Received: 19 May 2020 | Revised: 5 October 2020 | Accepted: 9 October 2020

DOI: 10.1111/eff.12581

ORIGINAL ARTICLE

Ecology of FRESHWATER FISH WILEY

Nowhere to hide: The importance of instream cover for stream-living Coastal Cutthroat Trout during seasonal low flow

Brooke E. Penaluna[1,2] | Jason B. Dunham[3] | Heidi V. Andersen[4]

[1]U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR, USA

[2]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

[3]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR, USA

[4]U.S. Department of the Interior, Bureau of Land Management, Corvallis, OR, USA

Correspondence
Brooke E. Penaluna, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.
Email: brooke.penaluna@usda.gov

Funding information
Watersheds Research Cooperative at Oregon State U; Oregon Department of Fish and Wildlife; USGS Forest and Rangeland Ecosystem Science Center; EPA STAR

Abstract

Through their multiple functions, refuges may be important for stream-living fishes, particularly during stressful events such as seasonal low flow or drought. Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* is an ideal study organism to understand the importance of refuge. During seasonal low flow, lower water levels limit access to refuge and emigration, survival of fish is low, and predation risk is high. Under these conditions, we studied patterns of cover use from field observations and tested predictions from multiple hypotheses about cover use in a semi-natural experiment. Boulders were the main cover selected by trout in natural streams. Trout disproportionately used cover near deeper water, and they selected larger-sized cover in shallower water. Trout showed plasticity to switch among behaviours, concealing under cover and emigrating as first options, followed by grouping, and then habitat shifting. Lack of feeding and growth suggested that perceived threat of predation was a more important driver of behaviour than foraging. Emigration was also linked to cover, with higher levels of emigration associated with less cover availability, revealing a potential link between refuge and demography through emigration. Except for feeding, the intensity of alternative behaviours can increase or decrease depending on refuge availability. Collectively, findings of this work indicate that cover can be considered a critical limiting resource along with other fundamental resources of food and space for stream-living fish.

KEYWORDS
emigration, habitat use, headwater streams, predation risk, refuge

1 | INTRODUCTION

The importance of refuges is arguably underappreciated by ecologists (Berryman & Hawkins, 2006), and the dependence of many animals on them may be increasing (Morelli et al., 2020). The immediate response of animals to environmental change is typically behavioural, with responses that are detectable in advance of measurable responses in growth, survival or other indicators of fitness (Beever et al., 2017; Berger-Tal et al., 2011). When an individual seeks refuge, also referred to as physical shelter or cover, it is assumed the intent is to avoid predators, evade competition or avoid harsh environmental conditions (Allouché, 2002; Orrock et al., 2013). However, the contingencies in how individuals use cover (Allouché, 2002), and the consequences of cover for individuals and populations remain uncertain (Smokorowski & Pratt, 2007).

For stream-living fishes, small streams are likely locations where cover may be particularly important. In the Pacific Northwest of the United States, for example, when lack of summer precipitation

creates seasonally low water levels (Tague & Dugger, 2010; Ward et al., 2020) resulting in less available cover, survival of trout is reduced (Berger & Gresswell, 2009) and vulnerability to predators is high (Steinmetz et al., 2003; Harvey and Nakamoto 2013; Penaluna et al., 2015). Although aquatic productivity (on a per-area basis) typically increases in summer owing to longer photoperiods and warmer stream temperatures (Bellmore et al., 2017), trout often exhibit low growth and consumption in streams (Jensen, 2017; Raggon, 2010). These observations could be explained by the threat of predation, by the lack of available cover and lack of feeding by fish, despite available food (Lima & Dill, 1990). However, without directly observing individual fish, it can be difficult to identify the processes underlying these patterns.

Here, we evaluate cover selected by Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* during seasonal low flow in relation to instream features that could potentially serve as cover in natural streams. Specifically, we considered cover used for concealment, based on the presumption that the threat of predation was driving fish to seek cover. Where available, fish may select from a host of stream features that can provide instream cover, including substrate, undercut banks, instream wood, flooded tree roots, vegetation, hydraulic features (e.g., turbulence, depth, turbidity), surface ice and human-constructed features (Allouché, 2002) that are in or near deeper water (Lonzarich & Quinn, 1995; Harvey and White 2017). To evaluate the selection of stream features providing concealment, we used a resource selection approach (Manly et al., 2002; Polivka, 2020). In addition to cover itself, we evaluated how selection of cover may be conditioned on availability of deep water for potential refuge, which could influence the importance of cover to fish (Power, 1984, 1987). We predicted that fish are more likely to use cover features that are in or near deeper water (Lonzarich & Quinn, 1995; Harvey and White 2016; Figure 1).

With knowledge of the type of cover selected by trout based on field observations, we further evaluated fish responses in a semi-natural experiment. We manipulated the availability of cover and the opportunity for emigration to evaluate growth and additional features of individual behaviours that we hypothesised were associated with cover availability. Emigration is a particularly important option for populations responding to cover manipulation (Gowan et al., 1994; McMahon & Matter, 2006). The behaviours we tracked included use of single cover features by more than one individual (sharing of cover), grouping, habitat shifting, feeding and emigration. Although it is difficult to identify the exact purpose of an expressed behaviour (Rosenblueth et al., 1943), it is useful to identify behavioural responses because of their implications for individual fitness and population processes. Accordingly, a better understanding of individual behaviour can help to identify details of how species can respond to changing environmental conditions (Beever et al., 2017; Berger-Tal et al., 2011) and how restoration of instream cover influences fish (Polivka, 2020).

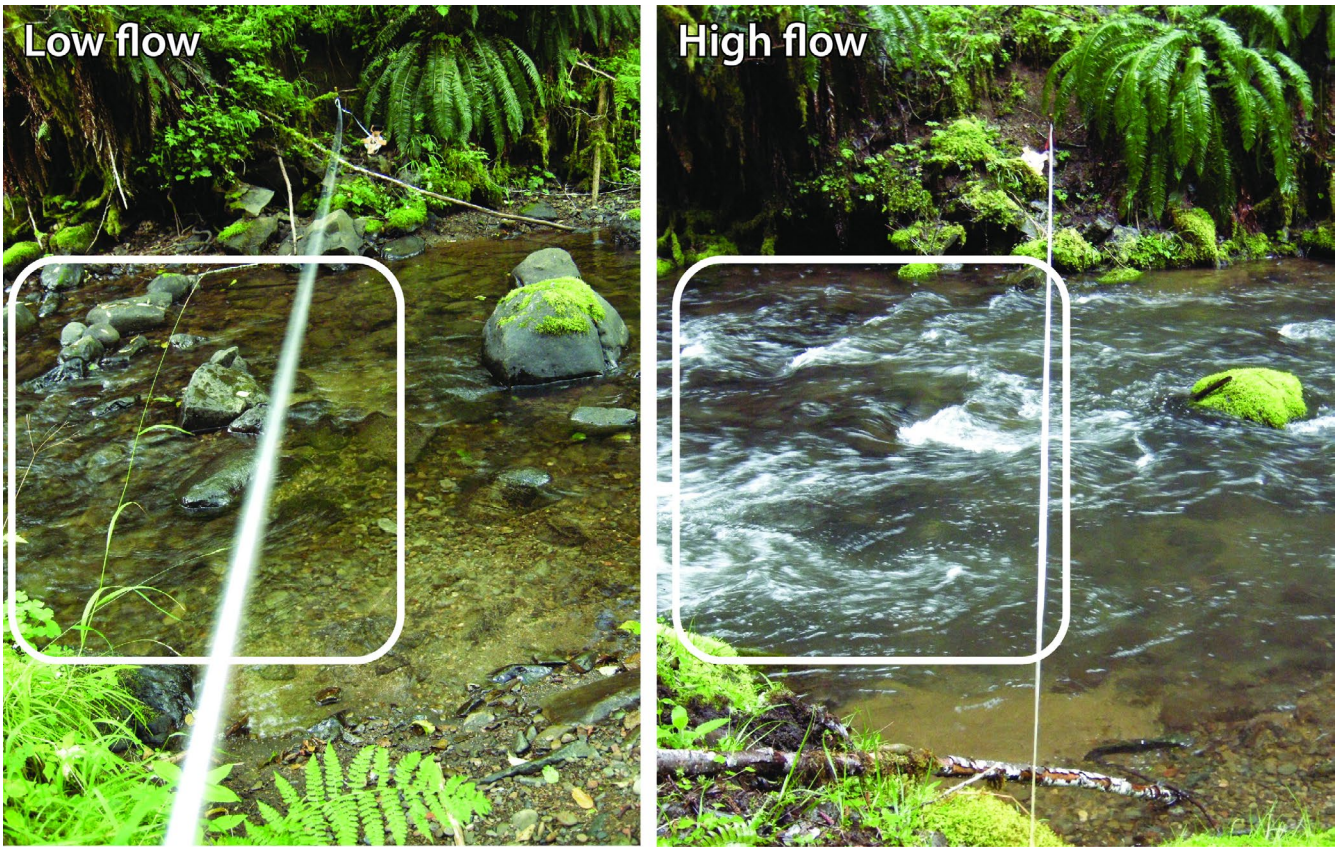

FIGURE 1 Instream cover availability during seasonal low and high flows highlighting greater availability of cover for fish during higher flows. Photographs show same transect in Rock Creek, Trask Watershed, western Oregon

TABLE 1 Characteristics of six western Oregon streams during seasonal low flow in 2007, including basin, stream, stream length and mean wetted width

Basin	Stream	Reach length (m)	Wetted width (m)	Number tagged	Fork length (mm)
Trask	Gus Creek	316	3.1	251	124 + 23
Trask	Pothole Creek	224	2.7	63	116 + 13
Trask	Rock Creek	286	3.5	98	114 + 14
Trask	Upper Mainstem Trask	200	3.0	97	123 + 20
Alsea	Flynn Creek	560	1.8	139	118 + 19
Hinkle	South Fork Hinkle	276	2.4	388	123 + 21

Note: Also included are number of tagged Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) and mean fork length in each stream reach.

We hypothesised several potential responses of trout to variation in availability of instream cover during seasonal low flow. Overall, we assumed trout expressed behaviours that reduced their perceived or actual vulnerability to predators, including using cover, aggregating in groups or emigrating altogether from semi-natural streams (Kerfoot & Sih, 1987). In the field study, we focused on selection of instream cover by individual fish, whereas in the experimental study, we were able to evaluate additional details of cover use. When cover was experimentally reduced, we expected that fish would use available cover, but that use of cover by more than one trout would increase. We predicted that grouping (presumably an antipredator response; Pavlov & Kasumyan, 2000) would be more likely when available cover was reduced. Given that fish that spend more time seeking cover or engaging in other behaviours (e.g., grouping) have reduced available time for feeding (Puckett & Dill, 1985), we predicted that feeding would be reduced when cover availability was reduced. Finally, we expected that reduced cover should lead to increased rates of emigration, as individuals sought to leave streams in presumptive search of more suitable locations (McMahon & Matter, 2006). Ultimately, we sought to evaluate the capacity of trout to cope with changes in their environment by understanding the condition-specific importance of cover to trout in small streams during seasonal low flow.

2 | METHODS

2.1 | Study area

We observed cover use by Coastal Cutthroat Trout during seasonal low flow (summer) in 200–560 m stream reaches in six streams (<1 m depth), including a range of habitats in three catchments, including the Trask, Alsea and Umpqua Rivers, Oregon (Table 1). These streams are mostly underlain by marine sandstones and shale, with intrusions of basaltic volcanic rock (Hicks & Hall, 2003). The climate is temperate maritime with mild, wet winters and warm, dry summers. Peak stream flows are flashy following winter rainstorms, with seasonal low flow generally between July and October (Segura et al., 2020; Surfleet & Skaugset, 2013) coinciding with declines in swimming costs (see supplementary materials). Study streams support Coastal Cutthroat Trout: the most abundant salmonid present relative to co-occurring species that included Rainbow Trout/steelhead (*O. mykiss*) and Coho Salmon (*O. kisutch*) juveniles. Sculpins (*Cottus* spp.) were also present and often the most numerous fish species present (Chelgren & Dunham, 2015). All fish used in this study were identified as Coastal Cutthroat Trout.

2.2 | Trout tagging and tracking

We implanted each trout (≥10 cm) with an individually coded 2.3-cm half-duplex passive-integrated transponder (PIT) tag (Oregon RFID, Portland, OR) in July of 2007. After a week of acclimation to allow time for trout to resume normal behaviour (Newby et al., 2007), we began tracking individuals to record characteristics of cover used for concealment and collected information on potentially available cover (from 1 August 2007 to 20 September 2007).

By actively wading into streams to measure habitat characteristics, we assumed that trout would flee or seek refuge in response. We assumed observed use of cover represented concealment or hiding behaviour that would be employed in response to actual predators or perceived threat of predation (Caro, 2005). To locate a tagged individual and ultimately identify characteristics of used cover, we deployed both a portable half-duplex PIT tag antenna that detected tags within at least 0.5 m of their location (Zydlewski et al., 2001) and a portable PIT tag reader (RS320 Stick Reader Allflex USA, Inc., Texas) that detected tags within at least 10 cm of their position. We recorded trout as using cover if a tag remained in a 10-cm radius for at least 20 s, and it was not a lost tag or a mortality (which was checked by eliciting movement by touching trout). Stream reaches were sampled for used cover two times each (one pass in an upstream direction and another in a downstream direction), with the exception of streams in the Trask River, which were sampled three times. We also randomly determined the order of sampling streams to ensure temporal and spatial interspersion of sampling.

2.3 | Quantification of used and available cover

We classified instream cover into categories that included large wood, woody material, turbulence, substrate, vegetation, undercut

banks and detritus. We quantified the exact depth of each location where a fish was detected using a stadia rod, but also categorically classified depth as a type of refuge if it exceeded 20 cm (Harvey & Stewart, 1991; Power, 1984; Harvey and White 2017). Large wood was defined as a piece of wood with a trunk both longer than 3 m and diameter >15 cm measured one-third of the way up from the base (Moore et al., 1999). We also noted the number of large wood pieces and whether the tree providing the wood was alive or dead. Woody material was defined as individual pieces or an accumulation of wood or branches <15 cm in diameter. Turbulence was considered cover when it obscured the overhead view of a 2.5-cm diameter Secchi disc. We measured substrate with a Wolman pebble count. Substrate referred to sediments of particle size >2 mm (b-axis dimension) used by trout as cover, mainly cobbles (b-axis dimensions of 64 mm to 256 mm) or boulders (b-axis dimensions >257 mm). Vegetation referred to instream and terrestrial vegetation overhanging within 40 cm of the stream surface (Inoue et al., 1997). Undercut banks were considered as any portion of the stream that flowed under a streambank often next to plants or tree roots. Detritus referred to a benthic organic matter mat composed of materials such as twigs and leaves that were at least 2 cm in depth.

We described used cover with a common set of descriptors for all streams, including depth of water (cm), proximity to deeper water (≥20 cm) for trout located in shallow water (≤20 cm depth), surface area of the cover (m^2), distance under substrate (cm) and whether substrate was embedded within fine (<2 mm, b-axis) bed material. Proximity to deeper water accounts for the complementary influence of deeper water on cover use (Schlosser, 1995; White & Rahel, 2008). Surface area may be a meaningful quantification of cover for trout, and hence, we multiplied the length of each cover item (a-axis) by its average width (b-axis). For all other cover types, we measured three widths, including longest width and two additional measurements at each end. Trout may use substrate or the interstitial spaces of a streambed as cover (Hartman 1963; Bustard and Narver 1975), similar to the hyporheic refuge hypothesis suggested for invertebrates (Palmer et al., 1992; Dole-Oliver, 2011). Hence, we considered embeddedness for substrate because interstitial spaces cannot be used as refuge by trout when the associated substrate is surrounded by fine substrates (Platts et al., 1983). Thus, we recorded substrate (gravel, cobble or boulder) as embedded when fines (and small organics) covered more than 25% of its surface (Platts et al., 1983) or interstitial space was inaccessible to trout. Even in cases where substrate appears embedded, it is possible that small tunnels, fissures or other points of access are available to trout to use as cover; thus, we also quantified the distance into the streambed that trout could potentially access.

We quantified characteristics of available habitat by randomly sampling points along transects perpendicular to the stream channel spaced every 2 m over the entire length of each stream (Table 3). At each point, we described the same set of stream features as for trout using cover, which allows for randomness and a representative sample of available habitat.

2.4 | Experimental setup

We conducted a manipulative experiment in the outdoor experimental streams at the Oregon Hatchery Research Center (http://www.dfw.state.or.us/fish/OHRC/) to approximate conditions experienced by trout during low flow periods. Water depth (Lonzarich & Quinn, 1995; Power, 1987), turbidity (Harvey & Railsback, 2009) and velocity (Bisson et al., 1988) were controlled by maintaining minimum flows, characteristic of average seasonal low flows. Drift and benthic inputs were naturally present in stream sections. We added 5 g (dry mass) of floating krill every other day to measure feeding behaviour.

We divided four experimental stream channels in half with 3-mm square-mesh screens to prevent fish movement among experimental units (Figure 2). The screens were placed perpendicular to the flow, creating 8 outdoor replicate stream sections (experimental units) that were 20 m long and 2 m wide, on average (wetted width). Although mesh screens prevented fish movements among experimental units, fish could move freely or enter emigration boxes at the up- and downstream end of each unit. Emigration boxes were accessible to all trout and constructed so that individuals had to enter through a narrow white tube into a small, white container to encourage only motivated trout to exit (McMahon & Matter, 2006). Emigration was open for 28 days following a 21-day period when it was closed. Continuous flow was supplied from an adjacent natural stream after being filtered through a 2-mm mesh stainless steel screen and then routed through a 679,648-L settling pond. To ensure that depth would not be used for refuge (Power, 1984), water depths were maintained at between 15 cm to 20 cm by managing incoming flows. We also removed larger substrate (>8-cm a-axis) that could have been used as instream cover. Water temperature ranged from 10 to 12°C and stream flows from 23 to 33 L/s. The entire experimental area was enclosed by a metal frame supporting black mesh screens that was 3.5–6.0 m above ground level, completely excluding potential predators. We examined stream shading in a post hoc exploratory measurement of canopy, because we were concerned about unequal shading from nearby trees that may have influenced behavioural responses of trout (Penaluna, Dunham, et al., 2015). We quantified stream shading with densiometer readings every 3 m along each section between 1,200 and 1,300 hr and summed the proportion of cover area in each cardinal direction.

We manipulated instream cover availability to have a high (0.01 m^2 of cover per m^2 of stream) or low (0.002 m^2 of cover per m^2 of stream) level. We randomly assigned each level of cover availability across four raceways or statistical blocks, thereby accounting for potentially dissimilar environmental conditions among locations. Hence, each level of cover availability was assigned to half of the eight replicate stream sections, resulting in four replicates each for high- and low-cover availability. In our field observations, we learned that substrate used by trout for concealment cover was equal to or greater in size than their body length, and thus, we built cover sized to slightly exceed the size of the largest trout (23.4 cm). Because we did not want to remove

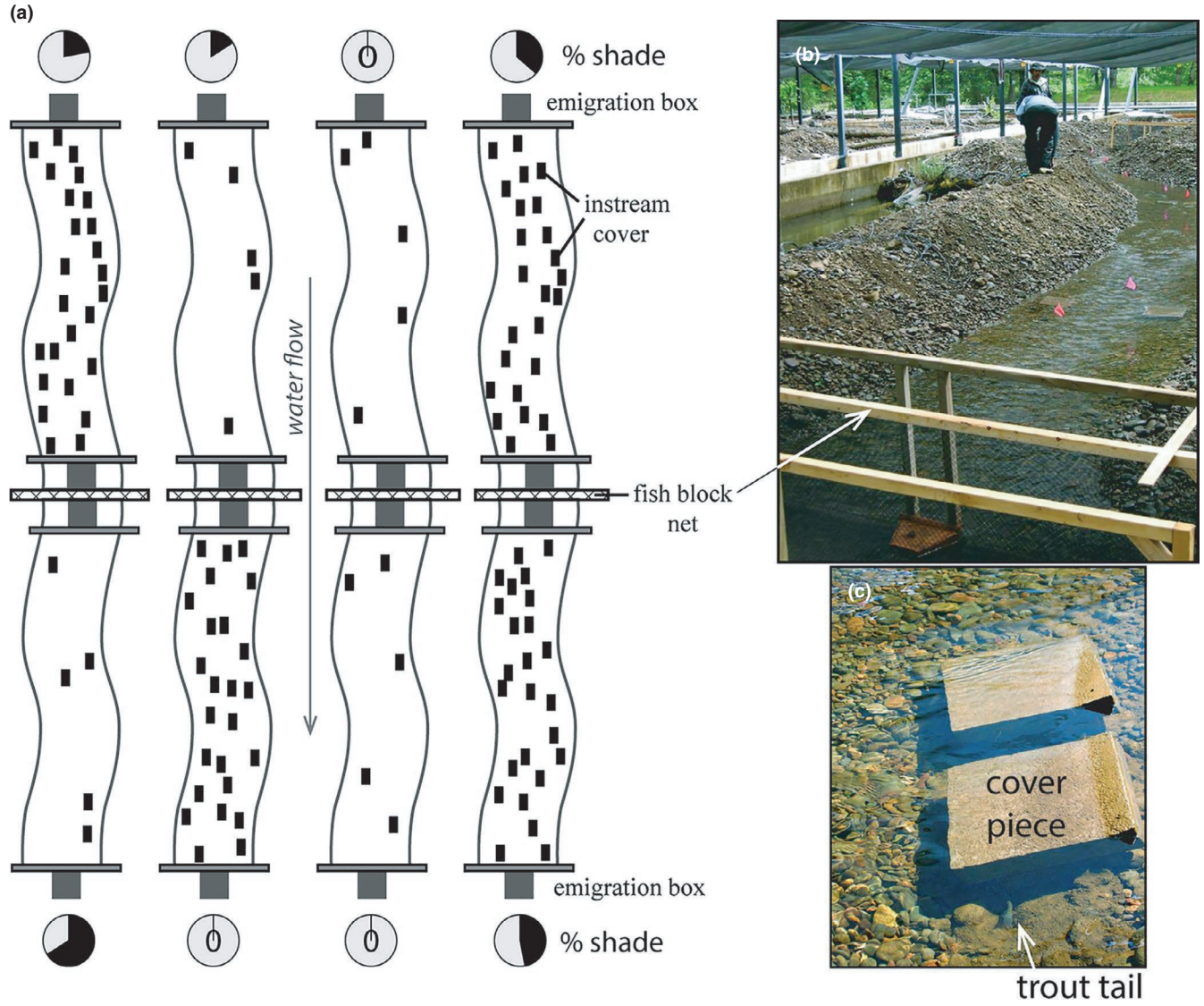

FIGURE 2 (a) Design of semi-natural experimental area with location of stream sections for low-density ($n = 4$) and high-density ($n = 4$) instream cover coupled with amount of shade for each stream section. Emigration boxes were placed at each end of a stream section. Mesh screens prevented fish passage to other stream sections as indicated by fish block nets. (b) Example low-density stream section with fish block net shown. All stream sections were 20 m long and 2 m wide (wetted width). (c) Adult Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) using instream cover piece. Each cover piece consisted of a 30.5- by 30.5-cm concrete paver top piece with a 30.5- by 20.3-cm paver bottom piece glued underneath in the centre, creating two 5.1- by 30.5-cm equal-sized spaces on each end for cover. This figure first appeared in Penaluna, Dunham, et al. (2015)

boulders from other natural streams (owing to the risk of transporting organisms from one stream to another and because we did not want to limit cover for organisms in the source streams), we designed standardised instream cover elements using cement pavers (Figure 2). Each piece of cover was assembled from pavers as follows: a 30.5 × 30.5-cm cement paver top piece with a 30.5 × 20.3-cm paver bottom piece glued underneath in the centre, creating two 5.1 × 30.5-cm equal-sized positions on each end. In each stream section, the placement of each instream cover piece was randomly distributed on a grid of 80 potential equally spaced locations.

During June 2009, we collected (by electrofishing) trout ranging from 9.4 to 23.4 cm (fork length) from nearby streams in the Alsea River watershed. This is the typical size range found during this time of year in the region. We measured (fork length, wet weight) and implanted each trout with a 2.3-cm half-duplex PIT tag (Oregon RFID, Portland, OR). We allowed fish three days to recover from tagging (Newby et al., 2007) and transferred 24 individuals to each of the experimental units using random assignments. Fish were allowed to acclimate to the experimental streams for three more days. We classified trout a priori into three initial fork length classes by dividing the overall length distribution of trout from the field into thirds. Our groups included small (9.4–14.9 cm), medium (15.0–19.4 cm) and large (19.5–23.4 cm) trout. We maintained comparable overall density and biomass in each stream section (0.4–0.6 fish m^2 and 1.30–1.34 g/m^2) and distributed individuals

with approximately equal numbers of trout from each of the three size classes per stream section (small = 13–16, medium = 4–7, large = 2–4).

2.5 | Behavioural responses of cover use, emigration, grouping and feeding

We examined cover use under two levels of availability (high, low) when stream sections were either open or closed to emigration. We examined emigration when emigration boxes were open. We identified individuals using cover or emigrating with a portable PIT tag reader (RS320 Stick Reader Allflex USA, Inc., Irving, Texas), allowing us to detect a link between cover use and emigration. We measured cover use as the proportion of trout that used cover (defined above) out of the number of trout present in each length class. We recorded cover use every fourth day throughout the experiment, allowing for 7 observations to identify consistency of use and whether trout shift among cover. We also recorded sharing of cover by trout. We quantified cover sharing as the number of times that ≥2 trout used any cover alcove or position (two positions per cover piece) at the same time. The length class of each trout that shared cover was also recorded. Each day, we recorded individuals that emigrated and determined the proportion of trout that emigrated for each length class relative to the total in a given class. We checked emigration boxes for the presence of individuals daily between 0,900 and 1,100 for the duration of the experiment. If an individual trout was found three times in the emigration box, we physically removed it from the experiment and counted it as an emigrant. Hence, individuals making local exploratory movements were not considered emigrants (modified from Keeley, 2001).

We defined grouping behaviour as observations where ≥3 individuals were present within a standardised body length (15 cm fork length) of each other and not using cover. Mean grouping (number of individuals recorded in groups) was calculated in each 20-m stream section. For each feeding event, we quantified feeding behaviour as the total number of nips at the water surface by trout and reported it as proportion of nips per trout out of the number of trout remaining (Noakes & Baylis, 1990). We released 5 g (dry mass) of floating dry krill all at once in one spot at midday every other day in the upstream end of each stream section. We allowed trout in stream sections to feed on drifting krill to cessation, which was determined as 60 s of no feeding action beyond last nip at the surface. Krill that was not eaten by trout collected after feeding in downstream screens and was immediately removed.

2.6 | Statistical analyses

All statistical analyses were performed in SAS software 9.3 (SAS Institute Inc., Cary, NC, USA).

We initially compared used and available features of cover across streams using pairwise nonparametric Wilcoxon rank-sum tests. Specific cover features compared for used and available observations included depth (cm), proximity to depth of 20 cm, surface area of cover (m^2), b-axis of boulders (mm) and distance under substrate (cm).

For analysis of selection of cover features, we used logistic regression on use-availability data (Johnson et al., 2006; Keating & Cherry, 2004) to evaluate the selection or relative probability of use of cover by trout in each stream (Allison, 1999; Manly et al., 2002). The logistic regression model (SAS PROC LOGISTIC procedure) related selection of cover by trout to surface area of cover (m^2), water depth (cm) and their interaction (to account for potentially context-specific selection of cover conditioned on depth). To examine collinearity among environmental predictors, we used Spearman rank correlation, omitting one predictor from each highly correlated pair ($r \geq 0.60$) to avoid multicollinearity. Hence, we did not include proximity to deeper water (≥20 cm) for trout in shallow water (≤20 cm depth) because results of the Spearman rank correlation showed that depth and proximity to depth of 20 cm were negatively associated ($r = -0.77$, $df = 515$, $p < .0001$), whereas surface area of cover and depth was not highly correlated ($r = 0.37$, $df = 514$, $p < .0001$). Model fit for selection was assessed using the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 2000) and the Pearson dispersion statistic (Allison, 1999).

For the manipulative experiment, we evaluated behavioural responses and growth using various models. Using a generalised linear mixed model (PROC MIXED procedure), we fit the model to the data to determine whether grouping and growth were a function of cover availability, whether the stream section was open or closed or their interaction. We analysed whether proportion of trout using cover was a function of trout size class, cover availability, whether the stream section was open or closed or their interactions using a generalised linear mixed model (PROC MIXED procedure) for a binomial-like response and logit link. We set blocks and repeated measurements of each stream section as random effects. We set size class and cover availability as fixed effects. Interactions were removed from the model because they did not improve the strength of the main effects (Ramsey & Schafer, 2002; Bolker et al., 2009). We also tested whether proportion of trout sharing cover and trout shifting among cover was a function of trout size class, cover availability or their interactions using a generalised linear mixed model (PROC MIXED procedure) for a binomial-like response and logit link. We set size class and cover availability as fixed effects. Cover availability, repeated measurements of each stream section and their interactions were removed from the model because they did not improve the strength of the main effects (Ramsey and Schafer 2002; Bolker et al., 2009). We analysed a potential link between cover use and emigration using the odds of using cover (PROC FREQ procedure), out of the five times that cover use was measured when emigration was closed, for trout that eventually emigrated versus trout that remained in stream sections. For all analyses, size class (small, medium, large), cover availability (high, low), and whether the stream section was open or not (open, closed) were analysed as categorical variables.

We examined whether the proportion and timing of emigrating trout were a function of trout size class, cover availability, whether the stream section was open or closed or their interactions using a generalised linear mixed model (PROC MIXED procedure) for a binomial-like response with a logit link. Based on our experimental design, we set blocks and repeated measurements of each stream section (to allow for different fish sizes) as random effects. We set cover availability and whether the stream section was open or closed as fixed effects. Size class and all interactions were removed from the model because they did not improve the strength of the main effects, measured by the magnitude of the *p*-value (Ramsey & Schafer, 2002; Bolker et al., 2009). To test whether the distributions of trout emigrants between low- and high-cover stream units differed, we used the two-sample Kolmogorov–Smirnov test (PROC NPAR1WAY procedure). This test is sensitive to small sample sizes and small counts in a class for the expected frequency (Zar, 1999), as was the case in our study, so we did not additionally account for blocks. We pooled the replicates of the number of emigrants for each cover type (low and high) to avoid zeros in our counts of a class, which in our case is number of emigrants per day.

3 | RESULTS

3.1 | Field study of cover selection

We implanted PIT tags in 1,036 Coastal Cutthroat Trout ranging in length from 10 to 20.4 cm for all six natural streams. Tracking of tagged individuals produced 285 detections of trout using cover. Of these, 190 unique individuals were observed (Table 2). We collected habitat characteristics and cover type for 797 randomly available points. Of these points, we removed 70% (562) from data analysis because they did not represent available cover (hereafter not used). The smallest surface area of cover used by fish was 0.002 m^2. To better represent what was available to fish for use as cover we removed all randomly available points with surface areas smaller than 0.002 m^2. This reduced the number of available points to 235. For the remaining 235 available points (considered to be truly "available" cover), substrate represented the largest per cent of available habitat at 92%. Of the available cover categorised as substrate, boulders accounted for 34% and cobble/gravel represented 57%. All other cover types combined represented the remaining 8% of the available cover.

Characteristics of cover used by trout differed from available cover and across cover types (Tables 3 and 4). Trout most frequently used substrate as cover (220 times, 78% of total detections) with boulders comprising the majority of use at 63%, cobble/gravel equalling 15% and large wood or woody material near 7% (Figure 3). All other cover types combined encompassed the remaining 15% of the total detections. When considering available habitat, however, cobble/gravel represented 57%, boulders were 34%, large wood and woody material were 6% and the remaining 3% represented other cover types.

For each potential cover type, we detected a statistically different mean for used versus available cover and depth. Trout also disproportionately used deeper water (Figure 3, Table 3) and locations closer to deeper water (>20 cm deep). For example, the furthest distance from deep water for used cover was 7.2 m, compared to 35.4 m for available cover. Trout used habitat with larger surface areas as cover more frequently than was available, especially wood. For substrate used as cover, the b-axis diameter was larger than for available substrate, and the distance under the boulder (space available for hiding) was larger for used boulders compared to available cover. The logistic regression model showed that selection of available cover by trout was positively associated with surface area of cover and with water depth and negatively associated with the interaction between water depth and surface area (Table 4). Compared to available cover, the interaction term suggested that trout used cover with smaller surface areas when it was located in deeper water. Hosmer–Lemeshow goodness of fit ($X^2 = 11.38$, $df = 8$, $p = .18$) and Pearson dispersion statistics ($X^2 = 497.22$, $df = 505$, $p = .59$) supported a good fit for the model.

TABLE 2 Summary of habitat characteristics for used refuge and available habitat, with repeat detections of individual Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) removed (*n* = number of samples) for 6 streams in western Oregon over the period of 1 August to 30 September 2007

Variable	*n*	Mean	*SD*	Range
Used refuge				
Depth (cm)	189	19.87	10.99	3–80
Proximity to depth 20 cm (cm)	190	71.04	108.92	0–720
Surface area of refuge (m^2)	187	0.71	1.35	0.002–7.2
B–axis of substrate (mm)	146	400	190.9	54–1310
Distance under substrate (cm)	146	29.4	14.7	4–109
Available				
Depth (cm)	233	9.03	6.41	1–40
Proximity to depth 20 cm (cm)	233	226.28	313.72	0–3540
Surface area of refuge (m^2)	233	0.22	0.48	0.003–4.15
B-axis of substrate (mm)	214	259.3	201.6	12–1200
Distance under substrate (cm)	215	7.1	13	0–90

Note: "Used" refers to detections of trout using refuge and "available" refers to randomly selected habitat points. The variables b-axis and distance under substrate refer only to refuge categorised as substrate.

3.2 | Experimental study

In the manipulative experiment, habitat availability affected the magnitude of emigration and cover use. We found that experimentally

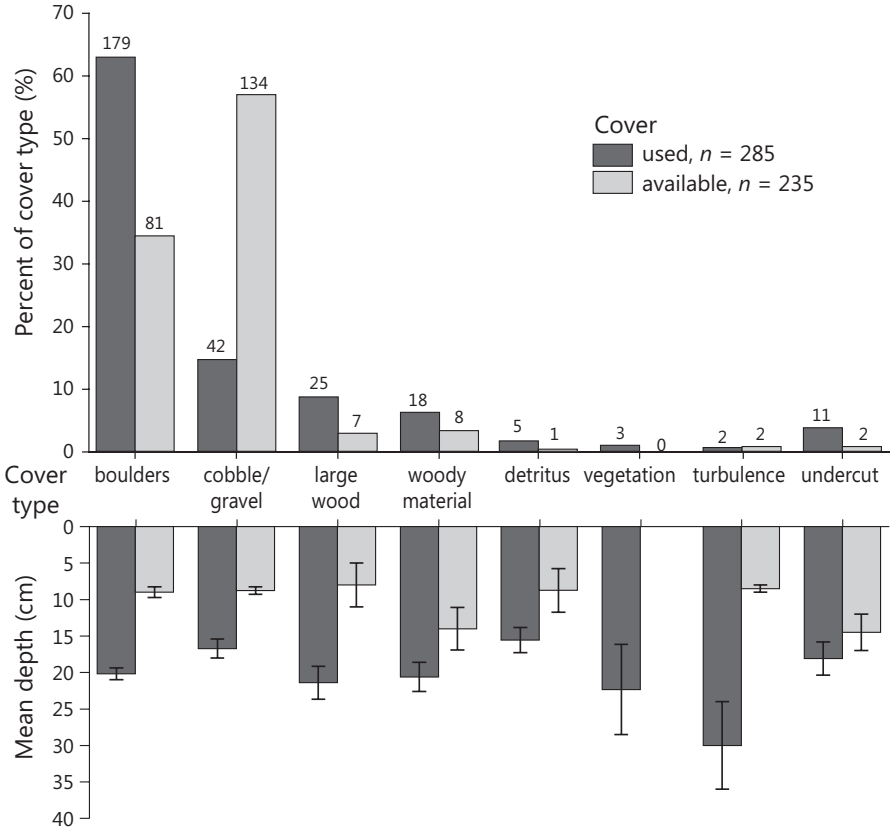

FIGURE 3 Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) used a wide variety of cover types found at different water depths, including boulders, cobble/gravel, large wood, woody material, detritus, vegetation, turbulence and undercut banks in six streams in western Oregon during seasonal low flow. For used cover, the number above the bar denotes number of detections. For available cover, the number above the bar is the number of that cover type identified as available in all streams combined (see methods for details on available cover)

TABLE 3 Wilcoxon rank-sum test z-statistic and P-values for the comparison of used cover characteristics versus available cover characteristics for six streams in western Oregon, USA, during seasonal low flow

Variable	z	*p*-value
Depth (cm)	−6.54	<.0001
Proximity to depth 20 cm (cm)	10.60	<.0001
Surface area of cover (m^2)	−10.44	<.0001
B-axis of substrate (mm)	−9.06	<.0001
Distance under substrate (cm)	−15.32	<.0001

lowering cover availability resulted in more individuals emigrating from those stream sections ($F_{1,19} = 32.76$, $p = .0001$, Figure 4a) and consequently lower overall trout densities. The probability of trout emigrating from low-cover stream sections was 3.5 times higher than from high-cover stream sections (95% CI: 2.22 to 5.56). Trout size was not a factor in emigration (Figure 4b). Emigration timing by trout differed between low- and high-cover stream sections (KS = 0.040, D = 0.080 $\alpha = 0.05$, D > KS critical value, so reject H_o that distributions are equal), with emigration being 5 d earlier and occurring at a faster rate in low-cover sections. One low-cover stream section was an anomaly in this analysis of day-to-emigration, as trout there behaved more similarly to high-cover stream sections. This anomaly stream section also had more shade (66%) than any other stream section (0%–47%).

The size of trout also played a role in the proportion of trout that used cover ($F_{2,40} = 17.07$, $p \leq .0001$, Figure 5a and b). Large trout were most likely to use cover, and they use cover 40.91 times more than either medium or small trout. Small trout shared cover positions most frequently, with an estimated 14% more sharing than the other size classes (95% CI: 0.07 to 0.23, Figure 5c and d). Medium-sized trout shared 3% of the time (95% CI: 0.01 to 0.09), and large trout did not share (95% CI: 0 to 0.01). Shifting among instream cover positions by trout depended on cover availability ($F_{1,33} = 80.06$, $p < .0001$), size of trout ($F_{2,33} = 124.84$, $p < .0001$) and

TABLE 4 Parameter estimates of logistic regression model for predicting cover selection by Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) in 6 streams in western Oregon, USA, during seasonal low flow with repeat detections of individual trout removed. All variables were log transformed

Variable	Estimated coefficient (β)	SE	*p*-value	Compared to available cover, used cover…
Intercept	−7.74	0.86	<.0001	–
Surface area	65.95	1.71	.0005	Had larger surface areas
Depth	2.82	0.32	<.0001	Was deeper
Depth * surface area	−1.72	0.60	.0045	Had smaller surface areas when located in deeper water

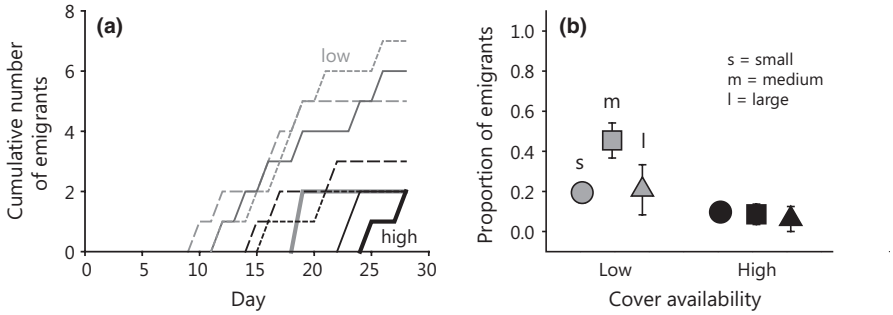

FIGURE 4 Relationship of (a) cumulative emigration by Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) per day in high-density (black, $n = 4$) and low-density (grey, $n = 4$) instream cover stream units of semi-natural experiments. Different line types represent results from one of four stream units for either high- or low-density cover and (b) proportion of trout that emigrate by length class of small: 9.4–14.9 cm (circle), medium: 15.0–19.4 cm (square), large: 19.5–23.4 cm (triangle) sized trout in high-density (black, $n = 4$) and low-density (grey, $n = 4$) instream cover stream units. Emigration boxes were checked daily

their interaction ($F_{2,33} = 18.08$, $p < .0001$). Shifting was an estimated 32 times more prevalent (95% CI: 29.10 to 34.39) for small trout in high-cover stream sections, whereas shifting occurred only slightly more often (estimated >4 times, 95% CI: 1.60 to 6.89), for large trout in high-cover stream sections.

When emigration was not possible, we found that trout were more likely to exhibit grouping behaviour regardless of cover availability ($F_{1,9} = 5.67$, $p = .04$). Average grouping per trout was estimated to be two more trout when emigration was not possible compared to when it was (95% CI: 0.11 to 4.45) which is approximately 8% more trout grouping. Trout group size was also higher in low-cover stream sections ($F_{1,9} = 3.17$, $p = .10$). Average group size was estimated to be almost three more trout in low-cover stream sections (95% CI: 0.74 to 6.18) than in high-cover stream sections representing 13% more trout having grouped.

Feeding behaviour of trout did not differ between stream sections with differing amounts of cover ($F_{1,3} = 0.25$, $p = .65$). For each feeding event, the average number of nips/trout was estimated to be less than half of a nip fewer per trout from low-cover stream sections (95% CI: −2.44 to 3.35). This lack of difference in feeding behaviour supports a lack of difference in average relative growth between stream sections for trout that emigrated ($F_{1,3} = 0.44$, $p = .55$) versus stayed ($F_{1,3} = 0.58$, $p = .50$). For trout that emigrated, the average difference in growth was estimated to be 0.88 more in high-cover stream sections as compared to low (95% CI: −3.31 to 5.07). For trout that stayed, the average difference in growth was negligible between stream sections because it was estimated to be <0.00 (95% CI: 0.00 to 0.00). For all statistical analyses, standard diagnostic plots suggested no deviations from mixed model assumptions.

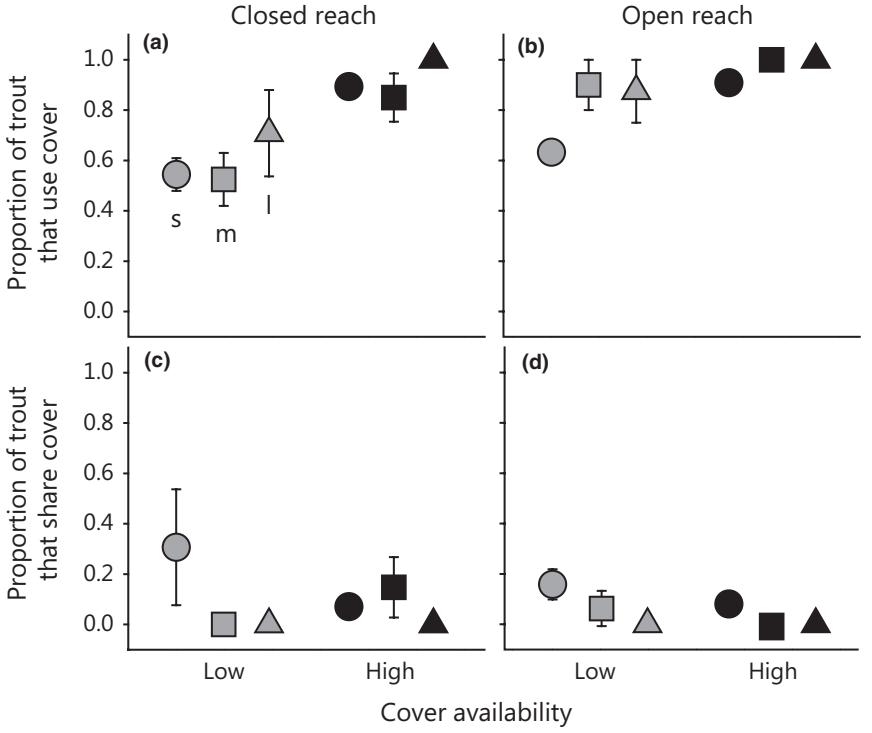

FIGURE 5 Relationship of proportion of Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) that use cover (mean ± SE) when stream section is either (a) closed to emigration or (b) open, and proportion of trout that share refuge (mean ± SE) when stream section is either (c) closed to emigration or (d) open in semi-natural experiments. Results are shown by size class small: 9.4–14.9 cm (circle), medium: 15.0–19.4 cm (square), large: 19.5–23.4 cm (triangle) in high-density (black, $n = 4$) and low-density (grey, $n = 4$) instream cover stream units

4 | DISCUSSION

We quantified cover use and selection by trout in natural streams and a semi-natural experiment to evaluate behavioural responses and population consequences of changing availability of cover. By integrating these findings, we suggest that trout primarily used cover as a refuge from predation during seasonal low flow. In natural streams, trout selected larger cover in shallower water, including boulders and large wood, although wood was less available. When cover availability was manipulated in semi-natural streams, trout concealed under cover or emigrated as first options, followed by grouping (a presumptive behaviour to swamp predators) and habitat shifting. The expression of most behaviours was associated with habitat availability, although observed rates of feeding were similar whether cover was abundant or scarce. The plasticity of trout to switch among such behaviours highlights a broad capacity for coping with environmental changes and the potential importance of behaviour for individuals and population processes.

Field observations of individually tagged trout allowed us to identify stream features that served as cover during low flow conditions. Trout in natural streams predominantly used boulders, probably because wood was not readily available, even though trout use a wide range of instream cover types during seasonal low flow (Boussu, 1954; Cunjak & Green, 1983; Fausch & White, 1981; Gresswell & Hendricks, 2007; Whiteway et al., 2010). Similarly, Harvey, Nakamoto & White, (1999) show that boulders are commonly used by trout in fall and winter even when availability of such boulders was limited. Greater instream cover may lead to increased survival (Berger & Gresswell, 2009). More generally, trout have been observed to select cover with lower ceiling spaces (Harvey & White, 2016), suggesting that boulders with such characteristics may be more important. In addition to boulders, trout also used smaller substrates for concealment, but they disproportionately used large wood and woody material. In the Pacific Northwest region, stream-living Coastal Cutthroat Trout are often associated with pools formed by large wood (Harvey et al., 1999; Rosenfeld et al., 2000). With the exception of Flynn Creek, the streams that we sampled exhibited low availability of wood, potentially owing to a legacy of stream simplification from human activities (Bilby & Bisson, 1998; McIntosh et al., 2000; Miller, 2010; Swanson & Lienkaemper, 1978). Where available, large wood is believed to provide many important benefits to fish and fish habitat (Gregory et al., 2003), including offering cover and influencing channel morphology (Lewis, 1969; Fausch & Northcote, 1992; Montgomery et al., 2003; Clark, Roni, & Burgess, 2019). As with other aspects of cover use, we would expect it to vary depending on the context within specific streams and most obviously dependent on availability of alternative features that could serve as cover.

As expected in the small streams we studied, trout were more likely to select larger cover for concealment where water depths were shallower. Condition-specific use of cover occurs in animals as they balance trade-offs of survival versus risk (Caro, 2005; Lima & Dill, 1990). Access to deeper water is an obvious asset in smaller streams, and there is much previous evidence indicating abundance of Coastal Cutthroat Trout increases with water depth (Bisson et al., 1988; Lonzarich & Quinn, 1995; Young, 1996) particularly during seasonal low flow (Heggenes et al., 1991). Fish may be expected to use deeper pools because deeper habitats offer refuge from terrestrial predators (Harvey & Stewart, 1991; Power, 1987). Depths of 20 cm or less are the more effective for feeding by many birds that hunt in freshwaters; thus, fish may avoid shallower water when possible (Power, 1984; Steinmetz et al., 2003). Although not focused on salmonids, an experimental study on Panamanian catfish (Loricariidae) in open pens found that the fish in water depths of 10–20 cm survived at lower rates than those held in deeper water (Power et al., 1989). However, as space and pool depths within streams decrease with declining flows, the importance of instream cover can increase. Other studies have also found that depth and cover jointly influence fish. Harvey and White (2017) found depth followed by distance to cover were key factors influencing feeding (harvest rate) of juvenile steelhead (*O. mykiss*). Heggenes et al. (1991) quantified habitat selection and found that a composite measure of depth and cover was the most important predictor of habitat selection for trout. Similarly, Lonzarich and Quinn (1995) found that the combination of depth and structure (cover) resulted in the highest overall fish densities and species richness in their study sites.

In the experimental study, trout regularly used cover in the semi-natural streams, with responses to cover often dependent on cover availability. Cover use was more frequently observed for larger trout. Sharing of cover in our study was generally infrequent, as also reported by Harvey and White (2016); however, when it occurred it was observed for small trout. It is possible that larger individuals in our study secured positions under cover first, followed by smaller individuals that may have been less likely to establish positions when cover was already occupied (Kvingedal & Einum, 2011), or that larger individuals were more likely to use cover owing to a potential higher risk of predation (Berger & Gresswell, 2009; Boss & Richardson, 2002; Orrock et al., 2013; Penaluna, Dunham, et al., 2015). In addition to potentially reducing predation, cover offers visual isolation from conspecifics, potentially reducing intraspecific competition (Allouché, 2002).

Trout shifted among cover positions, with more shifting occurring in high-cover stream sections and by small trout, as may be expected based on well-known size advantages in the relative competitive abilities of stream-living salmonids (Young, 2004). We found increased shifting by small trout (32 times higher), which may have been a consequence of their reduced ability to hold or defend occupied cover positions. Although shifting among habitats may not be as effective as holding within a single, desirable location, it may be the best available option for some individuals from the perspective of avoiding predators. For example, cyprinid fishes in lakes exhibit habitat shifting to pelagic habitats with stressful high temperatures, low food abundance and significant avian predation risk owing to the risk of predation by Largemouth Bass (*Micropterus salmoides*; Carpenter and Kitchell 1993).

Use of cover for concealment is just one of many potential anti-predator tactics that can be effective (Caro, 2005). Trout grouped or were more spatially proximate to one another when cover was limited in the experimental streams. We suspect that grouping was a response to limited availability of other options (e.g., cover available for concealment or emigration) perceived by individuals. Grouping may act to swamp predators or at least reduce the probability of predation-related mortality whereby group members benefit from predator dilution or confusion and from joint effort in vigilance behaviour (Godin, 1986). Living in groups entails costs of constraining opportunities to perform other vital activities, however, including feeding, growth and reproduction, and thus, behaviour of grouping is expected to occur when the benefits of the group exceed its costs. Predator swamping is also displayed by juvenile salmon during migration to reduce predation risk (Furey et al., 2016).

Feeding and growth of trout were negligible and did not differ between experimental streams with differing availability of cover. This may be evidence that growth in small streams may be constrained during seasonal low flows, especially if the threat of predation is high. Food availability can limit growth (Boss & Richardson, 2002; Wilzbach et al., 1986), but predation risk also limits growth by constraining foraging activity (Grand & Dill, 1997). Feeding tactics of individuals are likely influenced by selective pressures related to both survival and net energy intake (Harvey & White, 2016). For larger size Coastal Cutthroat Trout such as those considered herein, survival could be a dominant driver of behaviour during low flows (Berger & Gresswell, 2009), even if food is readily available.

Emigration is a common behaviour among mobile individuals, and it has been linked to population density, food availability (e.g., invertebrates in Snider & Gilliam, 2008), patch configuration (e.g., small mammals in Andreassen & Ims, 2001) and predator avoidance (e.g., insects in Poethke et al., 2010). Here, we add that emigration also depends on availability of cover, with emigration alone decreasing local densities of trout. When emigration is possible, yet cover is still limited; however, the use of available cover is more likely and individuals are less likely to group probably because overall density is lower, and they are able to successfully conceal under cover. Individuals that eventually emigrate used cover less often than remaining individuals, suggesting that emigrants leave because they are unable to successfully access or conceal under cover and seek to avoid predation risk, starvation or space limitations.

Although the importance of instream cover is widely accepted, it can be extremely difficult to define or clearly link to the demography. We examined this linkage by tracking emigration (McMahon & Matter, 2006). Linking populations to cover use requires a detailed understanding of individual behaviour (patterns of resource availability and use) and demography (Berryman & Hawkins, 2006). Immigration or movement into habitats with cover has been shown to be an important demographic response of fish in streams (Gowan & Fausch, 1996; White et al., 2011). Harvey et al., (1999) reported reduced movement by trout in relation to increased availability of cover, whereas Boss and Richardson (2002) reported no relationship between emigration and cover. Other studies have reported emigration to be influenced by food (Wilzbach, 1985), fish density (Mesick, 1988) or body size. Size-selective emigration is expected if larger individuals are motivated to move in search of higher levels of resources (Armstrong & Herbert, 1997; Gowan & Fausch, 2002; Hansen & Closs, 2009; Van Leeuwen et al., 2011) or when smaller less-dominant individuals are forced to emigrate to avoid intraspecific conflicts over limited resources (Chapman, 1962; Gowan & Fausch, 2002; Griffiths et al., 2013; Keeley, 2001).

5 | CONCLUSION

In conclusion, our findings identify what instream cover is and the role it can play among processes influencing fish in small streams. In agreement with the contentions of Allouché (2002), our results indicate that cover merits serious consideration among fundamental resources underlying population structure and dynamics. In addition to individual behaviour, availability of cover appears linked to demography through emigration. Although animals use cover to evade competition, minimise physiological stress and to optimise energy expenditure, we suggest that cover is used by trout in this study served as an actual or perceived predation refuge during seasonal low flow. The direct or indirect influences of predation can be significant for fishes, particularly in streams during seasonal low flow when access to emigration, deeper pools and cover availability are limited, as shown herein. Adding cover to streams may be a solution for managers in places where it is otherwise lacking (e.g., Roni & Beechie, 2013). Over longer time frames, if natural processes that allow for the generation of cover in streams, including recruitment and retention of large wood, are maintained, active additions of cover will be less necessary (Beechie et al., 2010). In this context, adding instream cover to streams can be viewed as an interim measure until natural cover-generating processes recover. Although the behavioural capacity of trout is plastic and adaptive over the short-term, showing their ability to cope with changes in their environment, especially when key resources are limited, it may alter fitness-related behaviours over the long-term including social structure and reproductive success (Berger-Tal et al., 2011) and merits further evaluation.

6 | CONTRIBUTIONS

B.E.P. generated all model data, ran models, completed model data analysis, collected experimental data and analysed experimental data. H.V.A. measured trout in field survey and completed field data analysis. J.B.D. advised B.E.P and H.V.A and secured funding. All authors contributed to manuscript preparation and ideas.

ACKNOWLEDGEMENTS

Funding for this work was provided by a U.S. EPA Science to Achieve Results (STAR) grant and a J Frances Allen scholarship from the American Fisheries Society to B.E.P. Additional funding

and support was provided by the USGS Forest and Rangeland Ecosystem Science Center, Watersheds Research Cooperative at Oregon State University and the Oregon Department of Fish and Wildlife. We thank David LG Noakes and the staff at the Oregon Hatchery Research Centre. Dave Leer, Doug Bateman, Steve Clark and others helped during the experiment. Matt Betts, Sherri Johnson, Steve Railsback, Dede Olson, Kelly Burnett and Ivan Arismendi provided comments on earlier drafts of our manuscript. We thank Ron Ptolemy, Robert Al-Chokhachy, Kyle Martens and an anonymous reviewer for their helpful comments. Lisa Ganio and Pat Cunningham provided advice on the statistical analyses. Kathryn Ronnenberg helped with figures. Fish collections were authorised by Oregon Department of Fish and Wildlife scientific taking permit #13881 and by Oregon State University Institutional Animal Care and Use Committee permit #3910. Use of trade or firm or product names here is for reader information only and does not constitute endorsement of any product or service by the U.S. Government.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author [BEP] on request.

ORCID

Brooke E. Penaluna https://orcid.org/0000-0001-7215-770X
Jason B. Dunham http://orcid.org/0000-0002-6268-0633

REFERENCES

Allison, P. D. (1999). *Logistic regression using the SAS system: Theory and application*. SAS Institute Inc.

Allouché, S. (2002). Nature and functions of refuge for riverine fish. *Bulletin Francais De La Pêche Et De La Pisciculture*, *365–366*, 297–324.

Andreassen, H. P., & Ims, R. A. (2001). Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. *Ecology*, *82*, 2911–2926. https://doi.org/10.1890/0012-9658(2001)082[2911:DIPVPR]2.0.CO;2

Armstrong, J. D., & Herbert, N. A. (1997). Homing movements of displaced stream-dwelling brown trout. *Journal of Fish Biology*, *50*, 445–449. https://doi.org/10.1111/j.1095-8649.1997.tb01372.x

Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., Roni, P., & Pollock, M. M. (2010). Process–based principles for restoring river ecosystems. *BioScience*, *60*, 209–222. https://doi.org/10.1525/bio.2010.60.3.7

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Smith, F. A., & Lawler, J. J. (2017). Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, *15*, 299–308. https://doi.org/10.1002/fee.1502

Bellmore, J. R., Benjamin, J. R., Newsom, M., Bountry, J. A., & Dombroski, D. (2017). Incorporating food web dynamics into ecological restoration: A modeling approach for river ecosystems. *Ecological Applications*, *27*, 814–832. https://doi.org/10.1002/eap.1486

Berger, A. M., & Gresswell, R. E. (2009). Factors influencing coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) seasonal survival rates: A spatially continuous approach within stream networks. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 613–632. https://doi.org/10.1139/F09-029

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P., & Saltz, D. (2011). Integrating animal behavior and conservation biology: A conceptual framework. *Behavioral Ecology*, *22*, 236–239. https://doi.org/10.1093/beheco/arq224

*Berryman, A. A., Hawkins, B. A., & Hawkins, B. A. (2006). The refuge as an integrating concept in ecology and evolution. *Oikos*, *115*, 192–196. https://www.jstor.org/stable/40234929

Bilby, R. E., & Bisson, P. A. (1998). Function and distribution of large woody debris. In R. J. Naiman & R. E. Bilby (Eds.), *River ecology and management: Lessons from the Pacific coastal ecoregion* (pp. 324–346). Springer-Verlag.

Bisson, P. A., Sullivan, K., & Nielson, J. L. (1988). Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society*, *117*, 262–273. https://doi.org/10.1577/1548-8659(1988)117<0262:CHHUAB>2.3.CO;2

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Boss, S. M., & Richardson, J. S. (2002). Effects of food and refuge on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarkii*) in coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1044–1053. https://doi.org/10.1139/f02-079

Boussu, M. F. (1954). Relationship between trout populations and refuge on a small stream. *Journal of Wildlife Management*, *18*, 229–239. https://doi.org/10.2307/3797719

Caro, T. (2005). *Antipredator defenses in birds and mammals*. The University of Chicago Press.

Chapman, D. W. (1962). Aggressive behavior in juvenile coho salmon as a cause of emigration. *Journal of Fisheries Research Board of Canada*, *19*, 1047–1080. https://doi.org/10.1139/f62-069

Chelgren, N. D., & Dunham, J. B. (2015). Connectivity and conditional models of access and abundance of species in stream networks. *Ecological Applications*, *25*, 1357–1372. https://doi.org/10.1890/14-1108.1

Clark, C., Roni, P., & Burgess, S. (2019). Response of juvenile salmonids to large wood placement in Columbia River tributaries. *Hydrobiologia*, *842*, 173–190. https://doi.org/10.1007/s10750-019-04034-x

Cunjak, R. A., & Green, J. M. (1983). Habitat utilization by brook char (Salvelinus fontinalis) and rainbow trout (*Salmo gairdneri*) in Newfoundland streams. *Canadian Journal of Zoology*, *61*, 1214–1219. https://doi.org/10.1139/z83-165

Dole-Olivier, M. (2011). The hyporheic refuge hypothesis reconsidered: A review of hydrological aspects. *Marine and Freshwater Research*, *62*, 1281–1302. https://doi.org/10.1071/MF11084

Fausch, K. D, & Northcote, T. G. (1992). Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 682–693. https://doi.org/10.1139/f92-077

Fausch, K. D., & White, R. J. (1981). Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 1220–1227. https://doi.org/10.1139/f81-164

Gowan, C., & Fausch, K. D. (1996). Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. *Ecological Applications*, *6*, 931–946. https://doi.org/10.2307/2269496

Gowan, C., & Fausch, K. D. (2002). Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes*, *64*, 139–153. https://doi.org/10.1023/A:1016010723609

Gowan, C., Young, M. K., Fausch, K. D., & Riley, S. C. (1994). Restricted movement in resident stream salmonids: A paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 2626–2637. https://doi.org/10.1139/f94-262

Grand, T. C., & Dill, L. M. (1997). The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): Ideal free distribution theory applied. *Behavioral Ecology*, *8*, 437–447. https://doi.org/10.1093/beheco/8.4.437

Gregory, S. V., Boyer, K. L., & Gurnell, A. M. (Eds.). (2003). The ecology and management of wood in world rivers. American Fisheries Society Symposium 37. American Fisheries Society.

Gresswell, R. E., & Hendricks, S. R. (2007). Population-scale movement of coastal cutthroat trout in a naturally isolated stream network. *Transactions of the American Fisheries Society*, *136*, 238–253. https://doi.org/10.1577/T05-196.1

Griffiths, J. R., Schindler, D. E., & Seeb, L. W. (2013). How stock of origin affects performance of individuals across a meta-ecosystem: An example from Sockeye Salmon. *PLoS One*, *8*(3), e58584. https://doi.org/10.1371/journal.pone.0058584

Hansen, E. A., & Closs, G. P. (2009). Long-term growth and movement in relation to food supply and social status in a stream fish. *Behavioral Ecology*, *20*, 616–623. https://doi.org/10.1093/beheco/arp039

Harvey, B. C., & Nakamoto, R. J. (2013). Seasonal and among-stream variation in predator encounter rates for fish prey. *Transactions of the American Fisheries Society*, *142*, 621–627.

Harvey, B. C., Nakamoto, R. J., & White, J. L. (1999). Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (Oncorhynchus clarki) during fall and winter. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 2161–2166.

Harvey, B. C., & Railsback, S. F. (2009). Exploring the persistence of stream-dwelling trout populations under alternative real–world turbidity regimes with an individual-based model. *Transactions of the American Fisheries Society*, *138*, 348–360. https://doi.org/10.1577/T08-068.1

Harvey, B. C., & Stewart, A. (1991). Fish size and habitat depth relationships in headwater streams. *Oecologia*, *87*, 336–342. https://doi.org/10.1007/BF00634588

Harvey, B. C., & White, J. L. (2016). Use of cover for concealment behavior by rainbow trout: Influences of cover structure and area. *North American Journal of Fisheries Management*, *36*, 1308–1314. https://doi.org/10.1080/02755947.2016.1207728

Harvey, B. C., & White, J. L. (2017). Axes of fear for stream fish: Water depth and distance to cover. *Environmental Biology of Fishes*, *100*, 565–573. https://doi.org/10.1007/s10641-017-0585-2

Heggenes, J., Northcote, T., & Peter, A. (1991). Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1364–1370. https://doi.org/10.1139/f91-163

Hicks, B. J., & Hall, J. D. (2003). Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. *Transactions of American Fisheries Society*, *132*, 468–482. https://doi.org/10.1577/1548-8659(2003)132<0468:RTACGS>2.0.CO;2

Hosmer, D. W., & Lemeshow, S. (2000). *Applied logistic regression*. John Wiley and Sons Inc.

Inoue, M., Nakano, S., & Nakamura, F. (1997). Juvenile masu salmon (*Oncorhynchus masou*) abundance and stream habitat relationships in northern Japan. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1331–1341. https://doi.org/10.1139/f97-036

*Jensen, L. R. (2017). *Factors influencing growth and bioenergetics of fish in forested headwater streams downstream of forest harvest*. Oregon State University. Master's thesis https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/1544bv18p.

Johnson, C., Nielson, S., Merrill, E., McDonald, T., & Boyce, M. S. (2006). Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management*, *70*, 347–357. https://doi.org/10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2

Keating, K., & Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management*, *68*, 774–789. https://doi.org/10.2193/0022-541X(2004)068[0774:UAIOLR]2.0.CO;2

Keeley, E. R. (2001). Demographic responses to food and space competition by juvenile steelhead trout. *Ecology*, *82*, 1247–1259. https://doi.org/10.1890/0012-9658(2001)082[1247:DRTFAS]2.0.CO;2

Kerfoot, W. C., & A. Sih (Eds.) (1987). *Predation: Direct and indirect impacts on aquatic communities*. University Press of New England.

Kvingedal, E., & Einum, S. (2011). Prior residency advantage for Atlantic salmon in the wild: Effects of habitat quality. *Behavioral Ecology and Sociobiology*, *65*, 1295–1303. https://doi.org/10.1007/s00265-011-1143-0

Lewis, S. L. (1969). Physical factors influencing fish populations in pools of a trout stream. *Transactions of the American Fisheries Society*, *98*, 14–19. https://doi.org/10.1577/1548-8659(1969)98[14:PFIFPI]2.0.CO;2

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640. https://doi.org/10.1139/z90-092

Lonzarich, D. G., & Quinn, T. P. (1995). Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Canadian Journal of Zoology*, *73*, 2223–2230. https://doi.org/10.1139/z95-263

Manly, B. F., McDonald, L. L., Thomas, D., McDonald, T., & Erickson, W. (2002). *Resource selection by animals*. Kluwer Academic Publishers.

McIntosh, B. A., Sedell, J. R., Thurow, R. F., Clarke, S. E., & Chandler, G. L. (2000). Historical changes in pool habitats in the Columbia River Basin. *Ecological Applications*, *10*, 1478–1496. https://doi.org/10.1890/1051-0761(2000)010[1478:HCIPHI]2.0.CO;2

McMahon, T. E., & Matter, W. J. (2006). Linking habitat selection, emigration and population dynamics of freshwater fishes: A synthesis of ideas and approaches. *Ecology of Freshwater Fish*, *15*, 200–210. https://doi.org/10.1111/j.1600-0633.2006.00130.x

Mesick, C. F. (1988). Effects of food and refuge on numbers of Apache and brown trout establishing residency in artificial stream channels. *Transactions of the American Fisheries Society*, *117*, 421–431. https://doi.org/10.1577/1548-8659(1988)117<0421:EOFACO>2.3.CO;2

*Miller, R. R. (2010). *Is the past present? Historical splash-dam mapping and stream disturbance detection in the Oregon Coastal Province*. Oregon State University]. [Master's thesis https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/4m90f001t

*Moore, K. M., Jones, K., & Dambacher, J. (1999). Methods for stream habitat surveys, aquatic habitat inventory project. Natural Production Program: Oregon Department of Fish and Wildlife.

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., & Meigs, G. W. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*, 228–234. https://doi.org/10.1002/fee.2189

Newby, N. C., Binder, T. R., & Stevens, E. D. (2007). Passive integrated transponder (PIT) tagging did not negatively affect the short–term feeding behavior or swimming performance of juvenile Rainbow Trout. *Transactions of the American Fisheries Society*, *136*, 341–345. https://doi.org/10.1577/T06-110.1

Orrock, J. L., Preisser, E. L., Grabowski, J. H., & Trussell, G. C. (2013). The cost of safety: Cover increase the impact of predation risk in aquatic systems. *Ecology*, *94*, 573–579. https://doi.org/10.1890/12-0502.1

*Palmer, M. A., Bely, A. E., & Berg, K. E. (1992). Response of invertebrates to lotic disturbance: A test of the hyporheic refuge hypothesis. *Oecologia 89*, 182–194. https://www.jstor.org/stable/4219870.

Pavlov, D. S., & Kasumyan, A. O. (2000). Patterns and mechanisms of schooling behavior in fish: A review. *Journal of Ichthyology*, *40*, S163.

*Penaluna, B. E., Dunham, J. B., & Noakes, D. L. G. (2015). Instream refuge and shade mediate avian predation on trout in semi–natural streams. *Ecology of Freshwater Fish*, *25*, 405–411. https://doi.org/10.1111/eff.12221

Platts, W. S., Megahan, W. F., & Minshall, G. W. (1983). Methods for evaluating stream, riparian, and biotic conditions. General Technical Report INT–138. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 10.2737/INT-GTR-138.

Poethke, H. J., Weisser, W. W., & Hovestadt, T. (2010). Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *American Naturalist*, *175*, 577–586. https://doi.org/10.1086/651595

Polivka, C. M. (2020). Habitat affinity and density-dependent movement as indicators of fish habitat restoration efficacy. *Ecosphere*, *11*, e03166. https://doi.org/10.1002/ecs2.3166

Power, M. E. (1984). Depth distributions of armored catfish: Predator-induced resource avoidance? *Ecology*, *65*, 523–528. https://doi.org/10.2307/1941414

Power, M. E. (1987). Predator avoidance by grazing fish in temperate and tropical streams: Importance of stream depth and prey size. In W. Kerfoot, & A. Sih (Eds.), *Predation: Direct and indirect impacts on aquatic communities* (pp. 333–352). New England University Press.

Power, M. E., Dudley, T. L., & Cooper, S. D. (1989). Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes*, *26*, 285–294. https://doi.org/10.1007/BF00002465

*Puckett, K. J., & Dill, L. M. (1985). The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour*, *92*, 97–111. https://www.jstor.org/stable/4534403. https://doi.org/10.1163/156853985X00398

Raggon, M. F. (2010). Seasonal variability in diet and consumption by cottid and salmonid fishes in headwater streams in western Oregon, USA. Oregon State University]. [Master's thesis https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/vt150p038

Ramsey, F. L., & Schaefer, D. W. (2002). *The statistical sleuth: A course in methods of data analysis*, 2nd ed. Duxbury Thomson Learning.

Roni, P., & Beechie, T. (2013). *Stream and watershed restoration: A guide to restoring riverine processes and habitats*. Wiley-Blackwell.

Rosenblueth, A., Wiener, N., & Bigelow, J. (1943). Behavior, purpose and teleology. *Philosophy of Science*, *10*, 18–24. https://doi.org/10.1086/286788

Rosenfeld, J., Porterand, M., & Parkinson, E. (2000). Habitat factors effecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarkii*) and coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 766–774. https://doi.org/10.1139/f00-010

Schlosser, I. J. (1995). Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, *303*, 71–81. https://doi.org/10.1007/BF00034045

Segura, C., Bladon, K. D., Hatten, J. A., Jones, J. A., Hale, V. C., & Ice, G. G. (2020). Long-term effects of forest harvesting on summer low flow deficits in the Coast Range of Oregon. *Journal of Hydrology*, *585*, art124749. https://doi.org/10.1016/j.jhydrol.2020.124749

Smokorowski, K. E., & Pratt, T. C. (2007). Effect of a change in physical structure and refuge on fish and fish habitat in freshwater ecosystems—a review and meta-analysis. *Environmental Reviews*, *15*, 15–41. https://doi.org/10.1139/a06-007

Snider, S. B., & Gilliam, J. F. (2008). Movement ecology: Size–specific behavioral response of an invasive snail to food availability. *Ecology*, *89*, 1961–1971. https://doi.org/10.1890/07-0715.1

Steinmetz, J., Kohler, S. L., & Soluk, D. A. (2003). Birds are overlooked top predators in aquatic food webs. *Ecology*, *84*, 1324–1328. https://doi.org/10.1890/0012-9658(2003)084[1324:BAOTPI]2.0.CO;2

Surfleet, C. G., & Skaugset, A. E. (2013). The effect of timber harvest on summer low flows, Hinkle Creek, Oregon. *Western Journal of Applied Forestry*, *28*, 13–21. https://search.proquest.com/docview/1434427871?accountid=28147. https://doi.org/10.5849/wjaf.11-038

*Swanson, F. J., & Lienkaemper, G. W. (1978). Physical consequences of large organic debris in Pacific Northwest streams. General Technical Report PNW-69. U.S. Department of Agriculture, Forest Service. Pacific Northwest Forest and Range Experiment Station. https://books.google.com/books?hl=en&lr=&id=dO1x5a4oCcMC&oi=fnd&pg=PA1&dq=Swanson,+F.+J.,+%26+Lienkaemper,+G.+W.+(1978).+&ots=n8XBGz_-5_&sig=Zarc7MaM1gNXVB8269DC2feO0gU#v=onepage&q&f=false. Accessed on 9/22/20.

Tague, C., & Dugger, A. L. (2010). Ecohydrology and climate change in the mountains of the western USA—a review of research and opportunities. *Geography Compass*, *4*, 1648–1663. https://doi.org/10.1111/j.1749-8198.2010.00400.x

Van Leeuwen, T. E., Rosenfeld, J. S., & Richards, J. G. (2011). Failure of physiological metrics to predict dominance in juvenile Pacific salmon (*Oncorhynchus* spp.): Habitat effects on the allometry of growth in dominance hierarchies. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 1811–1818. https://doi.org/10.1139/f2011-099

Ward, A. S., Wondzell, S. M., Schmadel, N. M., & Herzog, S. P. (2020). Climate change causes river network contraction and disconnection in the HJ Andrews Experimental Forest, Oregon, USA. *Frontiers in Water*, *2*, 7. https://doi.org/10.3389/frwa.2020.00007

White, S. L., Gowan, C., Fausch, K. D., Harris, J. G., & Saunders, W. C. (2011). Response of trout populations in five Colorado streams two decades after habitat manipulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 2057–2063. https://doi.org/10.1139/f2011-125

White, S. M., & Rahel, F. J. (2008). Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. *Transactions of the American Fisheries Society*, *137*, 881–894. https://doi.org/10.1577/T06-207.1

Whiteway, S. L., Biron, P. M., Zimmerman, A., Venter, O., & Grant, J. W. A. (2010). Do in–stream restoration structures enhance salmonid abundance? A meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 831–841. https://doi.org/10.1139/F10-021

Wilzbach, M. A. (1985). Relative roles of food abundance and refuge in determining the habitat distribution of stream–dwelling cutthroat trout (*Salmo clarki*). *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1668–1672. https://doi.org/10.1139/f85-208

Wilzbach, M. A., Cummins, K. W., & Hall, J. D. (1986). Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology*, *67*, 898–911. https://doi.org/10.2307/1939812

Young, K. A. (2004). Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology*, *85*, 134–149. https://doi.org/10.1890/02-0402

Young, M. K. (1996). Summer movement and habitat use by cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1403–1408. https://doi.org/10.1139/f96-054

Zar, J. H. (1999). *Biostatistical analysis*, 4th ed. Prentice Hall.

Zydlewski, G. B., Haro, A., Whalen, K. G., & McCormick, S. D. (2001). Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, *58*, 1471–1475. https://doi.org/10.1111/j.1095-8649.2001.tb02302.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Penaluna BE, Dunham JB, Andersen HV. Nowhere to hide: The importance of instream cover for stream-living Coastal Cutthroat Trout during seasonal low flow. *Ecol Freshw Fish*. 2021;30:256–269. https://doi.org/10.1111/eff.12581