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Use of streambed substrate as refuge by steelhead or rainbow trout *Oncorhynchus mykiss* during simulated freshets

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A flume was used to estimate the carrying capacity of streambed substrates for juvenile steelhead or rainbow trout *Oncorhynchus mykiss* seeking refuge from simulated freshets. The simulated freshets had mean water column velocities of *c.* 1·1 m s^{-1}. The number of *O. mykiss* finding cover within the interstices of the substrate was documented for different substrate sizes and levels of embeddedness. The availability of suitable refuges determined the carrying capacity of the substrate for *O. mykiss*. For the size of the *O. mykiss* tested [mean ± S.D. fork length (L_F) = 122 ± 12·6 mm], the number of interstices with depths ≥200 mm measured with a 14·0 mm diameter flexible plastic tube was the best predictor of the number of *O. mykiss* able to find cover ($r^2 = 0·75$). *Oncorhynchus mykiss* seeking refuge from freshets may need deeper interstices than those seeking concealment at autumn or winter base flows. The availability of interstices suitable as refuge from high flows may determine autumn and winter carrying capacity.

Key words: displacement; embeddedness; flood; high flows; interstitial; velocity.

INTRODUCTION

Salmonids in streams can use coarse substrates (cobbles and boulders) for visual isolation, concealment and for refuge from freshets (rapid increases in stream flow caused by rain or melting snow or ice). Large particles on or protruding from the streambed can reduce territory size and increase the density of salmonids by visually isolating them from one another (Kalleberg, 1958; Mesick, 1988; Imre *et al.*, 2002; Venter *et al.*, 2008). Some salmonids use the interstices of coarse substrates for concealment, which becomes increasingly important as water temperatures decrease in autumn and winter (Rimmer *et al.*, 1983; Cunjak, 1988; Griffith & Smith, 1993; Van Dyke *et al.*, 2010). A laboratory study conducted by Armstrong & Griffiths

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(2001) showed that the availability of concealment cover has the potential to set autumn or winter carrying capacity and in some streams concealment cover has been shown to limit the autumn and winter abundance of salmonids (Bjornn, 1971; Hillman *et al.*, 1987; Hvidsten & Johnson, 1992; Finstad *et al.*, 2009; Van Dyke *et al.*, 2009).

Freshets can reduce the number of salmonids in streams through direct mortality or displacement (Mason, 1976; Tschaplinski & Hartman, 1983; Jowett & Richardson, 1989; Quinn & Peterson, 1996; Bell *et al.*, 2001; Nislow *et al.*, 2002; Lonzarich *et al.*, 2009; Young *et al.*, 2010). Winter carrying capacity and smolt production of coho salmon *Oncorhynchus kisutch* (Walbaum 1792) have been increased in some cases by adding large woody debris or creating off-channel habitat to provide refuge from high flows (Cederholm *et al.*, 1997; Solazzi *et al.*, 2000). Heggenes (1988) concluded that the availability of coarse substrates allowed brown trout *Salmo trutta* L. 1758 to avoid displacement during large rapid increases in flow, and Makiguchi *et al.* (2009) inferred that boulders provide refuge for Formosan salmon *Oncorhynchus formosanus* (Jordan & Ōshima 1919) from typhoon-induced floods, but neither study directly documented the use of coarse substrates during high flows. Hartman (1963) found that at 12·5° C, the percentage of *S. trutta* 'hiding among stones' in an artificial channel increased from 0 to 45% as the velocity increased from 0·08 to 0·66 $\mathrm{m\,s^{-1}}$. At 0·5° C, 50% were hiding at 0·08 $\mathrm{m\,s^{-1}}$ and 100% were hiding at velocities between 0·25 and 0·66 $\mathrm{m\,s^{-1}}$. No other research was found that addresses the use of coarse substrates as refuge during high flows. Refuge from high flows may require deeper interstices than those used solely for concealment; therefore, in streams with freshets, high-flow refuge cover may be more limiting for steelhead or rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) than concealment cover. The present study determined how the number and depth of interstices occurring in substrates of different size distributions and levels of embeddedness affect the carrying capacity of *O. mykiss* exposed to high water velocities typical of freshets.

MATERIALS AND METHODS

Oncorhynchus mykiss used in the experiment had a mean ± S.D. fork length (L_F) of 122 ± 12·6 mm and were obtained from the Humboldt State University Fish Hatchery in Arcata, California. Experimental trials were conducted in a 1·5 $\mathrm{m^2}$ section of a 41301 recirculating flume at the USDA Forest Service Redwood Sciences Laboratory in Arcata, California, U.S.A. The upstream and downstream ends of the experimental unit were fenced with monofilament netting to contain the *O. mykiss*. Base flows of *c.* 0·2 $\mathrm{m\,s^{-1}}$ were maintained in the flume with a centrifugal pump (4541 $\mathrm{min^{-1}}$ capacity), which was augmented with a larger pump (37851 $\mathrm{min^{-1}}$ capacity) to generate test flows. Water temperature was maintained between 6·6 and 7·8° C by a heat pump.

Two types of streambed substrates were tested: (1) poorly sorted and (2) well-sorted, open-framework. In general, streambed substrates are poorly sorted (*i.e.* composed of a wide range of particle sizes) (Parker, 2008; Nelson *et al.*, 2010). The two poorly sorted substrates used in the experiment were re-creations of size distributions that had been measured in the field (Lisle & Hilton, 1999; unpubl. data). The finer of these mixtures had a D_{50} (the 50th percentile particle size) of 70 mm and the coarser mixture had a D_{50} of 150 mm. The following particle-size definitions were used: < 2 mm = sand, silt and clay; 2–64 mm = gravel; 64–256 mm = cobble; >256 mm = boulder. Open-framework, cobble-boulder substrates are well sorted (*i.e.* composed of a narrow range of particle sizes). Because they do not contain much fine material, they have larger interstices than poorly sorted substrates. Open-framework, cobble-boulder substrates can be found in steep canyon streams and are typically immobile except during very large infrequent floods (Grant *et al.*, 1990; Brummer & Montgomery, 2006; Scheingross *et al.*, 2013; E. T. Donaldson, unpubl. data). For the open-framework trials in this experiment, four particle-size ranges were tested: 45–64, 64–90, 90–128 and 128–180 mm. They were created by sorting natural river gravels to remove particles smaller or larger than the test range. Differing numbers of substrate layers (each layer with a depth equal to the D_{84} of the particle-size range being tested) were used to yield a similar total depth for all trials. Small gravel (5–10 mm) was added to the test substrates to create different levels of embeddedness. A layer of substrate was defined as 100% embedded when its interstices were filled.

Preliminary trials were conducted using large cobbles (128–256 mm) and boulders (>256 mm) to observe *O. mykiss* behaviour (*e.g.* use of interstices and territoriality) at base and high flows. During high flows, some *O. mykiss* took refuge in the substrate while others did not. Because one of the goals of the study was to establish the carrying capacity of various substrates and degrees of embeddedness, only those *O. mykiss* that sought refuge in the substrate during these preliminary trials were used in subsequent experimental trials.

One experimental trial was conducted on each combination of open-framework mixture and level of embeddedness. Three trials were conducted with each of the two poorly sorted mixtures (Table I). At the beginning of each experimental trial, 24 randomly selected *O. mykiss* were placed into the experimental unit at a mean water column velocity of $0{\cdot}2\ \text{m s}^{-1}$ and allowed to acclimate for 15 min. The flow was then increased with the larger pump. The simulated freshets had mean water column velocities of *c.* $1{\cdot}1\ \text{m s}^{-1}$. High flows were sustained for 60 min in each trial, after which all *O. mykiss* that had not found cover were collected. The substrate was then excavated to recover the remaining *O. mykiss*. In all but three of the 17 trials, all 24 *O. mykiss* were recovered. In each of those three cases, one *O. mykiss* was able to move past the netting to escape the experimental unit. Flexible plastic tubing (9·5 and 14·0 mm outside diameter) was used to measure the depth of interstices accessible from the substrate surface (Finstad *et al.*, 2007).

To determine the probe diameter and minimum interstitial depth that best explained the number of *O. mykiss* finding cover in each trial, the data were analysed using Poisson models and the Akaike information criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2002).

Let y_i be the number of *O. mykiss* finding refuge in trial i, and for a given depth threshold l_c, let x_i be the number of interstices of depth $\geq l_c$ cm of the substrate mixture used in trial i. The basic conceptual model is that the y_i for the different trials are independent Poisson variables with expected values linear in x_i: $E[y_i] = b_0 + b_1 x_i$, $b_0, b_1 > 0$, yielding the likelihood function: $L\left(\left\{y_i\right\}_i ; \left\{x_i\right\}_i, b_0, b_1\right) = L(b) = \prod_i e^{-b_0 - b_1 x_i}\left(b_0 + b_1 x_i\right)^{y_i}\left(y_i!\right)^{-1}$. Since $x_i = 0$ for sufficiently large values of l_c, it is necessary to include an offset term like b_0 to ensure that the likelihood is always defined.

Each model is therefore determined by: (1) probe choice (the 9·5 or 14·0 mm diameter probe) and (2) minimum interstitial depth l_c.

The statistical analyses did not use data from the open framework, 45–64 mm mixture or the poorly sorted mixtures because they had no interstices wide enough for the probes. Ten open-framework substrate mixtures used in the trials were analysed with the 14·0 mm diameter probe. The comparison of results using 14·0 mm *v.* 9·5 mm probes was limited to eight mixtures for which data using both probes were available.

The various models (*i.e.* the various combinations of probe widths and minimum interstitial depths) were compared using the AICc: $\text{AICc} = -2 \log L\left(\hat{b}\right) + 2K + 2K\left(K+1\right)\left(n-K-1\right)^{-1}$, where $\hat{b}$ maximizes the likelihood, K is the number of degrees of freedom (in this case 2) and n is the number of data points. Smaller values of AICc correspond to more strongly supported models. Likelihood ratios can be calculated directly from differences in AICc: if the absolute difference in AICc values between two candidate models is Δ, the model with the smaller AICc value can be said to be $\exp(\Delta/2)$ times better supported by the data than the other model.

Table I. Response of *Oncorhynchus mykiss* (24 individuals per trial) to substrates mixtures with different levels of embeddedness in simulated freshets

Trial substrate	Per cent embedded, by substrate layer*				*O. mykiss* finding cover		
(mm)	L1	L2	L3	L4	*n*	%	Density (fish m^{-2})
Open-framework							
45–64	0	0	0	0	0	0	0
64–90	0	0	0	–	8	33	5·3
64–90	100	0	0	–	2	8	1·3
90–128	0	0	–	–	9	38	6·0
90–128	50	0	–	–	7	29	4·7
90–128	100	0	–	–	2	8	1·3
90–128	100	50	–	–	0	0	0
128–180	0	0	–	–	15	63	10·0
128–180	50	0	–	–	16	67	10·7
128–180	100	0	–	–	8	33	5·3
128–180	100	50	–	–	5	21	3·3
Poorly sorted finer mixture							
Fine trial 1					1	4·2	0·67
Fine trial 2					0	0	0
Fine trial 3					0	0	0
Mean					0·33	1·4	0·22
Poorly sorted coarser mixture							
Coarse trial 1					1	4·2	0·67
Coarse trial 2					1	4·2	0·67
Coarse trial 3					2	8·4	1·3
Mean					1·3	0·56	0·87

*Layers were used in the open-framework trials to create a similar total depth of substrate and are numbered from lowermost (L1) to uppermost (L4). A zero (0) indicates a layer with no embeddedness and a dash (–) indicates that the layer was not used in a trial.

RESULTS

BEHAVIOURAL OBSERVATIONS

At base flow, the *O. mykiss* did not show any inclination to go into the substrate despite the availability of very large and deep interstices. As velocity increased, some *O. mykiss* began to seek cover in the substrate and enter interstices, while other *O. mykiss* never attempted to enter the substrate. At high flows, the *O. mykiss* within the interstices did not show any agonistic or territorial behaviour and in some cases they ended up side-by-side. After moving into the interstices, some *O. mykiss* were re-entrained into the main flow. Most *O. mykiss* eventually moved to the deepest extent possible within the substrate.

EXPERIMENTAL TRIALS

For the open-framework substrates evaluated with both probes, the 14·0 mm diameter probe better explained the number of *O. mykiss* finding cover than the 9·5 mm

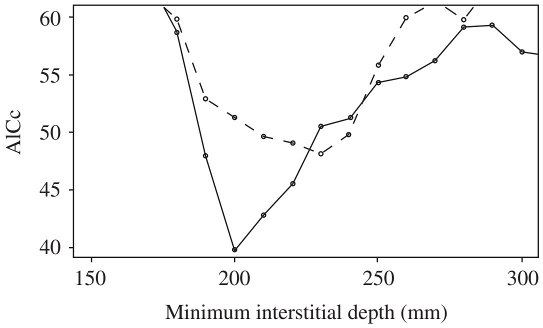

FIG. 1. Akaike information criterion (AICc) values for Poisson models of the number of *Oncorhynchus mykiss* finding cover as a function of the number of interstices that met different minimum depth thresholds as measured using 9·5 (_ _) and 14·0 mm (____) diameter probes ($n = 8$).

probe (Fig. 1). Support for the best-fitting model using the 14·0 mm probe was 73 times greater than support for the best-fitting 9·5 mm probe model. The best model fit for the 14·0 mm probe using all the observations for that probe size was for a minimum interstitial depth of 200 mm (Fig. 2). The 200 and 210 mm models were essentially indistinguishable by AICc; however, the 200 mm model was five times better supported than the 220 mm model and 99 times better supported than the 190 mm model. As expected from AICc values shown in Fig. 2, simple linear regressions of the number of *O. mykiss* finding cover, and the number of interstices ≥200 and ≥150 mm deep show that the ≥200 mm threshold much better explains the number of *O. mykiss* finding cover (r^2 of 0·75 compared with 0·10) (Fig. 3).

The two poorly sorted mixtures did not provide much refuge habitat (Table I). In the finer mixture, only one out of 72 *O. mykiss* tested found cover, whereas in the coarser mixture only four found cover. The few *O. mykiss* that found cover were able to wedge themselves against large cobbles or boulders and were moderately more successful in the coarser mixture, which contained 55% large cobbles and boulders (128–512 mm), than in the finer mixture, which had 32% large cobbles and boulders.

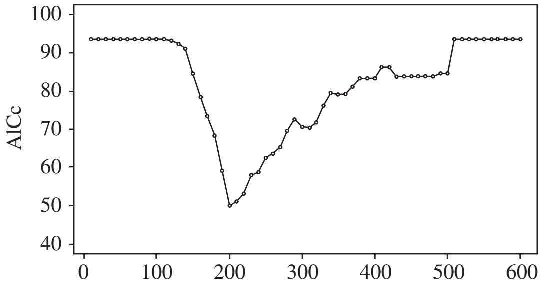

FIG. 2. Akaike information criterion (AICc) values for Poisson models of the number of *Oncorhynchus mykiss* finding cover as a function of the number of interstices that met different minimum depth thresholds as measured using a 14·0 mm diameter probe ($n = 10$).

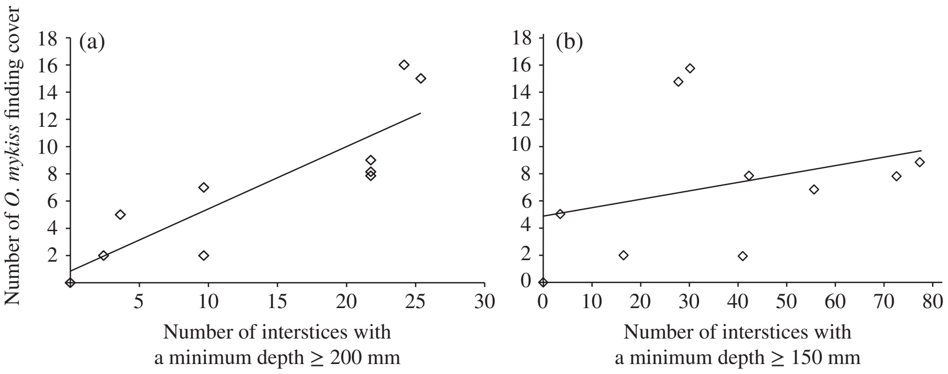

FIG. 3. Simple linear regression of the number of *Oncorhynchus mykiss* finding cover *v*. number of interstices with a minimum depth of (a) ≥200 mm ($y = 0{\cdot}46x + 0{\cdot}70$; $r^2 = 0{\cdot}75$) and (b) ≥150 mm ($y = 0{\cdot}062x + 4{\cdot}9$; $r^2 = 0{\cdot}10$), as measured using a 14·0 mm diameter probe. In (a), the two trials that had eight *O. mykiss* finding cover had the same number of interstices and for display the data points were offset.

DISCUSSION

In the present study, the number of interstices with depths ≥200 mm measured with a 14·0 mm diameter flexible plastic tube was a good predictor of the number of *O. mykiss* that found refuge from high flows. The 14·0 mm probe was a better predictor of refuge use than the 9·5 mm probe probably because it more closely approximated the head width of the test *O. mykiss*. Probes of different diameters and the use of different interstitial space depth thresholds may be necessary to best predict availability of high-flow refuge habitat for larger or smaller *O. mykiss*.

A smaller minimum depth threshold than 200 mm, such as 150 mm, would yield the same number of interstices ≥200 mm deep as the 200 mm threshold, with the addition of spaces with depths of 150–200 mm. Adding these shallower interstices to the number ≥200 mm deep greatly reduces the predictive power of the regression (Fig. 3). In one trial, two *O. mykiss* found refuge when there were four interstices with depths ≥200 mm. In this trial, there were 40 interstices with depths between 100 and 190 mm of at least 14 mm wide, but only two of the 24 *O. mykiss*, known from prior behavioural observations to seek refuge in the substrate, found a suitable refuge. No *O. mykiss* were able to find refuge in the 0% embedded, 45–64 mm substrate trial (Table I), indicating that coarse gravels would not provide high-flow refuge for the size of *O. mykiss* tested.

Why shallower interstices were unsuitable as high-flow refuge is not completely clear. The mean L_F of the test *O. mykiss* was 122 mm. Although *O. mykiss* were observed being re-entrained into the current from interstices deeper than their L_F, it is likely that in some cases the shallower interstices were narrow enough to allow an *O. mykiss* to wedge itself in sufficiently to avoid re-entrainment. The possibility was considered that deeper interstices were also wider and would allow easier access and that width was more important than depth in determining usability. The decrease in carrying capacity for all open-framework gravel mixtures with increasing embeddedness (Table I), however, shows this not to be the case, as the width of the interstices was unaffected by adding fine gravel, but the number of deep interstices was reduced.

Few *O. mykiss* found cover in the two poorly sorted mixtures, neither of which had interstices large enough to use as cover. As a greater number of *O. mykiss* found cover in trials with the coarser mixture than with the finer mixture, it is likely that poorly sorted substrates coarser than those tested would provide greater high-flow refuge habitat.

No agonistic behaviour by *O. mykiss* within interstices of the cobble and boulder substrate was observed in the behavioural observation trials. This may be due in part to the hatchery origin of *O. mykiss* used in the study. Hatchery Atlantic salmon *Salmo salar* L. 1758 were shown by Griffiths & Armstrong (2002) to be more willing to share concealment cover than wild *O. mykiss*. For *O. mykiss*, a hatchery origin does not necessarily preclude agonistic behaviour. Abbott & Dill (1985) found hatchery *O. mykiss* to be very aggressive during the summer, with considerable fin damage resulting from nipping. Wild *O. mykiss*, in an experiment examining concealment behaviour at low temperatures, sometimes shared spaces even though the available spaces far exceeded the number of test *O. mykiss* and the size of the spaces were sufficiently small that *O. mykiss* sharing a space were to some extent side-by-side (Gregory & Griffith, 1996*a*). When the number of interstices was more limited, Gregory & Griffith (1996*b*) found that aggression was variable among wild *O. mykiss*: in some cases sharing space with no aggression and in others a dominant *O. mykiss* would defend a territory within the interstice. They observed *O. mykiss* making contact with each other and unless one of them was a dominant *O. mykiss*, no aggression occurred, similar to what was observed in these trials. Several studies have documented the reduction or absence of territoriality or aggression in wild salmonids at cold temperatures (Chapman, 1962; Hartman, 1963; Glova, 1986; Fraser *et al.*, 1993; Heggenes *et al.*, 1993); aggressive behaviour may also decline during freshets. Hartman (1963) observed substantially reduced aggression in juvenile *S. trutta* in winter as velocities increased from 0·18–0·19 to 0·28–0·30 m s^{-1}.

Most studies of salmonids using interstices have documented their use for concealment at base flows and low temperatures during daylight hours (Campbell & Neuner, 1985; Contor & Griffith, 1995; Meyer & Gregory, 2000; Harwood *et al.*, 2002; Reeves *et al.*, 2010). Experiments by Gregory & Griffith (1996*a*) and Valdimarsson & Metcalfe (1998) strongly support the hypothesis that salmonids seek cover during the day to reduce predation risk when their swimming performance is impaired by low temperatures.

Most of the existing studies could not be used to assess whether salmonids seeking refuge from high flows required habitat different from those seeking only concealment as they did not report the width and depth of the interstices. Gregory & Griffith (1996*a*) measured the dimensions of the spaces they constructed for their experiment on *O. mykiss* concealment behaviour. Their spaces were all 195 mm deep, which is so close to the threshold found in this study to define suitable high-flow refuge, that their experiment sheds no light on whether concealment cover has a different threshold for suitability than high-flow refuge cover.

Finstad *et al.* (2007) developed the methodology employed in this study to quantify interstices and used experimental channels to test the suitability of substrates as cover for *S. salar* under low water temperatures (1·4–2·3° C) and low velocity (<0·005 m s^{-1}). The mean ± S.D. L_F of *S. salar* in their study (105 ± 9 mm) was somewhat smaller than the mean ± S.D. L_F of *O. mykiss* used in this study (122 ± 12·6 mm). They found a strong inverse relationship between the number of spaces available and the number of *S. salar* that they could observe (completely visible or partially concealed). Although they did not attempt to determine the minimum depths of interstices that could provide cover, *S. salar* in their experiments used shallower spaces than the *O. mykiss* in this study. They defined a minimum shelter depth to be 30 mm and the mean depth of interstices in their trials never exceeded 90 mm; and some *S. salar* used interstices too shallow to provide complete concealment. The infrequent use of spaces <200 mm deep under high flow conditions observed in this study, combined with the results of Finstad *et al.* (2007), suggests that interstices adequate for concealment can be much shallower than those needed as refuge from high flows.

High-flow refuge habitat of *O. mykiss* in streambed substrates is a function of both the size distribution of the framework and the level of embeddedness. For example, a streambed substrate composed of unembedded small cobbles may have a similar number of suitable interstices to a partially embedded substrate of larger cobbles and boulders. As opposed to time-consuming measurements of particle size and embeddedness, direct measurement of interstices may provide an efficient method for assessing the carrying capacity of substrates at high flows. Although this experiment focused on streambed substrates, the interstices provided by large wood and undercut banks could also be measured using the same approach.

Even though it is not necessary to measure embeddedness *per se* to determine the carrying capacity of streambed substrates for *O. mykiss* at high flows, understanding the degree to which stream substrates are embedded has management implications. Full or partial embedding of coarse substrates can reflect elevated fine sediment loading due to catchment disturbances. There are several approaches for defining and measuring embeddedness to assess habitat degradation, some of which consider only the surface layer (Sylte & Fischenich, 2007). This study indicates that *O. mykiss* refuge habitat can be reduced even if only subsurface layers are embedded. Fine sediments considered to be potentially detrimental to aquatic life are sometimes defined by a 2 mm or finer threshold (sand, silt and clay) (Cordone & Kelley, 1961; Chapman, 1988). This study demonstrates that larger particles, such as small gravel, can be detrimental.

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