

Title: A time-lapse photography method for monitoring salmon (*Oncorhynchus spp.*) passage and abundance in streams

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1 **Abstract**

2 Accurately estimating population sizes is often a critical component of fisheries research and
3 management. Although there is a growing appreciation of the importance of small-scale salmon
4 population dynamics to the stability of salmon stock-complexes, our understanding of these
5 populations is constrained by a lack of efficient and cost-effective monitoring tools for streams.
6 Weirs are expensive, labor intensive, and can disrupt natural fish movements. While
7 conventional video systems avoid some of these shortcomings, they are expensive and require
8 excessive amounts of labor to review footage for data collection. Here, we present a novel
9 method for quantifying salmon in small streams (<15m wide, <1m deep) that uses both time-
10 lapse photography and video in a model-based double sampling scheme. This method produces
11 an escapement estimate nearly as accurate as a video-only approach, but with substantially less
12 labor, money, and effort. It requires servicing only every 14 days, detects salmon 24 hrs. /day,
13 costs less than \$3000 per system, and produces escapement estimates with confidence intervals.
14 In addition to escapement estimation, we present a method for estimating in stream salmon
15 abundance across time, data needed by researchers interested in predator-prey interactions or
16 nutrient subsidies. We combined daily salmon passage estimates with stream specific estimates
17 of daily mortality developed using previously published data. To demonstrate proof of concept
18 for these methods, we present results from two streams in southwest Kodiak Island, Alaska in
19 which high densities of sockeye salmon spawn.

20 **Introduction**

21 Accurately estimating population sizes is often a critical component of fisheries research and
22 management. Managers use salmon (*Oncorhynchus spp.*) escapement estimates (salmon

23 remaining after harvest that enter freshwater to spawn) to develop stock-recruit curves and to
24 decide when to open and close fisheries. Researchers often need escapement data for studies
25 involving productivity, nutrient subsidies, and predator-prey dynamics. Although we have good
26 escapement data for many main-stem rivers used by migrating salmon, we have little escapement
27 data at smaller scales, including small streams where many salmon ultimately spawn. This is
28 regrettable given that large salmon stock-complexes are composed of dozens or hundreds of
29 distinct salmon populations, many of which spawn in first and second order streams. A
30 collection of small salmon populations spawning at different times and in different locations
31 tends to have more stable interannual abundance than a single homogenous population due to
32 “portfolio effects,” which results in more reliable returns and fewer closures for commercial
33 fisheries (Schindler et al. 2010). This stability arises from population diversity occurring at
34 small spatial scales (i.e. first and second order streams), so it is important that we have the tools
35 to investigate and understand these populations in order to effectively manage salmon for human
36 and wildlife consumers.

37 Watershed-scale escapement estimates do not effectively characterize the resources
38 available to wildlife consumers, because they do not tell us how long salmon are available to
39 consumers. In many watersheds, consumers cannot catch salmon while they migrate up the
40 relatively deep water of main-stem rivers; they must wait until salmon enter shallow spawning
41 streams where they are more easily caught. As a result, consumers interact with individual
42 salmon populations rather than entire stock complexes, and thus, watershed scale escapement can
43 be a poor estimate of the salmon available to consumers of conservation concern such as eagles,
44 bears and trout (Bentley et al. 2012, Schindler et al. 2013, Levi et al. 2015; Deacy et al. in press).
45 Also, consumers are easily satiated by even modest densities of spawning salmon, so the

Commented [MJ1]: For those not immersed in the world of salmon fisheries here is quite a nice review here (I learned a lot editing it): <https://www.msc.org/business-support/science-series/volume-02/best-practice-in-salmon-fisheries>

46 duration of spawning activity is likely just as important to consumers as the abundance of salmon
47 (Jeschke 2007). Despite the importance of small tributary salmon escapement to salmon
48 management, ecosystem function, and salmon conservation, existing methods of monitoring
49 salmon abundance do not perform well at these sites, because they are expensive, time
50 consuming, and alter salmon behavior.

51 Traditionally, anadromous salmonids (*Oncorhynchus spp.*) moving into large rivers or
52 streams have been counted by observers stationed at fish weirs, fences, and observation towers,
53 or by use of sonar stations (Table 1; Cousens et al. 1982). These methods can produce reliable
54 estimates; however, high labor and equipment costs make them too expensive for simultaneously
55 monitoring many streams. To fill this gap, researchers have experimented with systems that
56 record video of passing salmon using either under or above water cameras (Hatch et al. 1994,
57 Davies et al. 2007, Van Alen 2008). These video weir methods have three key advantages: 1)
58 footage can be counted long after the data are collected, allowing a small crew to monitor several
59 runs simultaneously; 2) periods with high salmon abundance can be counted more accurately by
60 reducing playback speed; and 3) fewer site visits reduce impacts on wildlife caused by human
61 presence. Although these benefits have made video enumeration an increasingly popular method
62 for counting salmonids, reviewing large amounts of video is required. The resulting personnel
63 costs make video weir methods impractical for many applications. A method is needed for
64 collecting escapement data that produces reliable estimates without thousands of hours of video
65 review or frequent site visits. Furthermore, some enumeration methods (i.e. weirs) can obstruct
66 natural movements of salmon and other fishes. This may not be a problem on main-stem rivers
67 if salmon tend to move consistently upstream, however, it is problematic in small streams where
68 diel movements into and out of streams is common (Bentley et al. 2014).

69 In addition to total escapement, studies focused on consumer responses to availability of
70 salmon need to know the number of living salmon in streams (hereafter in stream abundance)
71 across time. In stream abundance across time represents foraging opportunities better than gross
72 escapement when consumers are swamped by a pulsed resource, which is often the case for
73 consumers of spawning salmon (Armstrong and Schindler 2011). Typically, in stream
74 abundance data are collected using ground (Quinn et al. 2001) or aerial surveys (Neilson and
75 Geen 1981) which are repeated several times during a salmon run. Ground surveys work well on
76 streams that are easy to access, small enough to survey in a reasonable amount of time, and
77 where disturbing wildlife is not a concern. Aerial surveys may work well for less accessible sites
78 if visibility from the plane is not impeded by riparian vegetation or complex channel
79 geomorphology. Moreover, because salmon abundance in streams tends to change rapidly, these
80 methods only work well when the survey frequency is high. Furthermore, to collect reliable data
81 using aerial surveys, researchers need to correct for differences among observers (Bue et al.
82 1998). Here, we present an alternative method for estimating the number of living salmon in a
83 stream through the full duration of the run. The approach combines daily estimates of salmon
84 passage, collected using our time-lapse camera system, with a model of spawning salmon
85 mortality.

86 Our system requires service only every 14 days, detects salmon 24 hrs. /day, costs less
87 than US\$3000 per system, and produces escapement estimates with confidence intervals. This
88 system works on rivers and streams up to ~15m wide and ~1m deep. In addition, we present a
89 method for estimating in stream salmon abundance, data which are important for studies focused
90 on the response of wildlife consumers to salmon runs and nutrient subsidies. To demonstrate
91 proof of concept, we present results from two small streams with very high densities of salmon.

Commented [MJ2]: Would it be worth just saying "is cheap to implement". US\$3000 may be nothing in 10 years time!

92 **Methods**

93 *Approach*

94 To harness the advantages of remote camera systems without time-consuming video
95 enumeration, we utilized a “double sampling” scheme, which is often used when a variable of
96 interest is costly to measure, but an auxiliary variable is more easily measured and has a
97 predictable relationship to the variable of interest (Cochran 1977). The cheaper variable can be
98 measured for all of the sample units while the expensive variable is measured on a subsample of
99 units in order to model the relationship between the variables. Here, our variable of interest is
100 the number of salmon that pass into and out of a stream each hour, which we can accurately
101 quantify with an above-water video camera. The related auxiliary variable is the number of
102 salmon detected in time-lapse images each hour. The total time required to review footage is
103 low relative to video-only approaches because we only have to enumerate salmon in a subset of
104 the hour long sample units. We can determine the salmon passage for the remaining hours by
105 modelling the relationship between the subsample of hourly video counts and photo counts and
106 then using the model to predict salmon passage across the entire salmon run.

107 *Study Streams*

108 We developed this method on two streams used by spawning sockeye salmon: Meadow
109 and Southeast Creeks (Fig. 1a) in southwest Kodiak Island, Alaska. Meadow Creek is a second
110 order tributary to Karluk Lake. It has a mean width of 4.50 m and depth of 13 cm in the lower
111 0.8 km used by spawning salmon. Southeast Creek is a first order tributary to Red Lake that
112 flows out of a small spring pond. It has a mean width of 3.90 m and depth of 9.1 cm in the lower
113 2.7 km used by spawning salmon. Tens of thousands of salmon enter these streams annually to

114 spawn and bidirectional movement and pre-spawn mortality is common owing to a large number
115 of brown bears that prey on the salmon.

116 *Time lapse camera system*

117 To record time lapse images of passing salmon, we used a Reconyx® Hyperfire PC800
118 camera, programmed to take 3 photos in rapid succession (<1 sec. between frames) each minute,
119 24 hrs./day. Each three frame burst allowed us to detect the number and direction of travel (up
120 or downstream) of salmon passing the camera. We suspended the time lapse camera above the
121 stream using steel electrical conduit attached to a steel Big Game® Pursuit tripod tree stand
122 positioned adjacent to the stream (Fig. 1b). We attached the camera to the conduit with a
123 Camlockbox® ball mount which allowed us to easily aim the camera. To light the streambed at
124 night we secured an LTS® IR50 850nm infrared (IR) light to the tripod platform. Although
125 visible light would have worked well, we used IR light to avoid changing the behavior of salmon
126 and/or their predators with visible light. The Reconyx camera and infrared light were powered
127 by an 80 amp-hour deep-cycle battery charged by a 100W solar panel secured to the south side
128 of the tower.

129 To record video, we secured a video camera to the top of the tower. The video footage
130 was stored by a Digital Video Recorder (DVR) set to record D1 resolution, 30 frames per second
131 video from 12pm-8pm, the periods with the best quality video (good light) and the majority of
132 salmon movement activity. The video camera and DVR were powered by its own battery/solar
133 power system, identical to the one powering the Reconyx camera and IR light. To make passing
134 salmon easier to see, we secured 5.08 cm X 76.2 cm white High Density Polyethylene (HDPE)
135 contrast panels to the bottom of the stream below the cameras by attaching them to a heavy chain

136 (Alaska Department of Fish and Game Permit # FH-14-II-0076). The HDPE panels are buoyant
137 in water and the chain prevents the panels from floating off of the streambed. Using stainless
138 steel carabineers, we attached the chain to T-posts which we pounded into the margins of the
139 streambed. To prevent salmon from swimming under the panels, we pinned the chain to the
140 stream bed using several steel stakes.

141 We visited each camera system every two weeks from early June through early
142 September to switch out data cards and remove algae and debris from the contrast panels. Back
143 at our field station, we separately counted the number of salmon moving up and downstream past
144 the contrast panels during each three-photo burst. We only counted a salmon as passing if it
145 moved at least $\frac{1}{2}$ the length of the panels; we did not count stationary fish. Finally, we summed
146 upstream and downstream counts separately for each hour of the monitoring season. To ensure
147 consistent counting technique, each stream was counted by the same person for the entire season.

148 *Modelling salmon escapement (abundance)*

149 We used a model-based double sampling approach to estimate salmon escapement. We
150 modelled the relationship between video salmon counts and photo salmon counts for a non-
151 random subsample of hours, and then used this model to predict salmon passage for the entire
152 season. This is different from the “sampling-design approach” more commonly used to double
153 sample (Cochran 1977). If we had used the sampling-design approach, we would have counted
154 the salmon passing in a simple random subsample of video hours, and then calculated the total
155 escapement by multiplying the time lapse salmon count by the ratio of video counts to photo
156 counts in the subsample. However, the sampling design-based approach has two requirements
157 which are difficult to satisfy. First, to be random, every hour of the salmon run must be available

158 for sampling, meaning that video must be recorded throughout the entire run. A single day of
159 missed video (due to a power outage, insects sitting on the lens, etc.) could significantly bias the
160 resulting abundance estimates if the outage occurred on a day with relatively few or many
161 passing salmon. Second, the video must be high enough quality to assume 100% salmon
162 detection. This requirement can be difficult to meet because of glare and poor night-time video
163 quality. Rather than attempt to design a system that meets these strict requirements, we used a
164 model-based approach, where we model the relationship between video counts and time lapse
165 counts (Stephens et al. 2012). This framework allows us to select our sample of video-
166 enumerated hours non-randomly; our estimate of abundance is unbiased as long as the model is
167 correctly specified (Hansen et al. 1983, Gregoire 1998).

168 We selected 70 hours that spanned the full range of hourly time-lapse salmon counts,
169 from the hours with many salmon swimming downstream to hours with strong upstream
170 movement. Also, we selected hours where we were confident of nearly 100% detection,
171 excluding hours with bad glare or poor lighting. In total, we watched 70 hours of video for each
172 stream, however, because we considered up and downstream salmon movement independently,
173 this gave us a sub-sample of 140 values for each stream (70 upstream counts and 70 downstream
174 counts).

175 Next, we modelled video counts as a function of time-lapse photo counts for the
176 subsample. We compared four different models for each stream: first and second order linear
177 regressions and first and second order segmented or “split-point” linear regressions (Table 2).
178 The segmented regression allows the slope to differ across ranges of the predictor variable. This
179 makes sense for salmon swimming in a stream; salmon swimming upstream (positive values)
180 might move slower, and thus have a greater chance of being detected in a time-lapse burst. In

181 contrast, salmon swimming downstream (negative values) might move faster and have a lower
182 likelihood of detection. To address this possibility, we including segmented regression models
183 with the split-point (slope inflection point) constrained to zero. To assess relative model fit, we
184 compared Akaike's Information Criterion values (AIC_c; Akaike 1974). To validate models and
185 test for over-fitting, we performed leave one out cross validation (LOOCV; Kohavi 1995), and
186 used the resulting predictions to calculate the precision (mean squared error, MSE) and accuracy
187 (the percent difference between the predicted and actual escapement of the 70 hours for which
188 we watched video). Based on these metrics, we selected a top model for each stream.

Commented [MJ3]: I think it would be worth making it clear in your figure legend what the positive and negative values are. The figure should be understandable from the legend alone.

189 Using the top model for each stream, we predicted the salmon passage for all of the hours
190 of the monitoring period. The sum of these predictions is the estimated escapement. Because we
191 did not use random sampling to select our modelling subsample, it is inappropriate to use the
192 model variance to calculate confidence intervals for total escapement. Instead, we bootstrapped
193 our subsample with replacement (140 values to match our original subsample), refit our model
194 using the top model structure, and re-predicted the total escapement (Efron and Tibshirani 2003).
195 We repeated this 10,000 times and used the 2.5 and 97.5 percentile values as upper and lower
196 95% confidence intervals of total escapement.

Commented [MJ4]: best

Commented [MJ5]: I'm not completely clear on why this is necessary (probably my ignorance). If I'm reading this correctly is there the potential that you are imposing normality on data that may not be? I assume you bootstrapped using a mean and s.d. from your original samples? If these are count data should your model assume poisson?

197 *Modelling number of living salmon in streams*

198 To model in stream abundance across time, we took daily escapement estimates
199 (upstream moving salmon minus downstream moving salmon), and applied mortality estimates
200 from the literature. Carlson et al. (2007) investigated the relationship between stream
201 width/depth and stream life (number of days from salmon stream entry to death) on a range of
202 tributaries to Nerka and Aleknagik Lakes, Alaska which are morphologically similar to our focal

203 streams. The three main sources of mortality for spawning sockeye salmon were senescent
204 death, predation (mostly by bears), and stranding. They found that salmon spawning in
205 wider/deeper streams tended to have longer stream lives. The authors' explanation was that
206 salmon in shallow/narrow streams experienced higher predation rates which selects for more
207 rapid reproductive cycles and consequently earlier deaths. Because of this interaction between
208 stream morphology and salmon stream life, it is probably inappropriate to use a single estimate
209 of stream life across streams with varying morphology. We used the results of Carlson et al.
210 (2007) to create a model of stream life as a function of stream morphology.

Commented [MJ6]: Equation 1?

211 Assuming salmon in our streams were equally likely to die by stranding, predation, and
212 senescence as they were in the Carlson study, we calculated a weighted average of the mean
213 stream life for each of the Carlson et al. (2007) streams. We then used this weighted average
214 stream life as the response variable and stream width and depth as predictor variables in a simple
215 linear regression model. Because stream depth and width were strongly correlated ($r = 0.90$),
216 including both variables in the model resulted in collinearity. We thus selected between depth-
217 only and width-only models by comparing AIC_c scores. We then used the top model to predict
218 the mean stream life of sockeye salmon in Meadow and Southeast Creek, using field
219 measurements of stream morphology measured in 2014 as predictors. There was a strong
220 positive correlation between the mean and pooled standard deviation (Hedges 1981) of stream
221 life in the Carlson data ($r = 0.95$, $p = 0.004$); therefore, rather than model the standard deviation
222 (SD) of stream life separately from the mean, we assumed stream life SD was proportional to the
223 mean ($SD = 0.499 * \text{mean stream life}$).

Commented [MJ7]: What was the weighting used?

224 To calculate in-stream abundance each day, we summed the number of salmon that
225 entered on that day with the predicted number of surviving salmon from the previous days:

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227
$$\text{Living Salmon On Day } x = \sum_{t=1}^N P_x + P_{x-t} S_t$$

228 where P_x is the number of salmon that passed into the stream on day x , P_{x-t} is the number of
 229 salmon that passed into the stream t days before day x , S_t is the proportion of those salmon
 230 surviving to day x , and t is an index of days. The values of S_t are from the cumulative
 231 distribution function of survival which we modelled above. N is the number of days it takes for
 232 survival (S_t) to reach zero, which varies based on the survival model (it will be larger on deeper
 233 streams where stream life is greater).

234 To understand the sensitivity of in-stream abundance models to changes in stream life
 235 estimates, we calculated in-stream abundance for each stream across a range of stream life
 236 values. We then used percent change in maximum abundance to assess the impact of changing
 237 stream life. Because the amount of time consumers have access to salmon is at least as important
 238 as peak abundance, we also calculated the duration of the salmon run, defined as the number of
 239 days where abundance was at least ten percent of the maximum in stream estimate from the un-
 240 altered model. This (admittedly arbitrary) ten percent threshold was an attempt to set a lower
 241 limit on the salmon density below which benefits to consumers decline.

242 Results

243 *Salmon Escapement*

244 Of the suite of models relating video counts to time lapse counts for Meadow Creek, the
 245 top model was the segmented first order model (Table 2, Fig. 2). It had the lowest AIC_c
 246 (1534.3), best precision (MSE=3556), and best accuracy (+3.0%). The segmented models likely
 247 explained more variation than the unsegmented models because salmon had different detection

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Commented [MJ8]: You have used some fairly complex stats here. Could you share the packages you used? You should cite them using citation("packagename"). I could not open the r code you deposited.

250 rates while swimming upstream versus downstream (salmon swim slower against the current), in
251 the relatively steep gradient of Meadow Creek. Using the top model, the predicted escapement
252 for Meadow Creek was $30,509 \pm 9,494$ (95% confidence intervals).

253 The top model for Southeast Creek was the first order regression which had the lowest
254 AIC_c (1732.2), best precision (MSE=14167), and best accuracy (+3.1%). In contrast to Meadow
255 Creek, the segmented model only explained slightly more variation than the first order model,
256 but required an additional parameter. This suggests salmon in Southeast Creek have a similar
257 detection rate whether they are swimming up or downstream, which is likely because Southeast
258 Creek has a relatively flat gradient and low velocity. The total escapement for Southeast Creek
259 was $65,355 \pm 4,305$ (95% confidence intervals). For Southeast Creek, the escapement estimates
260 were not very sensitive to the model selected (maximum difference of only 4.4%) (Fig. 3). This
261 contrasts with Meadow, where the difference between the highest and lowest estimate was 38%.

262 *Modelling number of living salmon in streams*

263 The model with depth as a predictor ($AIC_c = 27.5$) explained more variation than the
264 width model ($AIC_c = 31.9$), so we used this model to predict mean stream life for our two
265 streams. Meadow Creek had a predicted mean stream life of 7.1 days (SE=3.5) while Southeast
266 Creek (which is shallower), had a predicted stream life of 5.9 days (SE=3.0). Using these values,
267 we found the predicted salmon abundance over time in each stream were quite different;
268 abundance peaked at just over 11,000 sockeye on July 11th in Meadow Creek and the run was
269 finished around August 16th (Fig. 4). In contrast, Southeast Creek had two distinct peaks in
270 abundance: the first on July 21st with just over 15,000 sockeye and the second peaking at 4,645

271 on August 29th. Thus, although the total escapement in Southeast Creek was more than double
272 that of Meadow Creek, the peak salmon abundance was only 29% higher in Southeast.

273 In general, the in stream abundance models were quite sensitive to changes in stream life
274 estimates. Increasing mean stream life in Meadow Creek by 2 days, from 7.1 to 9.1 days,
275 increased the estimated maximum abundance by 14% (Fig. 5). The effect was even greater on
276 Southeast Creek, with a 22% increase in abundance from a 2 day increase in mean stream life.
277 Increasing the standard deviation had the opposite effect: a 1 day increase in SD of stream life
278 decreased the maximum abundance by 5% and 3% on Meadow and Southeast Creeks,
279 respectively. The sensitivity of salmon run duration (defined as the number of days with at least
280 10% of the maximum salmon abundance), to changes in mean and SD of stream life was less
281 clear. On Meadow Creek, increasing mean stream life by 2 days increased the salmon run
282 duration by 2 days (from 40 to 42 days) and increasing stream life SD by 1 day resulted in no
283 measurable increase in salmon run duration. In contrast, the same changes on Southeast Creek
284 resulted in an 5 day and 2 day increase in salmon run duration for changes to the mean and SD of
285 stream life, respectively. This difference is likely because Southeast Creek has two distinct
286 peaks in salmon abundance, and a 2 day increase in stream life is a larger proportional change
287 compared to Meadow creek.

288 Discussion

289 Researchers and managers increasingly acknowledge the important role of small salmon
290 populations in generating stable returns for commercial fisheries and for supporting wildlife of
291 high economic and commercial value (Schindler et al. 2010, Beacham et al. 2014). Many
292 existing salmon monitoring tools were designed primarily for large streams and rivers and are

ineffective or too expensive for monitoring the salmon populations that use small streams for spawning. The time-lapse salmon counting system presented here proved to be a low-cost, time-efficient, and accurate method for counting salmon in streams less than 15m wide. This method only required bi-weekly site visits, which is ideal for remotely monitored sites and studies involving the response of wildlife to spawning salmon. These benefits will allow managers and researchers to quantify salmon in streams where it was previously too difficult or expensive. In addition, we presented a method for estimating the number of living salmon in a stream across the run, data which are particularly important for consumer-resource studies.

To estimate in stream salmon abundance, we developed a model of salmon stream life (number of days a salmon survives following spawning stream entry) based upon data collected in the Wood River system, Alaska (Carlson et al. 2007). These data are specific to the sites and years where they were collected; differences in water level, intensity of predation, and salmon abundance are all likely to change these values. For these reasons, future users of the method we demonstrated here should estimate stream life in their own systems, rather than relying on the model developed using the Carlson et al. (2007) data. This is particularly important because a sensitivity analysis showed our in stream salmon estimates were quite sensitive to changes in estimated stream life (Fig. 5); a two day increase in stream life increased the estimated maximum abundance by 14% on Meadow Creek and 22% on Southeast Creek.

Similarly, a good escapement estimate is only possible if users accurately model the relationship between time lapse and video counts (Hansen et al. 1983). This is critical given the large differences in abundance estimates resulting from small differences in model structure or fit (Table 2, Fig. 4). It is important to consider multiple model shapes; different stream morphologies or salmon species may produce different salmon run patterns. For example, steep

316 streams are likely to produce models with different slopes for salmon swimming upstream and
317 downstream. The segmented model structure can account for this pattern, and thus should
318 always be included in the candidate model set. Also, a polynomial model might be appropriate
319 for streams that experience high densities of spawners. In general, a polynomial model is needed
320 if time-lapse detection of passing salmon changes with salmon run intensity. For example, as
321 salmon reach high densities, they may not be able to move upstream very quickly because of
322 crowding. This could result in relatively higher detection at high run intensities. In this case, a
323 polynomial model would likely model the relationship better than a first order model.
324 Regardless of the model shape, it is important that users use standard model diagnostics and
325 good sense to fit the best model possible.

326 From four years of testing this method on different streams and different sites within
327 streams we have learned several important lessons. First, this counting system is most accurate
328 and requires the least effort when located where flow is rapid but the water surface is smooth.
329 The rapid flow prevents salmon from loitering above the contrast panels (which can introduce
330 noise into the time-lapse counts), while the smooth water surface makes it easy to see passing
331 salmon. Second, this system works best in shallow streams. Deep streams (>1 m) were
332 problematic because salmon were more likely to swim at different depths, which caused their
333 outlines to overlap and made counting more difficult. It was also more difficult to light deep
334 streams at night. We found that our infrared lights did not light passing salmon adequately if
335 streams were more than one meter deep. Using conventional flood lights (visible light) solves
336 this problem; however, it negates the advantages of using IR lights, which is invisible to humans,
337 fishes, and most wildlife. Third, it is important to orient the camera away from the sun

Commented [MJ9]: It would be interesting to know whether light does affect passage of salmon.

338 (northward in the northern hemisphere), because otherwise the surface of the water reflects glare
339 towards the camera.

340 Although this new method increases the breadth of sites that can be monitored, it has
341 some limitations. As with other methods, the turbidity associated with high flow events can
342 make seeing passing salmon difficult or impossible. Fortunately, these events tend to be brief in
343 the small streams for which we designed this system. Also, it can be difficult to distinguish
344 among species if a site has multiple species migrating at the same time. Finally, this system can
345 only monitor streams up to 15_m wide. Beyond this width, counting accuracy is likely to
346 decrease as the salmon in the images become more distant. One potential solution is to use two
347 camera towers on opposite banks, each viewing one half of the stream.

348 Using this system, it can be difficult to accurately model the relationship between time-
349 lapse counts and salmon passage if escapement is less than two or three thousand salmon. This
350 is because at low escapement, hourly time-lapse counts tend to vary little, regardless of the
351 relative intensity of the run. This makes it difficult to effectively model the relationship between
352 time-lapse photo counts and video counts. One solution to this problem is to increase observer
353 effort by either increasing the length of the sampling unit (e.g. from one to two hours) or by
354 increasing the sampling frequency (e.g. 3-photo burst every 30 seconds). This would increase
355 the contrast between weak and strong runs, but also increase the time required to review photos
356 and/or video. Another solution is to use a model from a stream with similar features (width,
357 depth, velocity, etc.), although we know from the data presented here that models can differ
358 greatly among streams (Table 2). For example, if we had used the Southeast Creek model to
359 estimate Meadow Creek escapement, we would have overestimated by 89% compared to the
360 Meadow Creek top model.

361 In general, salmon researchers should strive to minimize their impact on natural salmon
362 behavior. In small streams such as those monitored here, spawning salmon tend to move up and
363 downstream frequently (Fig. 4, top), a behavior that may be a strategy for avoiding predators
364 (Bentley et al. 2014). Salmon monitoring methods such as weirs have the potential to limit these
365 movements. This could allow predators such as bears to catch salmon more easily, which could
366 decrease salmon spawning success rates and alter trophic interactions with salmon consumers. A
367 key strength of the method presented here is that it allows salmon to move freely and allows
368 natural interactions with salmon consumers.

369 As with many resources used by wildlife, salmon availability is very patchy in space and
370 time (Armstrong and Schindler 2011). This presents a challenge for researchers and managers
371 interested in using sampling to estimate their abundance; the more patchy or pulsed the salmon
372 run, the less accurate a random sampling method will be without large amounts of effort. Here,
373 we overcame this challenge by using a model-based design instead of a random sampling-based
374 design. This allowed us to relax the demands on our camera system; rather than requiring
375 complete video coverage, we merely needed hours of video that represented the full range of
376 salmon run intensities. Given the ubiquity of patchy (in space) or pulsed (in time) resource
377 availability, we suspect that this approach to double sampling could be usefully employed in a
378 variety of natural resources applications.

379 The salmon counting method that we present here expands the range of salmon spawning
380 habitats that can be realistically monitored. Compared to existing methods, our solution is less
381 expensive, less time consuming, and less detrimental to salmon and the wildlife that use them.
382 The data produced can help improve our understanding of how population dynamics at small
383 scales creates stability at the watershed scale. Lastly, due to their low cost and relative

384 portability, these systems would be ideal for monitoring salmon populations of conservation
385 concern. For example, they could produce baseline and ongoing data on the abundance of
386 salmon spawning downstream of mines or other resource development projects.

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