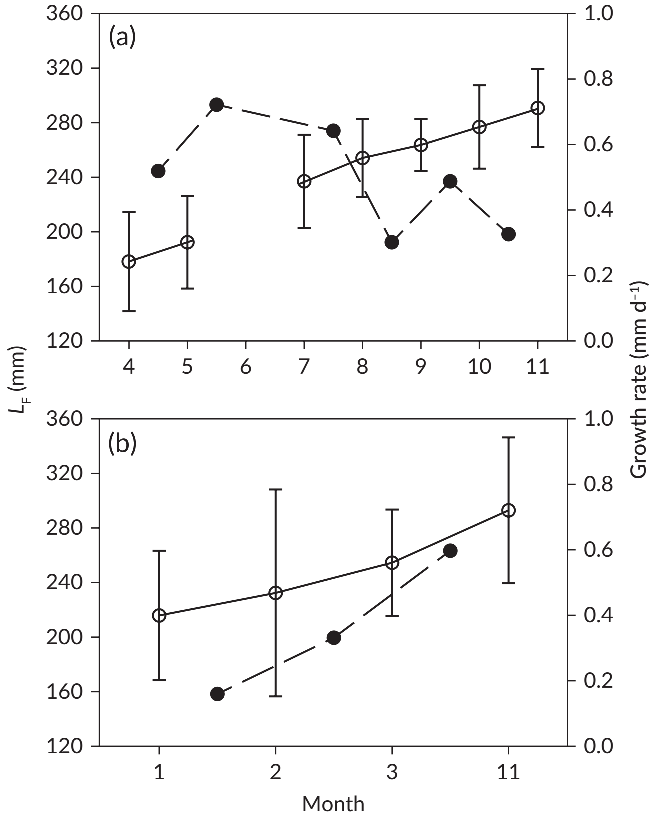

FIGURE 7 Mean monthly fork length (L_F; –○–, ± SD), and growth rate (--●--) of (a) new migrants and (b) veteran migrating anadromous *Oncorhynchus clarkii clarkii*, captured in Eld Inlet, South Puget Sound Washington in 2015

life stages of *O. c. clarkii* either remained at or returned to our study beach. Using a length-based cohort analysis, Duffy and Beauchamp (2008) estimated marine growth in central and south Puget Sound ranging from 0.39 to 0.63 mm d^{-1} during spring, similar to the present study. Growth remained high throughout the sampling period, but we observed variation in monthly mean growth rates for fish during their first and second marine migrations. For new migrants, growth rates

TABLE 1 Number of anadromous *Oncorhynchus clarkii clarkii* sampled and recaptured in Eld Inlet, South Puget Sound, Washington in 2015

Date 2015	Sample (*n*)	Recaptures (%)
15 January	45	–
26 February	97	16.5
24 March	54	44.4
26 March	29	86.2
22 April	28	10.7
20 May	50	22.0
25 June	0	0
21 July	12	33.3
17 August	31	25.8
16 September	7	42.9
14 October	51	15.7
23 November	21	38.1
23 December	2	50.0
Total	427	

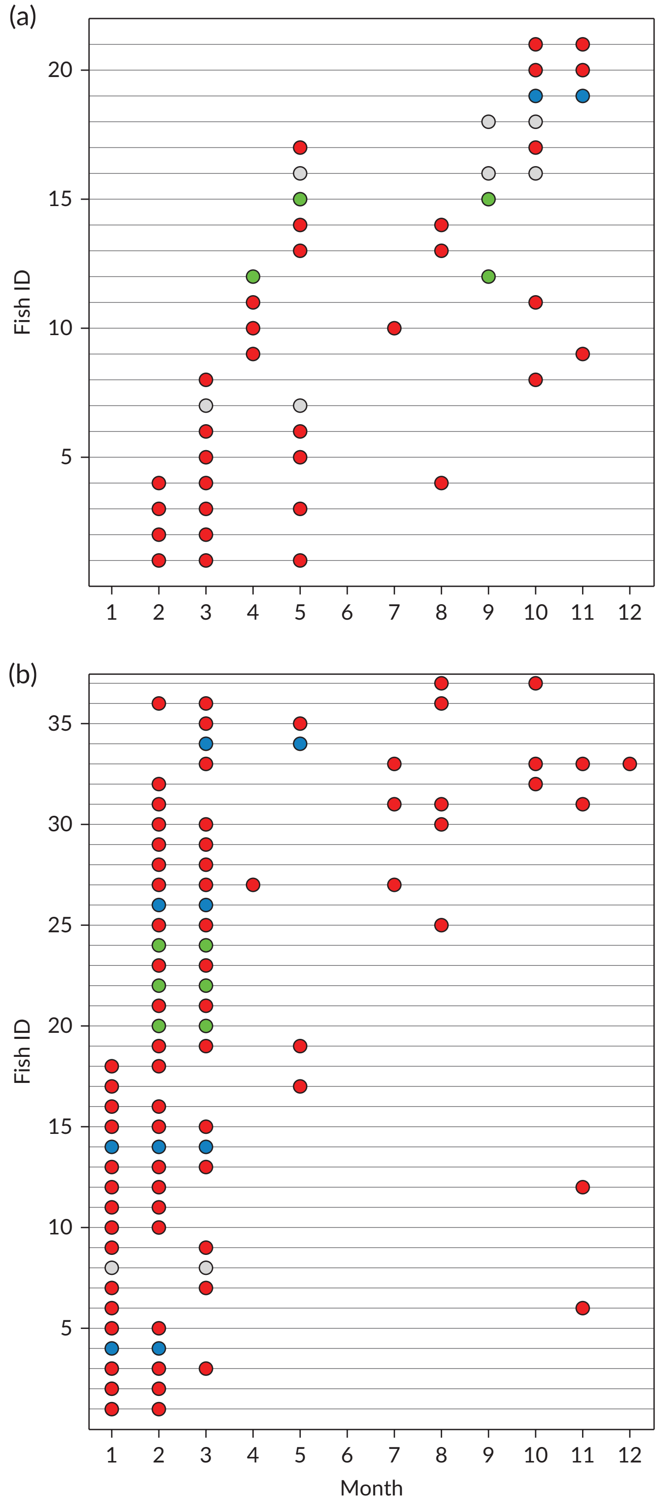

FIGURE 8 Month of recapture for anadromous *Oncorhynchus clarkii clarkii* of (a) new migrants and (b) veteran migrants. Each horizontal line represents an individually identified fish (Fish ID) captured on more than one occasion in Eld Inlet, South Puget Sound Washington in 2015. Streams of origin are ●, Kennedy Creek; ●, McLane Creek; ●, Skookum Creeks; ○, undetermined

increased during spring from April–August and were declining throughout the fall. Similarly, growth increased for veteran migrants from January to April. We suspect that this variation in growth rates observed at our study beach was related to seasonal variation in sea-surface temperature and availability of Chum Salmon *Oncorhynchus keta* (Walbaum 1792) eggs and fry, which have been shown to comprise 46% of *O. c. clarkii* diet in the marine environment during winter and spring (Jauquet, 2008).

Predictable species and stock-specific migratory pathways have been well documented for *Oncorhynchus* spp. and other migratory marine vertebrates (Block *et al*., 2011; Byron and Burke, 2014; Quinn & Myers, 2004), but definitive information on movements following the early marine residency period is lacking for anadromous fish. In this study, we documented the potential for anadromous fish to return to a previously occupied location in the marine environment. Using radio tags, Hayes *et al*. (2011) found similar results in a single bull trout *Salvelinus confluentus* (Suckley 1859) individual that repeatedly used one area in the marine environment. Our documentation of *O. c. clarkii* exhibiting high site fidelity immediately upon marine entry and throughout their life to a relatively small area (< 200 m of sampled area) suggests *O. c. clarkii* may be extremely susceptible to perturbation of shoreline habitats and other anthropogenic effects. Because the inlet where this study took place contains numerous small beaches of undisturbed habitat interspersed between large areas of shoreline habitats that have been heavily modified, additional work needs to be done to better understand if other beaches are as well used as that of our study.

The high recapture rate of anadromous *O. c. clarkii* observed at the study beach is consistent with predictions that short-lived, fast growing animals have a tendency to exhibit site fidelity (Switzer, 1993). While it is plausible that larger-bodied *Oncorhynchus* spp. migrate throughout the ocean opportunistically based on environmental conditions and food resources (Healey, 2000; Kallio-Nyberg *et al*., 1999; Losee *et al*., 2014), a growing body of evidence suggests that anadromous *Oncorhynchus* spp. display some degree of fidelity to migratory pathways and offshore feeding areas, possibly as a mechanism of bet-hedging in a highly variable ocean environment (Burke *et al*., 2014; Quinn *et al*., 2011; Weitkamp, 2010). *Oncorhynchus* spp. exhibit a high degree of variability in abundance of adult returns, but this variability can be explained in large part by variability in ocean conditions during the first month of ocean residence (Losee *et al*., 2014; Miller *et al*., 2013; Pearcy, 1992), when juvenile salmon migrate rapidly (up to 40 km d^{-1}, Fisher *et al*., 2014) to offshore feeding areas. The 1 to 5 years following the early marine migration represents a time-period where survival rates are relatively stable for *Oncorhynchus* spp. (Beamish & Mahnken, 2001; Pearcy, 1992). Behaviour and movement of Pacific salmon during this period is largely unknown, but it has been shown that Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) and coho salmon *Oncorhynchus kisutch* (Walbaum 1792) follow predictable, heritable migratory pathways to these offshore feeding areas (Burke *et al*., 2014; Putman *et al*., 2014; Weitkamp, 2010) largely independent of variability in environmental conditions (Weitkamp, 2010). It is probable that these genetically controlled migrations are leading salmonids and other large marine predators to feeding areas that consistently result in adequate conditions for growth and survival (Block *et al*., 2011). Future research aimed at improving understanding of salmonid movement patterns in offshore habitats would probably be beneficial to those tasked with recovering salmonid populations and modelling stock specific harvest rates, particularly if large bodied ocean migrating P *Oncorhynchus* spp. prove to exhibit site fidelity during ocean residency as *O. c. clarkii* have here been shown to do, albeit on a much smaller spatial scale.

For *O. c. clarkii*, these results highlight the importance of nearshore feeding areas and add support for conservative regulations in marine waters. As the second largest estuary by surface area in the United States, Puget Sound has the potential to offer robust fishing opportunities for *O. c. clarkii* as they remain in nearshore tidal waters for much of their life (Gelfenbaum *et al*., 2006). However, anthropogenic modification of shorelines in Puget Sound have significantly diminished quality and availability of habitat. For instance, in Eld Inlet, where this study took place, the percentage of armoured shoreline more than doubled between 1992 and 2002 (Morrison *et al*., 1993). The effect of this habitat modification on distribution of nearshore fishes that overwinter in Puget Sound has not been well documented but could result in reduced fish abundance and increased pressure from anglers on the limited habitat remaining. A comprehensive management approach that identifies stocks of concern and protects habitat adjacent to these populations' natal streams could contribute to long-term sustainable fishing opportunity for anadromous cutthroat trout.

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Author Contribution

J.P.L., ideas, data generation, data analysis, manuscript preparation and funding.

A.M.C., ideas, data generation, data analysis and manuscript preparation.

P.D.D., ideas, data generation, data analysis, manuscript preparation and funding.

H.S.F., ideas, data generation, data analysis, manuscript preparation.

T.R.S., ideas, data generation, data analysis, manuscript preparation and funding.

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