

**Estimation of the abundance and
apparent survival of spawning Arctic
grayling in Red Rock Creek;
Red Rock Lakes National Wildlife Refuge**

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APPROVAL

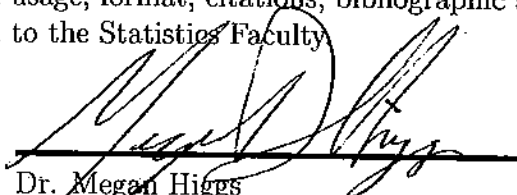
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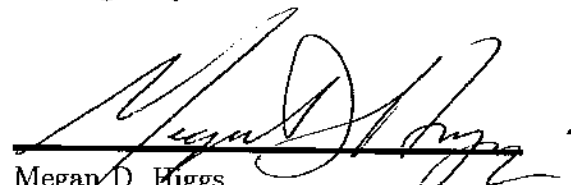
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1 Abstract

Concerns about a potentially declining population and low survival for the last remaining native population of adfluvial Arctic grayling in the lower 48 states (Red Rock Lakes National Wildlife Refuge) motivated a long-term monitoring effort (1975 to present). The species is currently under review for a potential listing under the Endangered Species Act. That decision requires estimates of abundance and survival. The 38-year legacy data set from the monitoring effort was used to produce minimum abundances based on fish counts, along with estimates of both abundance and apparent survival based on mark-recapture methods intermittently applied over the years. The sampling design of the monitoring effort necessitated a simulation study to partially understand the degree of bias in abundance estimates resulting from spatially restricted sampling during electrofishing. Estimated abundances in the system range from a few hundred individuals (1995: 122 (95% confidence interval: 101, 154)) to over 2000 (2012: 2535 (95% confidence interval: 2509, 2545)). Estimated annual apparent survival ranged from 0.15 (95% confidence interval: 0.05, 0.28) in the period 1993 to 1994, to 0.82 (95% confidence interval: 0.49, 0.99) in the period from 1994 to 1995. Simulations suggest that abundance estimates are biased high and variable with low detection and spatially restricted sampling.

Contents

1	Abstract	1
2	Introduction	3
2.1	Project Goals	4
3	Project Background	5
3.1	Study Area	5
3.2	Available Data	6
3.3	Practical Problems and Limitations of Inference	8
3.3.1	Spatial concerns	8
3.3.2	Temporal concerns	9
3.3.3	The importance of communication	10
4	Abundance and Survival	11
4.1	Minimum Abundance	11
4.2	Abundance Estimates based on a Mark-Recapture Design	12
4.2.1	Capture histories	12
4.2.2	Closed population abundance estimation: the Lincoln-Petersen estimator	13

4.2.3	Open population survival estimation	15
4.3	Summary	16
5	Methods	17
5.1	Minimum Abundance	17
5.2	Abundance and Survival Estimates	19
5.2.1	Capture histories	20
5.2.2	Closed population abundance estimates	21
5.2.3	Apparent survival estimates	25
5.2.4	Simulation study: abundance with uncatchable fish and varying detection probability	27
6	Results	30
6.1	Minimum abundances based on counts	30
6.2	Closed Population Abundance Estimates	31
6.2.1	1994, 3 occasions (upstream trap, electrofishing, downstream trap) .	35
6.2.2	1995, 2 occasions (upstream trap, downstream trap)	36
6.2.3	1998, 2 occasions (upstream trap, downstream trap)	37
6.2.4	2002, 2 occasions (upstream trap, downstream trap)	37
6.2.5	2010, 2 occasions (upstream trap, downstream trap)	37
6.2.6	2012, 3 occasions (upstream trap, electrofishing, downstream trap) .	37
6.2.7	2013, 3 occasions (upstream trap, electrofishing, downstream trap) .	38
6.3	Apparent Survival Estimates	38
6.3.1	1993 to 1996	39
6.3.2	2010 to 2013	39
6.4	Simulation study	40
7	Discussion	40
7.1	Abundance Estimation	42
7.2	Apparent Survival Estimation	42
7.3	Simulation Study	43
8	Future Work	44
8.1	Age-specific Survival	44
8.2	Simulations for Spatial Heterogeneity in Distribution	44
8.3	Revised Sampling Design	45
9	Acknowledgements	45
10	References	45
11	Appendix A: Fish counts through trap	48

2 Introduction

Arctic grayling (*Thymallus arcticus*) are a salmonid that occupy cold, freshwater lacustrine and fluvial environments throughout much of the high latitudes in North America (Northcote, 1995; Armstrong, 1986). Management and conservation efforts over the last century have noted that grayling are occupying a smaller and smaller portion of their historic range, e.g. they were extirpated from Michigan in the 1930s (Scott and Crossman, 1973; Hubbs and Lagler, 1958) . Though still present in Montana, grayling range and abundance have suffered a decline (Liknes and Gould, 1987; Kaya, 1992; Rens and Magee, 2007). Both the size and distribution of the population of adfluvial Arctic grayling in the Centennial Valley, Montana have considerably contracted during the recorded history of the valley. Once abundant and widely distributed, the extant population occupies a small fraction of its historic range (Rens and Magee, 2007; Kaya, 1992; Nelson, 1954). It is now thought to be limited to Upper Red Rock Lake, with the predominate tributary of Red Rock Creek (Hagen, 1996). Recent work suggests that this population of adfluvial grayling is genetically distinct from other populations with different life histories, even the proximal population of fluvial grayling in Big Hole River drainage (Figure 1) (Peterson and Ardren, 2009; Everett, 1986).

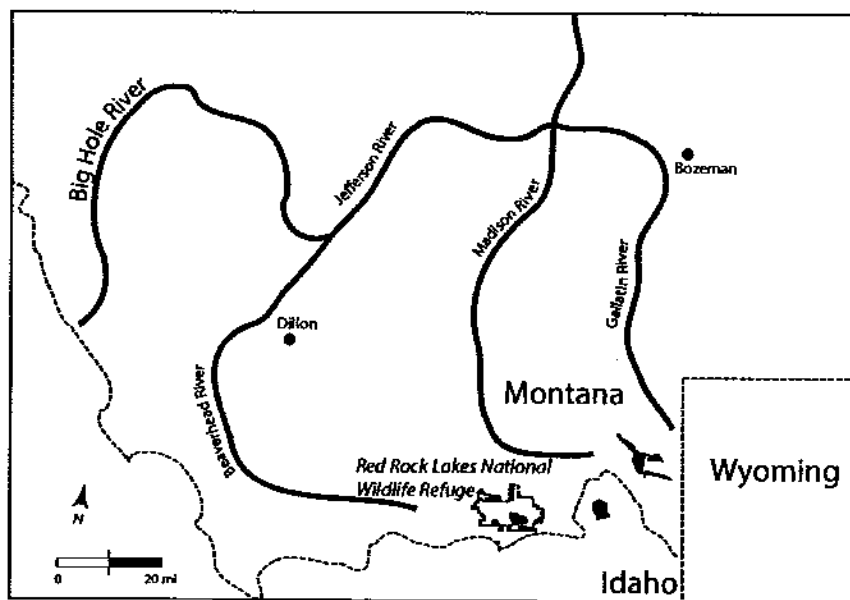


Figure 1. Regional map. Red Rock Lake National Wildlife Refuge is located in the Centennial valley in far southwestern Montana, just north of the Idaho border and to the west of the Montana-Wyoming border.

The U.S. Fish and Wildlife Service is interested in conserving this distinct population of Arctic grayling, and has considered a potential listing of this population as a species of concern under the Endangered Species Act (a final decision was delayed to 2014). Consequently, we require estimates of historic abundance and survival to adequately inform the listing decision using a data set from the monitoring effort. Though monitoring of the grayling population began as far back as the 1950s, consistent and well-documented efforts began in 1975 and have progressively increased in effort and scale to the present.

2.1 Project Goals

We desire estimates of the historic abundance and survival of spawning grayling in Red Rock Creek. The goal is to use a long-term monitoring data set that is an amalgamation

of different sampling designs and methodologies to estimate the abundance of spawning grayling and the apparent survival rate between years. The method(s) developed to produce the estimates will be used to inform an ongoing adaptive management plan for Arctic grayling.

3 Project Background

The monitoring effort in the Centennial Valley has largely focused on the spawning population of adults utilizing Red Rock Creek. In the spring of each year, sexually mature adult grayling (between two and three years old in this system (Shepard and Oswald, 1989)) leave Upper Red Rock Lake and enter the creek, migrating upstream to suitable spawning habitat (Figure 2). Biologists involved in the project suspect the start of the spawning run is triggered by a combination of water temperature and discharge (Hagen, 1996), both heavily influenced by spring weather and winter snowpack conditions. The spawning run begins in late April to early May and concludes in early to late June. Once the spawning run is complete, grayling migrate back downstream (over the course of days to weeks) to the lake in which they spend the remainder of the year. The monitoring effort allows inference only to the population of spawning grayling, a population that serves as an implied proxy for the size of the population in the entire system.

3.1 Study Area

Red Rock Creek is a tributary to Upper Red Rock Lake and is a cold-water stream that cuts through a variety of landscapes from the headwaters to the lower reaches near the lake.

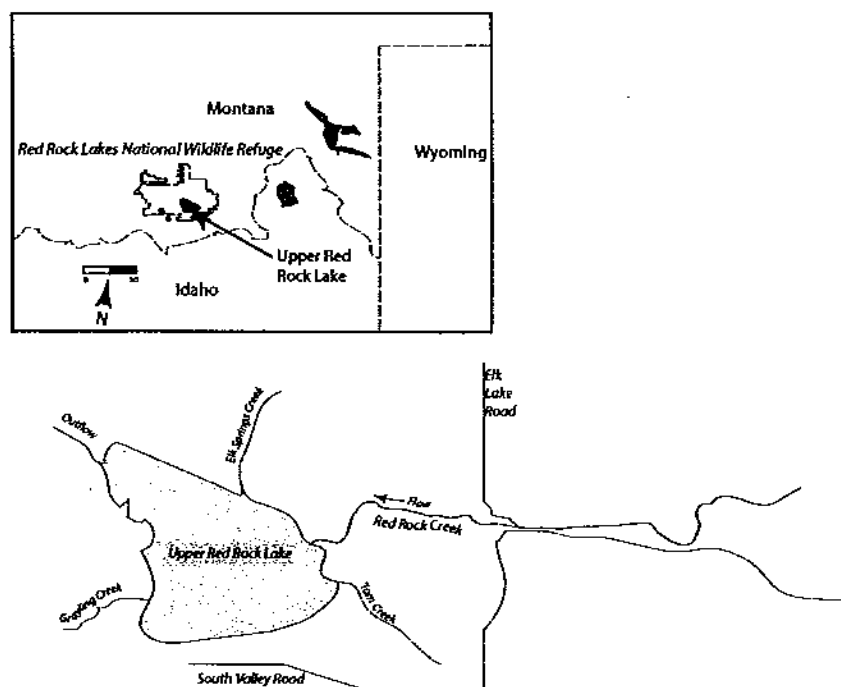


Figure 2. Study Area. Upper Red Rock Lake is the primary habitat for Arctic grayling; each spring sexually mature fish spawn in Red Rock Creek. The creek has been the focus of the monitoring effort under the assumption that it is the overwhelmingly used tributary for spawning.

Over its course, it flows through private land in the upper reaches of the tributary subject to grazing pressure as well as federally protected land on the refuge itself (near the mouth) and exhibits a variety of morphologies from braided to highly sinuous. During the general spawning season from late April to late June water temperatures range from 2°C to 29°C, and discharge ranges from 11 cfs to 250 cfs.

3.2 Available Data

The data used to estimate the abundance of grayling are the result of decades of work by technicians and scientists in the Red Rock Lakes National Wildlife Refuge. From 1975 to

2013 various intermittent efforts have been made to sample the population of grayling in Red Rock Creek to monitor for long-term changes in the abundance of the species. Two methods have been used to estimate the number of spawning adults each year: a fish trap (1994-1996, 1998, 2000-2002, 2010 and 2012) and an electrofishing transect (1975, 1978-1989, 1993, 1994, 2000-2002, 2005-2012).

The fish trap is a barrier located approximately 2 miles upstream from the mouth of Red Rock Creek. It is located and designed so that fish traveling upstream to spawn (or downstream to return to the lake post-spawning) are corraled into a holding area from which they can be removed, tagged or given a disfigurement mark (in some years), and have individual attributes such as sex, length, and weight recorded. The tags permit individual identification of fish whereas disfigurement marks only identify the year in which the fish was observed. The installation and removal of the trap is, ideally, timed to catch and observe as many of the fish as possible during a spawning run. At 100% capture efficiency, an individual would be seen in the trap during both the upstream and downstream records.

Electrofishing has been the most often used sampling method in the monitoring effort for grayling. Each year, biologists and technicians select a stretch of the tributary upstream of the fish trap, then exhaustively electrofish that section in a single pass, referring to length of the tributary thus sampled as the 'transect'. Over the history of the monitoring effort, the locations of the starting and ending points have been variable (and thus the length of the transect). The section is fished in a single pass in a day or two, during which individual attributes of caught fish (sex, length and weight) are recorded. In some years, disfigurement marks or tags are given to the fish in an effort to identify different cohorts of fish. The technicians limit the possibility of repeatedly catching the same fish by sampling a subsection of the transect, holding all fish in a live well on the

boat until the end of the subsection, then processing all the fish in a batch and waiting to release them until the sampling of the next subsection is underway.

3.3 Practical Problems and Limitations of Inference

As a mosaic of efforts and ideas, the sampling methodologies used over the last 38 years place both spatial and temporal limitations on the inferences of abundance for each year.

3.3.1 Spatial concerns

The fish trap is located approximately 2 miles upstream from the mouth of the tributary (Figure 3).

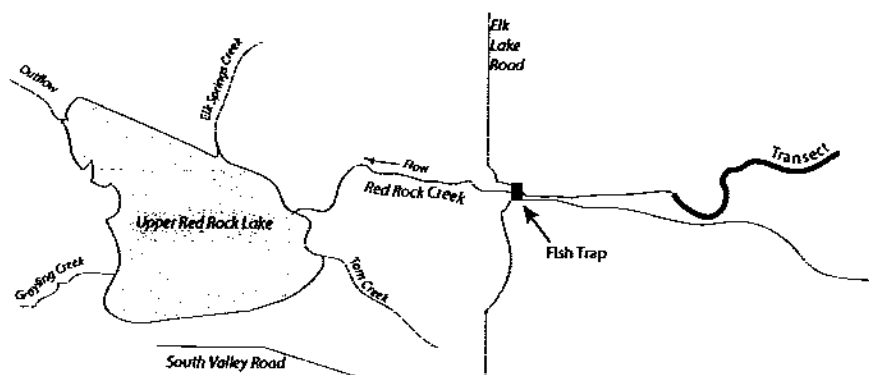


Figure 3. Idealized locations for the two sampling methods used in the monitoring effort: the fish trap (located approximately 2 stream miles upstream from the mouth of Red Rock Creek) and the electrofishing transect section (variously located upstream of the trap though the downstream end is consistently upstream of the fish trap).

The stretch below the trap contains spawning habitat and likely supports a large proportion of the total fish leaving the lake to spawn in the spring. The position of the fish trap therefore further limits inference for the population size to those grayling that spawn above the trap. Both the location and length of the electrofishing transect

are often selected in deference to logistical concerns such as technician availability, high water and navigation of the tributary, and the need to acquire gametes for off-site and remote-site incubators for grayling fry. Consequently, the same stretch of the tributary may not be sampled in consecutive years. The variation in both the length and location of the transect means that the transect does not cover the entire population known to be upstream of the trap.

3.3.2 Temporal concerns

Temporal concerns are particularly problematic for the study insofar as a spawning population only ephemeraly occupies the tributary, *i.e.* sampling efforts are trying to hit a moving target. Ideally the fish trap is installed prior to the beginning of the spawning run, is maintained throughout, and then removed after declining counts of fish in the downstream trap suggest the end of the spawning run. In high-water years the trap may be temporarily washed out due to high flows (potentially removed for the entire season in extreme cases) or in some cases simply bypassed by fish. Each case results in a decline in trap efficiency because less of the population is caught and/or tagged. In the worst-case scenario, the complete removal of the trap for the season simply means that the capture session cannot be used to help estimate abundance.

As previously mentioned, the existing data set is the result of a variety of individual efforts over time. In an ideal year, the day of electrofishing would come close to the peak of the spawning run when as many fish as possible are upstream from the trap. In several years the electrofishing occurred early, when low counts of fish in the trap suggested comparatively few fish were upstream. Consequently, using the electrofishing sample as a recapture event further limits the scope of inference to the spawning population above the trap at the time of sampling.

3.3.3 The importance of communication

I struggled with the interpretation of a data set that was an amalgamation of a variety of individual efforts. For example, it took several conversations with biologists involved in the project to adequately understand the deviations from the ideal implementation of the trap, e.g. many previously unmarked fish showed up in the downstream trap on multiple occasions.

Grayling spawning behavior is suspected to depend upon water temperature. At lower temperatures they will hold in deeper pools, and only move onto the active spawning grounds of riffles at higher temperatures. The result of this movement is that fish may pass through the upstream trap, then subsequently caught again very quickly in the downstream trap. It is at the technician's discretion whether to then release the fish on the upstream or downstream side of the trap. If he or she determines the fish is still in pre-spawning condition, the fish is released on the upstream side of the trap but recorded as being captured in the downstream trap. This subtlety has clear implications for analysis.

I was provided with a scattered record of the specific locations and lengths of the electrofishing transects. Interviews with biologists and technicians indicated these were variable among years and thus the degree to which the transect was representative of the distribution of the spawning population is unknown.

Furthermore, each individual sampling event (either trap or transect) has a widely variable effort at marking fish. In multiple years, no marks or tags were given to fish, or such marks were not recorded upon subsequent observation/capture. Coupled to that lack of information, in some years in which tags were given to fish, the biologists and technicians occasionally ran out of tags. For example, in 2012 approximately 1000 fish were captured and handled after tags had run out.

4 Abundance and Survival

4.1 Minimum Abundance

The simplest metric for tracking changes in the size of a population is the number of unique fish counted during a sampling occasion, which provides a minimum number of fish in the population. The primary limitation of using counts of unique fish as a proxy for the size of the population is that it does not account for imperfect detection or spatial/temporal limitations in the sampling. We know that an electrofishing transect does not detect all of the available fish within the sampling transect, nor does the transect cover the entire stretch of spawning habitat in Red Rock Creek or necessarily coincide with the peak of the spawning run (Appendix A includes plots of the numbers of fish through the traps, indicating problems with detection and the dates of electrofishing). Similarly, the fish trap suffers from imperfect detection owing to high flows and structural problems that allow fish to bypass the trap at times. Minimum abundances based on fish counts have two primary limitations: 1) they are underestimates of the population size due to imperfect detection, and 2) they are not comparable across years due to variation in detection resulting from differences in the timing and the extent of the sampling. The latter limitation implies these data should not be used to draw conclusions about trends in population size over time.

In recognition of the limitations of minimum abundances based on fish counts, the monitoring effort has made several attempts to utilize mark-recapture style sampling to actually estimate abundance and year to year apparent survival of grayling during the spawning run.

4.2 Abundance Estimates based on a Mark-Recapture Design

Mark-recapture describes a well-developed suite of study designs that attempt to estimate demographic parameters of a population such as abundance, survival, detection probabilities, immigration into a population, and emigration from a population (Kéry and Schaub, 2012; Amstrup et al., 2010; Williams et al., 2002). Fundamentally, all of the designs attempt to estimate these parameters by dealing with the problem that animals are imperfectly detected. These methods depend upon the assignment and recording of unique identifications for each animal upon capture at each sampling occasion. The individual records are then compiled into a capture history.

4.2.1 Capture histories

The capture history is a matrix in which each column represents a capture occasion, each row represents an individual, and each cell is either 1 (animal was captured) or 0 (animal was not captured). For example, a study with two capture occasions (an initial 'mark' event during which captured individuals are given unique identification tags/marks and a second 'recapture' event) can be represented as:

ID	Mark	Recapture	Interpretation
1	1	1	Individual 1 was marked at first event and recaptured
2	0	1	Individual 2 was not captured at first event, was subsequently captured
3	0	1	Individual 2 was not captured at first event, was subsequently captured
⋮	⋮	⋮	⋮
9	1	0	Individual 9 was marked at first event and not recaptured
10	1	1	Individual 10 was marked at first event and recaptured

or in condensed form as:

possible history	number of individuals with history
11	a
10	b
01	c

The relative proportion of marked to unmarked individuals in a recapture event, in addition to total numbers of animals captured, is then used to estimate detection probabilities at each sampling occasion which, depending upon the model, allows for estimation of population parameters such as survival, abundance, etc. (Amstrup et al., 2010).

4.2.2 Closed population abundance estimation: the Lincoln-Petersen estimator

Consider a hypothetical study interested in the population of rabbits within a defined geographical area. We would like to estimate the abundance of rabbits and therefore treat the population as 'closed', or of fixed size, for the course of the study. On an initial trapping occasion (the 'mark' event) 8 rabbits (m_1) are captured and given unique identifying marks. During a second trapping occasion (the 'recapture' event) 12 rabbits are captured (n_2) of which 5 were previously marked (r_2). The capture history would look like:

An intuitive estimate of the population size is a ratio between the two capture occasions:

$$\frac{m_1}{N} = \frac{r_2}{n_2} \implies \frac{8}{N} = \frac{5}{12}$$

Rearranging the proportion for N yields the classic Lincoln-Petersen estimator (Nichols, 1992; Seber, 1982; White, 1982) for the size of a population based upon two trapping oc-

1	1	The 5 rabbits caught on both occasions
1	1	
1	1	
1	1	
1	1	
<hr/>		
1	0	The 3 rabbits initially marked and not recaptured
1	0	
1	0	
<hr/>		
0	1	The 7 rabbits not caught on the first occasion, but caught on the second
0	1	
0	1	
0	1	
0	1	
0	1	
0	1	

casions.

$$\hat{N} = 8 \times \frac{12}{5} = 19.2$$

or approximately 19 rabbits. The estimator (and associated standard error) has been more formally derived from a multinomial approach to the problem, and has been extended to multiple (> 2) capture occasions and typically uses the maximum likelihood approach to obtain estimates and confidence intervals (Williams et al., 2002).

There are a variety of models used to estimate abundance in a mark-recapture framework (Kéry and Schaub, 2012; Amstrup et al., 2010; Williams et al., 2002), all of which attempt to address one or more of the three potential sources of heterogeneity in capture probabilities: temporal (model M_t), behavioral (M_b) and individual (M_h) (notation from (Otis et al., 1978), (Pollock et al., 1990)). For example, a M_t model allows for different probabilities of detection at each capture and subsequent recapture event. A behavioral model (M_b) allows changes in detection probability based on whether or not an animal has previously been captured, and M_h allows for difference detection probabilities at each

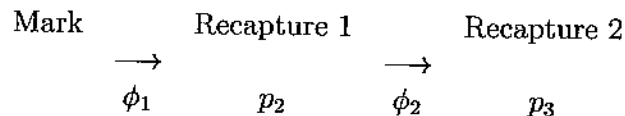
capture and recapture occasion for individuals. All possible combinations of heterogeneity, in addition to the simplest model wherein capture probabilities are fixed (M_0), yield eight traditional models for closed populations: $M_0, M_t, M_h, M_b, M_{th}, M_{bh}, M_{tb}, M_{tbh}$.

4.2.2.1 Assumptions The intuitive approach highlights the fundamental assumptions for the estimator (Amstrup et al., 2010):

1. the population must be closed over the course of the study, i.e. no births (or immigration) or deaths (or emigration), and
2. each capture event constitutes a random sample from the population.

4.2.3 Open population survival estimation

An open population is one in which births and deaths (or immigration and emigration) change the size of the population between sampling events (Amstrup et al., 2010). Births and deaths can not be separated from immigration or emigration. In the simplest case, the mark-recapture study design can be used to estimate the survival of individuals between sampling occasions. For a three-event study (an initial mark event and two subsequent recapture events), the parameters of interest are



The probability of an individual encounter history is now the product of both survival and detection. For example, the probability of an encounter history for an individual seen on all three occasions (an encounter history of 111) is $\phi_1 p_2 \phi_2 p_3$, read as “the individual survived to the second occasion and was detected, then survived to the third occasion and was detected.” In other words, the individual has to survive from the mark event, be seen on the first recapture event, survive to the second event, and be seen on the second

event. Problematic for inference are individuals who are seen at some point and then never seen again. For example, an individual with encounter history 100 (marked, then never seen again) may have survived between the first and second occasions and simply not have been detected. Alternatively, the individual may have died (emigrated) after the first event. In this case the probability of the encounter history is $(1 - \phi_1) + \phi_1 \cdot (1 - p_2) \cdot (1 - \phi_2) + \phi_1 \cdot (1 - p_2) \cdot \phi_2 \cdot (1 - p_3)$, read as “the individual died (emigrated) after the first occasion *or* survived to the second interval, was not detected and then died (emigrated) after the second occasion *or* survived between all the occasions and was never detected.” Estimation of the parameters uses the method of maximum likelihood derived from the multinomial distribution (Williams et al., 2002).

4.2.3.1 Assumptions The open population analysis assumes (Amstrup et al., 2010):

1. all of the individuals present in the population at each of the sampling occasions have the same probability of detection and the same probability of survival until the next sampling occasion (assumed to be 1 under a closed population model),
2. no mark loss,
3. sampling is essentially instantaneous, i.e. no immigration and emigration occur during the sampling process, and
4. all apparent emigrations (either deaths or true emigration) from the population are permanent.

4.3 Summary

Mark-recapture methods rely upon the assignment of unique marks to individuals. At each recapture event, the relative proportion of marked to unmarked fish is used to estimate (in this study) the apparent survival between occasions (open population), or the abundance and probability of detection (closed population). Each model has a set of

assumptions, violations of which can bias the resulting estimates and standard errors to a degree depending on the severity of the violation. In this study, the capture histories for individuals are the combination of two methods, the fish trap and electrofishing transect, both of which have potential violations of key assumptions.

5 Methods

Two of the primary goals of the study are to estimate the abundance of fish in each year, and the apparent survival of fish between years. Over the course of the monitoring effort, a variety of methods have been used to quantify the size of the spawning population in each year (Table 1). These methods vary over the years, from years in which only electrofishing was utilized (e.g. 1975), years in which the upstream trap was monitored (e.g. 1996), and years in which multiple methods were used (e.g. 2000). Additionally, unique marks were given to fish in only a subset of years.

These available data allow for two types of abundances of spawning grayling: a minimum abundance based on the raw counts of fish at each occasion (the only method available in the absence of unique marks for individuals) and an estimate of abundance within a year based on modeling using capture histories from the mark-recapture design (closed population). When unique marks were applied to individuals in subsequent years, modeling of capture histories under an open population model also permits estimates of year-to-year survival across years.

5.1 Minimum Abundance

The two sampling methodologies, the fish trap and electrofishing transect, are two very different methods of sampling the population and each has its own limitations for esti-

Year	Method	Identifiers	Capture History
1975	tran	none	none
1978	tran	none	none
1979	tran	none	none
1980	tran	none	none
1981	tran	none	none
1982	tran	none	none
1983	tran	none	none
1984	tran	none	none
1985	tran	none	none
1986	tran	none	none
1987	tran	none	none
1988	tran	none	none
1989	tran	none	none
1993	tran	unique	none
1994	tran, up, down	unique id	3 occasion
1995	up, down	unique id	2 occasion
1996	up	unique id	none
1998	up, down	disfigurement, unique id	2 occasion
2000	tran, up, down	none (tran) disfigurement	2 occasion
2001	tran, up	disfigurement	2 occasion
2002	tran, up	disfigurement	2 occasion
2005	tran	unique id	none
2006	tran	unique id	none
2007	tran	unique id	none
2008	tran	none	none
2009	tran	none	none
2010	tran, up, down	none (tran), unique id (trap)	2 occasion
2011	tran	unique id	none
2012	tran, up, down	unique id	3 occasion
2013	tran, up, down	unique id	3 occasion

Table 1. The long term monitoring effort has used a variety of methods over its history. 'tran' refers to the electrofishing transect, 'up' to the upstream trap and 'down' to the downstream trap. The marks refer to either unique identifying tags or non-unique disfigurement marks given to individuals in each year of interest.

—mating the abundance of grayling. The transect is a single snapshot in time during a spawning run; if it is too early or too late the count of fish may not be a good index for the true size of the spawning population. It is also unknown how well the electrofished sections captured the spatial distribution of the spawning population upstream of the trap. For example, if the grayling are uniformly distributed upstream from the trap, the number of fish caught in the transect is proportional to the fraction of the total spawning

habitat the transect represents; this distribution is unknown, however. The fish trap is a more continuous record designed to capture the size of both the upstream and downstream migrations, yet high water flows periodically reduce trapping efficiency or force the removal of the trap altogether.

For years in which counts of fish are available from multiple methods (for example, a year in which both the upstream trap and down stream trap were monitored and an electrofishing transect was run), it is problematic to combine the different counts into a single number for a year. I simply chose the largest count as the minimum abundance for the year. For example, in a three occasion year (upstream trap record, electrofishing transect, downstream trap record) the reported minimum abundance is simply the largest count from amongst the three sampling occasions. For biologists, this has the practical interpretation of the absolute minimum number of spawning fish in the system within a year. Given the variety of methods used within each year, as well as the varied effort for each method between years (e.g. in some years the fish trap efficiency was greatly reduced due to high water, the length of the transect varied, etc.), it is unlikely that minimum abundances based on counts are directly comparable between years. As a result, minimum abundances are unlikely to be useful for tracking trends in the size of the spawning population over time.

5.2 Abundance and Survival Estimates

Abundance estimates based on a mark-recapture design require at least two capture occasions using unique identifiers within a single year, a criterion met in 1994, 1995, 1998, 2000, 2001, 2002, 2010, 2012 and 2013. Estimates of survival between years use pooled capture histories (the combination of multiple within year mark-recapture occasions into a single capture history for each year) and were available for each year from 1993 to 1996

and 2010 to 2013.

5.2.1 Capture histories

Within each year the trap was operated there were potentially two occasions to mark and recapture fish (the upstream migration and downstream migration). The entire record from the upstream trap was treated as a single occasion, similarly for the downstream trap. Note that each record is the result of daily monitoring from the time the trap is installed to the time the trap is removed. If electrofishing was also run that year, there were three occasions: the upstream migration recorded at the trap, the electrofishing transect, and the downstream migration at the trap. These occasions were used to estimate annual abundances under the assumption of a closed population. Then, to estimate apparent survival across years under the open population model, I pooled the multiple capture events within each year into a single capture event, recording whether or not an individual was seen at all during that year. This apparent survival is actually the result of two separate probabilities: the probability that a fish survives and the probability that a fish returns to spawn above the trap.

In years with both a trap record and an electrofishing transect, I treated the upstream trap as a single mark event, the subsequent electrofishing transect upstream from the trap as a recapture event, and the downstream trap as the final recapture event for the season. However, as noted above, the transect does not cover all of the spawning habitat upstream from the trap. Consequently, there are potentially many fish for whom the probability of recapture at the second occasion is zero. In years with only a trap record, I treated the upstream trap record as the mark event and the downstream record as the recapture event. However, if the trap was removed prior to the complete downstream migration of the spawning run, the fish lingering in the system had a recapture probability of zero. It is

this violation of the assumption of equal catchability that motivated investigation of the methods via computer simulations in an effort to understand how violation of assumptions may affect inferences about abundance.

Technicians ran out of tags in 2012 while processing fish at the trap; as a result, approximately 1000 fish were handled at the trap that were not tagged with individually identifying marks. It is likely that many of the fish seen in 2013 were present in 2012 and the lack of the tag potentially introduces a sizeable source of error into the estimate of survival from 2012 to 2013.

5.2.2 Closed population abundance estimates

The biological and practical realities of the monitoring effort suggest that, *a priori*, M_t (different capture probabilities at each occasion within a year) is the most appropriate model. Each sampling method used (upstream trap, downstream trap, or electrofishing) represents a different amount of effort over a different amount of time, and I expect those differences to manifest as heterogeneous detection probabilities. Essentially, the temporal heterogeneity in detection probability in model M_t is also heterogeneity due to differences in the method used on each occasion. I am assuming the lack of a trap response (M_b) and with no information of individual variation in spawning behavior (M_h), I simply fit M_t and the homogeneity model M_0 . The latter model was included in deference to the convention of comparing more complicated models to the simplest model available.

I ran the models using a variety of software packages (MARK (White and Burnham, 1999), Rcapture (Baillargeon and Rivest, 2007), mra (McDonald, 2012)) before ultimately deciding to adopt a Bayesian approach. Though all methods arrived at similar results for most problems, the need to explicitly write out the distributions of the likelihood forced me to think much more critically about the assumptions behind each model. I found

the Bayesian approach to be a much more intuitive representation of the physical and observation processes at work in the model.

Bayesian estimation of abundance introduces a computational hurdle that is not present in likelihood estimation. Depending upon the parameterization of the model, the number of parameters may change at each iteration of the MCMC algorithm (Kéry and Schaub, 2012), requiring a more sophisticated formulation of the model. Royle and Dorazio (2007) described the problem for the model wherein we estimate the probability of capture for each individual observed in the capture history. As the length of the parameter vector for capture probabilities is equal to the size of the population, each update to the size of the population changes the dimension of the parameter space of the probabilities. One solution to the problem is data augmentation, described in Kéry and Schaub (2012), originated by Tanner and Wong (1987) and introduced to recapture analysis by Royle and Dorazio (2007). The technique essentially reparameterizes the model as an occupancy model (modeling the probability of being present) through the addition of an arbitrary number of individuals (who are never observed) to the capture history. This effectively embeds the observations inside a larger model, and then allows us to estimate the occupancy rate, or probability that an individual is observed.

After augmentation, the capture history matrix consists of the observed data and an arbitrary number of individuals that were never seen (rows of all 0s). Using a latent indicator variable (z_i equal to 1 if an individual is in the observed data set and 0 otherwise) allows estimation of the population size as the sum of the vector of latent variable indicators, i.e. it counts the number of those individuals observed. The addition of unobserved individuals makes the estimation of the detection probability problematic, therefore the latent variable indicator is used again to constrain estimation of the probability of detection to those individuals actually seen.

For example, model M_0 (fixed detection probability) is (notation and structure from (Kéry and Schaub, 2012)):

Model M_0

$y_{i,j} \sim \text{Bernoulli}(p)$, whether an individual i is observed on occasion j ,

$p \sim \text{Bernoulli}(z_i v)$, the probability of detection for individual i on occasion j ,

$z_i \sim \text{Bernoulli}(\omega)$, whether an individual i was captured at least once,

priors

$\omega \sim \text{Beta}(1, 1)$

$v \sim \text{Beta}(1, 1)$.

Uniform(0,1) (or, equivalently, Beta(1,1)) priors were used for each parameter. Prior selection is a topic of vigorous debate, and there are several choices available in the quest for a 'noninformative' prior such as the Uniform(0,1) (Beta(1,1)) prior, or Jeffrey's prior, a Beta(1/2, 1/2). At large sample sizes, the resulting posterior distributions are 'practically indistinguishable' when used with a binomial likelihood (Link and Barker, 2009). The Uniform(0,1) prior was chosen for convenience.

The model changes only slightly to allow for different detection probabilities at each capture occasion (M_t , the most *a priori* reasonable model for the data):

Model M_t

$y_{i,j} \sim \text{Bernoulli}(p_j)$, whether an individual i is observed on occasion j ,

$p_j \sim \text{Bernoulli}(z_i v_j)$, the probability of detection for individual i on occasion j ,

$z_i \sim \text{Bernoulli}(\omega)$, whether an individual i was captured at least once,

priors

$$\omega \sim \text{Beta}(1, 1)$$

$$v_j \sim \text{Beta}(1, 1)$$

I used JAGS (Just Another Gibbs Sampler Plummer (2003)), a program that uses MCMC methods to implement Bayesian models to approximate the posterior distribution for each parameter. I assessed convergence using the Gelman-Rubin statistic, \hat{R} (or, phonetically, ‘Rhat’) (Gelman and Hill, 2007). \hat{R} is “approximately the square root of the variance of the mixture of all the chains, divided by the average within-chain variance.” In other words, small values of Rhat indicate that the variance of the chains is comparable to the variance inside each chain, suggesting convergence; I assumed convergence at values of \hat{R} less than 1.01. I monitored the effective sample size, increasing the number of iterations until it exceeded 100 for each parameter. Additionally, I visually assessed convergence using trace plots, making sure that the chains appeared to be well-mixed and converging to the targeting distribution. The appropriate burn-in period, and concomitant discarding of non-converged simulations, was also decided upon using trace plots.

I initially compared models using the *deviance information criterion* (DIC, Spiegelhalter et al. (2002)) an information-theoretic criterion similar to the Akaike information criterion (AIC). DIC is useful for Bayesian modeling because it is readily calculated from the samples of the targeting distribution generated by the MCMC method, and is appropriate for hierarchical modeling wherein the number of parameters (the complexity penalty in AIC) is more difficult to calculate. DIC is an approximation to the expected predictive deviance, useful when the goal is to pick a model with “the best out-of-sample predictive power” (Gelman et al., 2013), or the model that best describes hypothetical, new data produced from the underlying physical processes governing spawning abundance. The interpretation is similar to that for AIC in that the lower the score, in general, the better

the predictive power of the model.

Given the variations in sampling methodology and effort, model M_t is the most reasonable model for the data. Model comparison in this case amounts to a 'check' that the additional complexity in model M_t relative to model M_0 is warranted, acknowledging that it is possible that detection probabilities for the upstream and downstream trap could be similar for years in which water and monitoring conditions were ideal. However, the use of DIC to compare models is tempered by practical realities in several cases below. If there is a good, practical reason to favor one model over another, DIC is disregarded.

5.2.3 Apparent survival estimates

Similar to closed population abundance estimates, estimates of apparent survival in open populations can be obtained by a variety of models incorporating various sources of heterogeneity in capture probabilities and survival rates (review in Lebreton et al. (1992)). The Cormack-Jolly-Seber models are a broad class of models allowing variation in both parameters as a function of time, behavior and individual heterogeneity (Pledger et al., 2003; Williams et al., 2002; Amstrup et al., 2010). *A priori*, a model incorporating temporal heterogeneity (between and among years) makes biological and practical sense in the context of the monitoring effort, given the concern for the violations of the underlying assumptions. I also included a model in which apparent survival rates and detection probabilities are constant between and among years both in deference to convention and in acknowledgment of the possibility that the data do not support the additional complexity of the model in which apparent survival rates and detection probabilities are allowed to vary. In pooled capture histories (an amalgamation of trap data and/or transect data), the detection probability is simply the probability that an individual is observed by any method throughout the spawning run.

I chose to use the state-space formulation of the models to estimate survival and detection probabilities (Gimenez et al., 2007; Royle, 2008) as an aesthetic choice, given the elegant decomposition of the observed data into two separate processes. The parameterization relies upon the separation of the true state $z_{i,t}$, a binary latent variable that describes an individual i as in the sampled population (1) or not (0) at time t , from the process by which we observe spawning grayling during sampling with less than perfect detection. The former takes the value of 1 for an individual at first capture and subsequent states of the individual at additional capture occasions are modeled as realizations from a Bernoulli process with a rate parameter defined by the state at the previous time step and the survival rate (ϕ) (Kéry and Schaub, 2012). Formally, the latent state is

$$z_{i,f_i} = 1, \text{ and } z_{i,t+1} | z_{i,t} \sim \text{bernoulli}(z_{i,t}\phi_{i,t}),$$

where f_i denotes the occasion (i) of first capture for an individual. This is separate from the observation process, which is modeled as a realization from a Bernoulli process with rate parameter defined from the state $z_{i,t}$ and the detection probability (p_t , assuming temporal-heterogeneity in the probability of detection) :

$$y_{i,t} | z_{i,t} \sim \text{bernoulli}(z_{i,t}p_{i,t}),$$

where $y_{i,t}$ is either 0 (not detected) or 1 (detected) at time t . The latent indicator variable $z_{i,t}$ in the rate parameter guarantees that only individuals who are available for sampling at time t are used to estimate the detection probability.

The homogeneity model restricts both detection probabilities and survival to be constant across individuals and capture occasions within a year, *i.e.* it has a reduced parameter space ϕ, p , resulting in the following model:

observation process

$$y_{i,t} | z_{i,t} \sim \text{bernoulli}(z_{i,t}p)$$

state process

$$z_{i,f_i} = 1$$

$$z_{i,t+1} \mid z_{i,t} \sim \text{bernoulli}(z_{i,t}\phi)$$

priors

$$\phi \sim \text{Beta}(1, 1)$$

$$p \sim \text{Beta}(1, 1).$$

A model allowing survival rate and detection to change at each capture occasion looks like the model above, but with ϕ and p also indexed by time: ϕ_t and p_t . Given the variety of sampling methods (and efforts associated with those methods) used in the long term monitoring effort, this is the most reasonable model, i.e. it allows the probability of detection to change between years.

Models were compared using the *deviance information criterion* (DIC) in the same manner as were models for abundance (section 5.2.2). *A priori*, a model with varying apparent survival rates and detection probabilities is the most reasonable given the variation in sampling methodologies and effort over the years. Model comparison in this case is done in deference to the convention of comparing a more complicated model to the most simple model.

5.2.4 Simulation study: abundance with uncatchable fish and varying detection probability

The ideal case for making inference about abundance is a year in which the upstream trap (occasion 1), electrofishing transect (occasion 2) and downstream trap (occasion 3) were each mark/recapture occasions with high probabilities of detection. Results from the closed-population models suggest that the upstream trap operates with approximately

50% efficiency (i.e., capturing 50% of the fish moving upstream), and the downstream trap with an efficiency that varies between approximately 10% and 50%. The variation is the result of the downstream trap being washed out or removed in years with high water, i.e., the trap missed a portion of the downstream migration post-spawning. We are also interested in changing the sampling design for the monitoring effort in the future, using only the upstream trap and electrofishing transect, and removing the downstream trap. Given the presence of uncatchable fish, we would like to understand how relying upon only the upstream trap record and the electrofishing record could potentially influence inference about abundance.

I investigated the influence on abundance estimates of varying the detection probability for the fish trap and eliminating the downstream trap using three scenarios (Table 2). Closed population models suggest detection probability for an well-operating trap is close to 50%, that detection probability drops when the trap is impaired due to high water. Reasonable distributions for detection probabilities are a Uniform(0.4, 0.6) for a well-operating trap, and a Uniform(0.05, 0.25) for an-impaired trap.

Scenario 1			Scenario 2			Scenario 3	
Occ 1	Occ 2	Occ 3	Occ 1	Occ 2	Occ 3	Occ 1	Occ 2
$p_{1,2,3} \sim U(0.4, 0.6)$			$p_{1,2} \sim U(0.4, 0.6)$		$p_3 \sim U(0.05, 0.25)$	$p_{1,2} \sim U(0.4, 0.6)$	

Table 2. Three scenarios were used to investigate the influence of detection probability (p) and a reduced number of occasions on abundance estimates. Occasion 1 (Occ 1) is the upstream fish trap, occasion 2 is the electrofishing transect, and occasion 3 is the downstream trap. For each realization of the simulation, a probability of detection (p_i) for each occasion ($i = 1, 2, 3$) was randomly drawn from an appropriate distribution.

The limited length of the electrofishing transect means that some portion of the population marked during the upstream migration has a zero percent chance of recapture. This

spatial restriction represents a potentially large problem for estimating abundance in a population assumed to be closed. Estimated detection probabilities for the electrofishing transect are likely biased low due to the limited spatial extent of the electrofishing section. Therefore, within each of the three scenarios, I investigated the influence of changing the proportion of the population available for recapture on abundance estimates, allowing the proportion to vary from 0.05, 0.25, 0.50, 0.75 to 0.95

Thus, the simulation study varied two separate factors to investigate their potential influence on abundance estimates: the probability of detection (either through reducing the probability of detection or reducing the number of occasions), and the proportion of fish available for recapture during the electrofishing transect.

For each realization within a scenario, I first fixed the size of the population at 1000 fish. I then generated capture histories for each occasion. For the fish trap (occasions 1 and 3), I randomly drew a probability of detection from the appropriate distribution (Table 2) and generated an encounter history for each individual. For the electrofishing transect (occasion 2 in all scenarios), I first specified the proportion of the population available for recapture, then generated a capture history for each available individual using a probability of detection randomly drawn from the appropriate distribution; unavailable individuals were automatically given a '0' (undetected). I assembled the capture history for each individual on each occasion, and produced a capture history for each scenario.

Using the capture history, I then ran the model M_t (from above) via JAGS to obtain the posterior distribution for abundance, using the posterior mean for abundance as a point estimate and quantiles (0.025 and 0.975) to express the uncertainty in the estimate. I then ran 1000 iterations of each scenario (1, 2, and 3) at each proportion of fish available for recapture (0.05, 0.25, 0.50, 0.75, 0.95).

6 Results

The results include minimum abundances based on fish counts, as well as abundances and apparent survival rates based on a mark-recapture design. Minimum abundances are provided for every year of the monitoring effort. Estimated abundances (from mark-recapture) are provided for the years in which the sampling methodology was appropriate (i.e. at least two capture/recapture occasions and unique identifiers given to each fish), and compared to minimum abundances. Finally, estimates of apparent survival are reported for the two intervals (1993 to 1996, 2010 to 2013) during which the sampling methodology allowed estimates (i.e., unique identifiers given in each consecutive year and at least one sampling occasion per year).

6.1 Minimum abundances based on counts

Minimum abundances (Table 3, Figure 4) represent the absolute minimum number of spawning grayling in Red Rock Creek each year and are based on the largest number of individual fish handled during each of the three sampling methods (upstream trap, electrofishing and downstream trap). For the years 1975, 1978 to 1993, and 2003 to 2010, minimum abundance estimates is only available based on the electrofishing transect. Caution is required in comparing these numbers across years due to the ephemeral nature of the spawning run and the timing of the traps and the electrofishing transect. It is unlikely that minimum abundances based on fish counts are appropriate for monitoring trends in the population size over time.

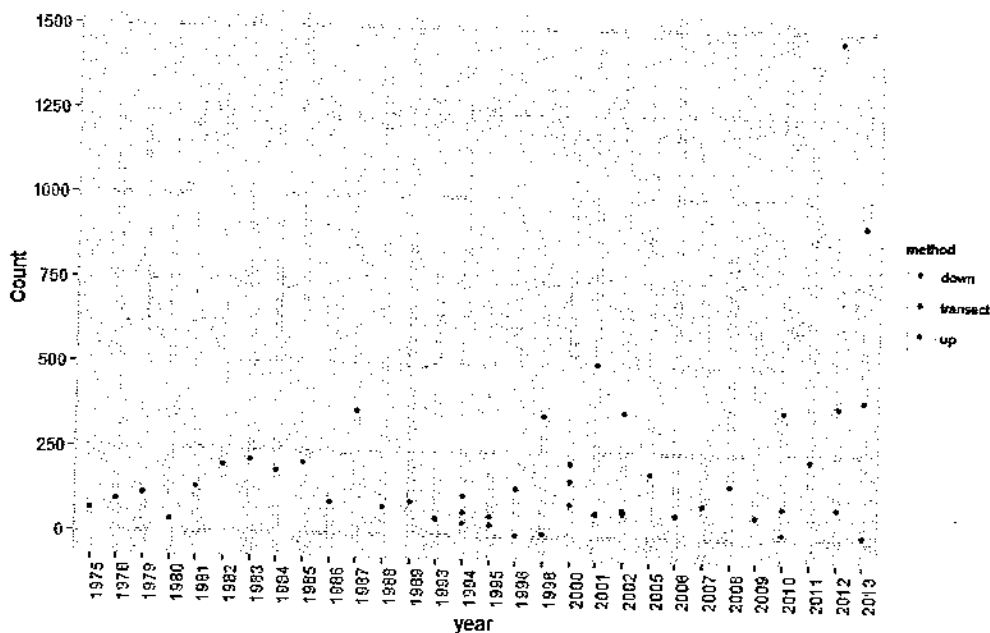


Figure 4. The largest count of fish for any sampling method in a given year is the minimum abundance. up=upstream trap, down=downstream trap, and transect=electrofishing transect.

6.2 Closed Population Abundance Estimates

Models (M_0 and M_t) were run with 5 chains and 10,000 iterations. Traceplots (example in Figure 5) suggested that 1000 iterations should be discarded for burn-in. \hat{R} values less than 1.01 were assumed to indicate adequate convergence. For two years, 2000 and 2001, the chains failed to converge in the MCMC algorithm due to the very small number of recaptures in each year.

For the years in which abundance estimates were possible (1994, 1995, 1998, 2002, 2010, 2012, and 2013), the relative symmetry of the approximate posterior distribution for the abundance (Figure 6) from the either model M_0 or M_t suggest the mean is an appropriate summary statistic for the posterior.

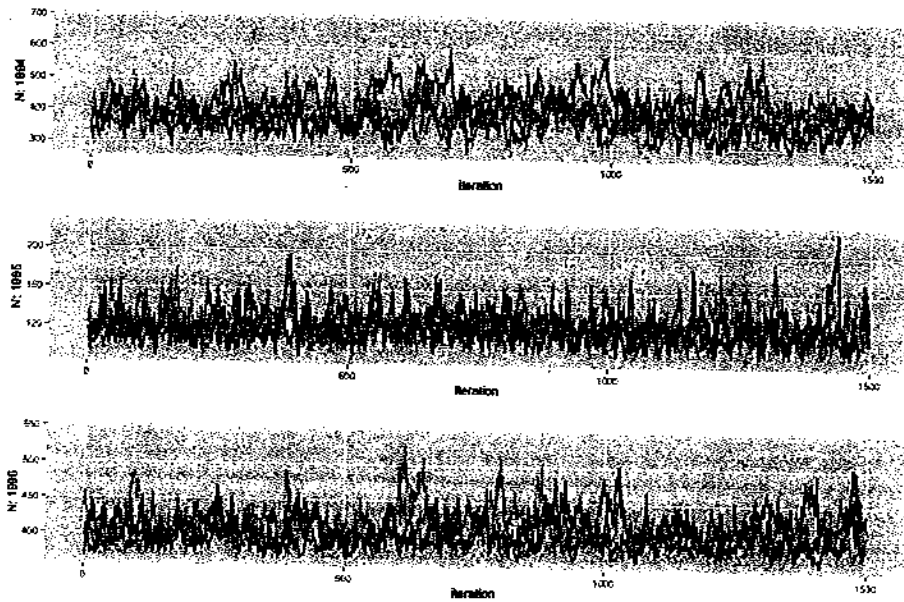


Figure 5. The appropriate period for burn-in was assessed using trace plots. Examples from 1994, 1995, and 1998 are included above.

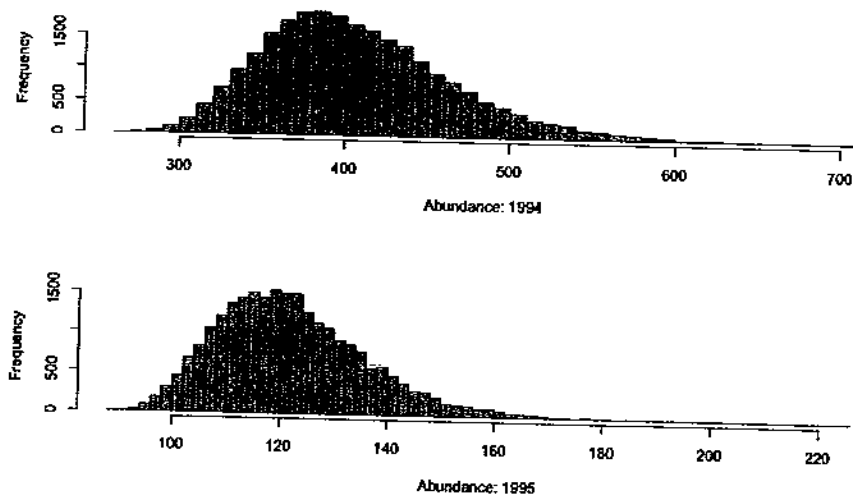


Figure 6. The relative symmetry of the approximate posterior distribution for abundance suggests the mean is an adequate summary statistic. Examples from 1994 and 1995 are included above.

year	method	count
1975	tran	61
1978	tran	91
1979	tran	112
1980	tran	35
1981	tran	131
1982	tran	196
1983	tran	214
1984	tran	182
1985	tran	205
1986	tran	90
1987	tran	360
1988	tran	80
1989	tran	95
1993	tran	46
1994	tran	35
1994	up	116
1995	up	54
1996	up	140
1998	up	354
2000	up	212
2001	tran	71
2002	tran	69
2005	tran	187
2006	tran	65
2007	tran	94
2008	tran	153
2009	tran	61
2010	tran	91
2010	up	372
2011	tran	229
2012	down	1466
2013	up	925

Table 3. Minimum abundances based on fish counts are the result of the electrofishing transect ('tran'), upstream trap ('up'), or downstream trap ('down').

Estimated abundances vary greatly between years (4) from 122 in 1995 (95% CI: 101, 154) to 2535 in 2012 (95% CI: 2509 to 2545). Given the variety of sampling methods and efforts, I *a priori* expected the data to support model M_t in each year. However, in three out of the seven years (1995, 2002 and 2010) for which abundance estimates were available, DIC results (Table 4) suggest that the model with constant detection probability (M_0) is more supported by the data. Details of model selection in those cases is discussed below.

Year	Model	DIC	Estimate and 95% CI	Scope of Inference
1994	M_0	3539.6	518 (391, 698)	4/28-7/15
	M_t	3116.3	407 (317,536)	
1995	M_0	829.4	122 (101,154)	5/4-8/5
	M_t	832.9	121 (100, 152)	
1998	M_0	8043.7	962 (765,1254)	4/22-6/29
	M_t	4607.7	411 (377,463)	
2002	M_0	2255.0	1251 (1121,1305)	4/25-6/30
	M_t	2541.9	1230 (1060,1304)	
2010	M_0	3692.4	1285 (1100,1380)	5/3-6/15
	M_t	11205.0	593 (481,760)	
2012	M_0	8110.9	2540 (2525,2545)	4/23-6/14
	M_t	6939.4	2535 (2509,2545)	
2013	M_0	7539.0	1145 (1085,1215)	4/16-5/22
	M_t	4999.4	934 (910,971)	

Table 4. Abundance estimates based upon a closed-population model of capture histories suggest the size of the population of spawning grayling above the trap varies substantially between years. Model comparison results are included to illustrate not only the top model, but also both the occasional equivocal comparison (e.g. 1995) and to illustrate the importance of considering temporal heterogeneity in detection probability.

Hereafter, I report the results from the top model for each year (Figure 7).

Though occasionally regarded as a nuisance parameter in mark-recapture studies, the probability of detection in this study is valuable for both informing us about trap efficiency and potentially explaining why, in some years, the expectation for M_t to be the best model is violated.

6.2.1 1994, 3 occasions (upstream trap, electrofishing, downstream trap)

In 1994, all three sampling methods were available (upstream trap, electrofishing transect and downstream trap). For model M_t , the posterior mean for abundance was 413 (322 to 547) individuals. The posterior means for time-dependent detection probabilities were 0.29 (0.21,0.38) for the upstream trap, 0.02 (0.01, 0.04) for electrofishing and 0.21 (0.15, 0.28) for the downstream trap.

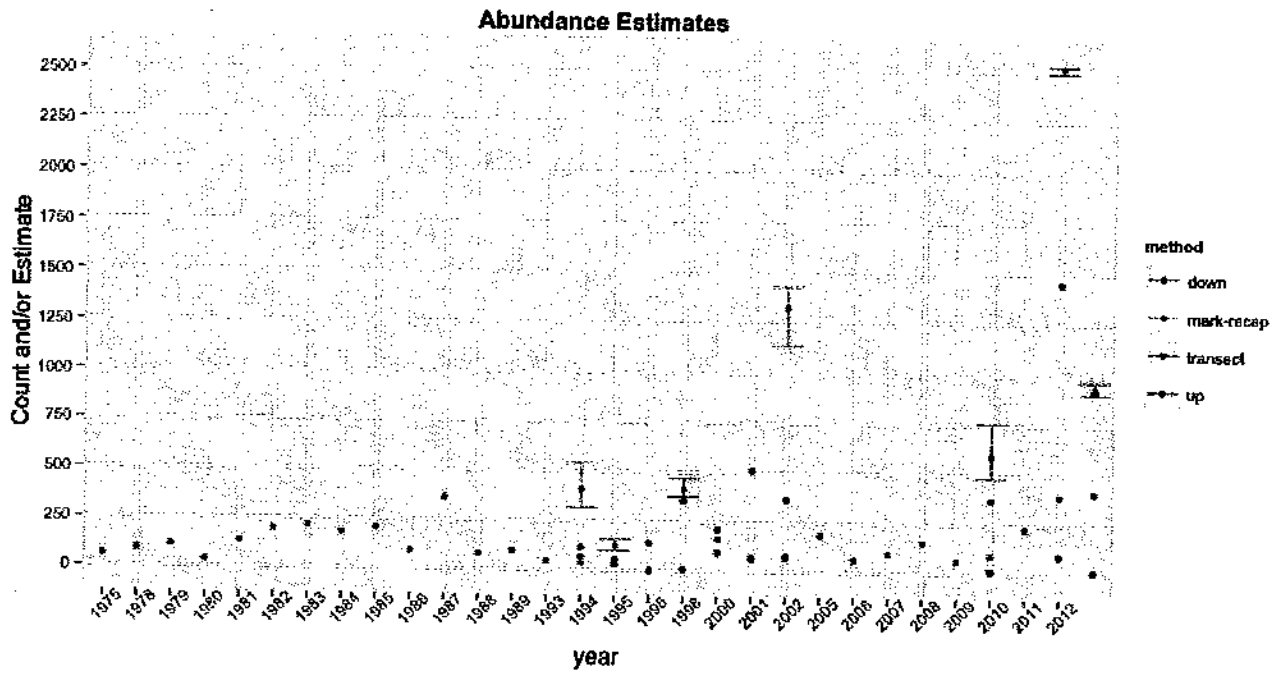


Figure 7. Minimum abundance and estimated abundance highlight the weak correlation between minimum abundance and abundance estimates based on mark-recapture (down=downstream trap, up=upstream trap, transect=electrofishing transect, mark-recap=mark recapture estimate).

6.2.2 1995, 2 occasions (upstream trap, downstream trap)

Model comparison results for this year are equivocal (Table 4). For model M_0 , the posterior mean for the distribution for abundance was 122 (100, 155), and the mean of the constant detection probability, p , was 0.45 (0.34, 0.57). For model M_t the posterior mean for abundance was 121 (100 to 152) individuals. The posterior means for the time-dependent detection probabilities were 0.46 (0.33, 0.59) for the upstream trap and 0.45 (0.33, 0.59) for the downstream trap. The similarity in the estimates of abundances and detection probabilities for the two models explain why the additional complexity intro-

duced with temporal heterogeneity (differences in trap efficiency) is not favored with a DIC comparison.

6.2.3 1998, 2 occasions (upstream trap, downstream trap)

For model M_t the posterior mean for abundance was 411 (376 to 467) individuals. The posterior means for the time-dependent detection probabilities were 0.86 (0.75, 0.94) for the upstream trap and 0.12 (0.09, 0.16) for the downstream trap. High water and structural problems in 1998 dramatically reduced trapping efficiency later in the season.

6.2.4 2002, 2 occasions (upstream trap, downstream trap)

For model M_0 , the posterior mean for abundance was 1251 (1121, 1305), and the posterior mean for the constant detection probability, p , was 0.18 (0.16, 0.22).

6.2.5 2010, 2 occasions (upstream trap, downstream trap)

This year saw a dramatically reduced downstream trap detection probability due to the breach and subsequent removal of the trap just as large numbers of grayling were starting to migrate downstream. For that reason, model M_0 is not at all appropriate. For model M_t , the posterior mean for abundance was 593 (481, 760). The posterior mean for the detection probability of the upstream trap was 0.62 (0.47, 0.76), and 0.07 (0.04, 0.09 for the downstream trap).

6.2.6 2012, 3 occasions (upstream trap, electrofishing, downstream trap)

For model M_t the mean for the posterior distribution of abundance was 2536 (2510 to 2545) individuals. The posterior means for the time-dependent detection probabilities were 0.13

(0.12,0.14) for the upstream trap, 0.07 (0.06, 0.08) for the electrofishing transect, and 0.46 (0.44, 0.48) for the downstream trap.

6.2.7 2013, 3 occasions (upstream trap, electrofishing, downstream trap)

For model M_t the posterior mean for abundance was 1068 (1031 to 1109) individuals. The posterior means for the time-dependent detection probabilities were 0.82 (0.78,0.83) for the upstream trap, 0.36 (0.33, 0.37) for the electrofishing transect, and 0.03 (0.02, 0.04) for the downstream trap.

6.3 Apparent Survival Estimates

For two time periods (1993 to 1996, 2010 to 2013) two models were run assuming constant survival and detection probability between years, and allowing for year-specific apparent survival and detection. Note apparent survival encompasses several processes discussed earlier including the probability of survival between years, the probability that, conditional upon survival an individual returns to spawn above the trap, and that the return is timed to coincide with trap operation. Similar to the estimation of abundances in the previous section, traceplots suggested that 1000 iterations should be discarded for burn-in. \hat{R} values less than 1.01 were assumed to indicate adequate convergence. The relative symmetry of the approximate posterior distributions suggest the mean is an adequate summary statistic.

Model comparison is less guided by practical realities in survival estimates than in abundance estimates, largely due to relative ignorance about the main drivers for apparent survival from year to year when compared to the well-characterized and obvious problems in detection probabilities. A simple DIC comparison approach suggests that constant survival and detection is the best model for both time periods (Table 5 and Table 6).

Model	DIC	1994	1995	1996
ϕ, p	299.6	$p = 0.25$ (.12, .46), $\phi = 0.41$ (0.24, 0.66)		
ϕ_t, p_t	325.1	$p = 0.15$ (.05, .28), $\phi = 0.87$ (0.60, 0.99)	$p = 0.82$ (0.49, 0.99), $\phi = 0.11$ (0.07, 0.18)	$p = 0.45$ (0.14, 0.95), $\phi = 0.44$ (0.13, 0.95)

Table 5. Apparent survival and detection probability estimates (mean of the approximate posterior distribution and 95% CI) for 1993 to 1996.

However, practical differences in the fish trap and electrofishing methodologies (including both timing and effort) suggested *a priori* that a model allowing for varying apparent survival and detection probabilities makes the most practical sense. In contradiction to a simple DIC comparison, I subsequently report the results from the year-specific apparent survival and detection probability due to the fact that the model makes the most practical sense.

6.3.1 1993 to 1996

For the model with year-specific survival and detection, the posterior mean for survival from 1993 to 1994 was 0.87 (0.59, 0.99), from 1994 to 1995 was 0.11 (0.07, 0.19), and from 1995 to 1996 was 0.46 (0.13, 0.95). Detection probabilities were similarly varied; 1994 was 0.15 (0.06, 0.28), 1995 was 0.81 (0.46, 0.99) and 1996 was 0.44 (0.13, 0.93).

6.3.2 2010 to 2013

This interval is problematic due to the approximately 1000 fish that were handled without being assigned unique identification tags in 2012. The resultant, artificial, decrease in trap efficiency for this time period suggests a model with time-varying detection probability again makes the most practical sense.

Modeling separate survival and detection probability yields posterior means for apparent survival probabilities of 0.86 (0.65, 0.94) from 2010 to 2011, 0.31 (0.23, 0.34) from

Model	DIC	2011	2012	2013
ϕ, p	1436.7	$p = 0.21 (.16, .27), \phi = 0.63 (0.53, 0.74)$		
ϕ_t, p_t	3115.1	$p = 0.06 (.03, .07),$ $\phi = 0.86 (0.65, 0.94)$	$p = 0.43 (0.30, 0.47),$ $\phi = 0.31 (0.23, 0.34)$	$p = 0.45 (0.18, 0.97),$ $\phi = 0.52 (0.18, 0.74)$

Table 6. Apparent survival and detection probability estimates (mean of the approximate posterior distribution and 95% CI) for 2010 to 2013.

2011 to 2012 and 0.52 (0.18, 0.74) from 2012 to 2013, and detection probabilities of 0.06 (0.03, 0.07) in 2011, 0.43 (0.30, 0.47) in 2012 and 0.45 (0.18, 0.97) in 2013.

6.4 Simulation study

I used simulations to investigate the potential effect of the spatial restriction of the electrofishing section, *i.e.* some unknown proportion of fish known to be upstream of the fish trap are unavailable for recapture, and to investigate how abundance estimates would change if we removed the fish trap and relied only upon the upstream trap and electrofishing section (Figure 8).

The results suggest at low proportions of the population available for recapture, abundance estimates for all three simulations are comparatively much more variable than those estimates at higher proportions. Unsurprisingly, the two-occasion study has higher variation than either of the three occasion simulations, though the point estimates are roughly comparable, with the ‘truth’ set as $N=1000$ individuals.

7 Discussion

The monitoring effort over the last 38 years has produced a legacy data set that is an amalgamation of methodologies and efforts, and as a result inference to the changing population of grayling over the years is problematic. The inference about abundance

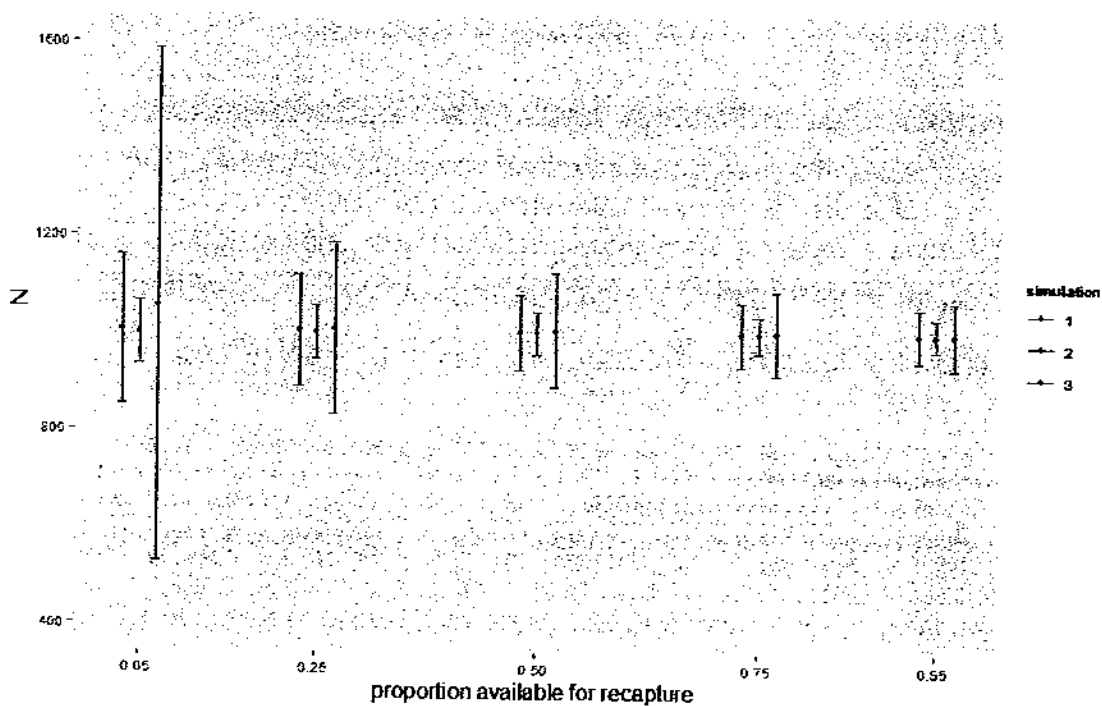


Figure 8. Posterior means and 95% confidence intervals for abundance estimates in the simulation study suggest that at high proportions of the population available for recapture, estimates from scenarios 2 and 3 are close to those from the ideal case, scenario 1. Simulation scenario 1 was a three occasion study in which every occasion had a detection probability drawn from a *Uniform*(0.40, 0.60) distribution. Scenario 2 was a three occasion study in which the first two occasions had detection probabilities drawn from a *Uniform*(0.40, 0.60) distribution, and the last occasion had a detection probability drawn from a *Uniform*(0.05, 0.25) distribution. Scenario 3 was a two occasion study in which each occasion had a detection probability drawn from a *Uniform*(0.40, 0.60) distribution.

and apparent survival rates produced through this work are the best effort to extract information using the available data; the problems encountered in the analysis and then partially quantified through simulations should help to guide future monitoring efforts.

7.1 Abundance Estimation

Though abundance estimates for individual years are comparatively straightforward to produce, it is problematic to compare inter-annual abundance estimates given the nature of the population under study and the varied sampling methodologies and efforts used to monitor them. We are monitoring a spatially ephemeral population, and abundance estimates in each year are constrained to those days during which monitoring was active. The length and timing of active monitoring is influenced by abiotic factors such as temperature and water flow. Compounding the difficulty is the lack of a lengthy time series with which to compare estimates, i.e. the intermittent sampling effort has produced two intervals of four consecutive years as its longest interval. Finally, the degree to which the abundance of the spawning population is coupled to the population of grayling in Red Rock Lake is unknown. Therefore, extreme caution should be used when drawing any conclusions regarding the population trend.

This work has provided a frame of reference for abundance estimates, however. Minimum abundances based on counts (Figure 7), correlate only weakly with abundance estimates from the mark-recapture design, suggesting the former should be used with great caution if making conclusions about population trends.

It is unknown how the fluctuations reflect population dynamics or year-specific abiotic factors that influence the timing and size of the spawning run such as water temperature and discharge or simply differences in sampling.

7.2 Apparent Survival Estimation

Guided by the practical realities of variations in sampling methodology and efforts, the most reasonable model is one in which apparent survival and detection are allowed to

vary between years. The estimated apparent survival is highly variable between years for both intervals (1993 to 1996 and 2010 to 2013), as is the probability of detection on each occasion. The latter is a reasonable conclusion given the variation in sampling methods and efforts over the years. The variation in apparent survival is also reasonable, considering that this is apparent, and not true, survival. Apparent survival is the probability that the individual survives the year, returns to spawn, and that return is timed to coincide with the trap monitoring effort. This uncertainty is further compounded by breeding site fidelity for Arctic grayling, which is unknown in this system. If breeding site fidelity is low, and grayling spawn below the fish trap in some years, it further reduces estimates of the apparent survival.

Conclusions based on the 2010-2013 interval will continue to be hampered by the approximately 1000 non-tagged fish handled in 2012, though reasonable estimates based on hypothetical and reasonable capture histories suggest that overall survival in that period was in the neighborhood of 0.60.

7.3 Simulation Study

Encouragingly, when the proportion of the population available for recapture during the electrofishing transect gets close to 0.50 the abundance estimates and associated variation are roughly comparable for all three simulation scenarios. The two occasion study (upstream trap and electrofishing transect) yield estimates that are quite close to the three occasion study with a very low detection probability at the third occasion, and not grossly different than the ideal three occasion study. Under the structure of the model, this suggests that we can remove the downstream trap from the sampling design and still be within a few hundred fish of the estimate based on three occasions.

A limitation of the simulation study is the assumption that fish are evenly distributed

in the stream. Though abundance estimates resulting from varying proportions of fish available for recapture during the electrofishing transect are compensated for by artificially depressing the detection probability, the model still assumes that those fish available for recapture are a random sample from the larger population of fish spawning above the trap. If breeding site fidelity is high for individual spawning grayling, this model misses an important source of heterogeneity in detection probability, and the model with individual heterogeneity (M_h) is applicable in this case. Not taking individual heterogeneity into account artificially depresses detection probability; the results from the simulation study suggest this lowered detection probability increases the uncertainty in abundance estimates.

8 Future Work

8.1 Age-specific Survival

Several years in the legacy data set have scale ages available for individual fish, which should allow for an age-length key to be constructed and then applied to fish caught in years lacking ages. Once the key is applied to individuals, age-specific apparent survival rates can be estimated. We would expect survival to change for different age classes of fish, and this modeling approach can be extended to examine survival for specific cohorts of grayling greater than or equal to the spawning age.

8.2 Simulations for Spatial Heterogeneity in Distribution

The spatial distribution of Arctic grayling upstream of the fish trap is unknown, e.g. they could be distributed roughly uniformly upstream, grouped in pools along the stream,

massed near the fish trap, etc. A set of simulations should be run that incorporate different spatial distributions, sampling methodologies and detection probabilities to quantify the degree to which abundance, survival and detection estimates vary.

8.3 Revised Sampling Design

We changed the sampling design for 2013 so that the entire section of tributary upstream from the fish trap will be electrofished. Each subsection of the electrofishing transect (delineated by convenience) will be geographically identified to provide at least some information on the spatial distribution of grayling. I can then use that record and compare it to 2010 through 2012 and have an estimate for how I should inflate (or deflate) capture numbers to account for the spatial limitations of the previous transects.

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11 Appendix A: Fish counts through trap

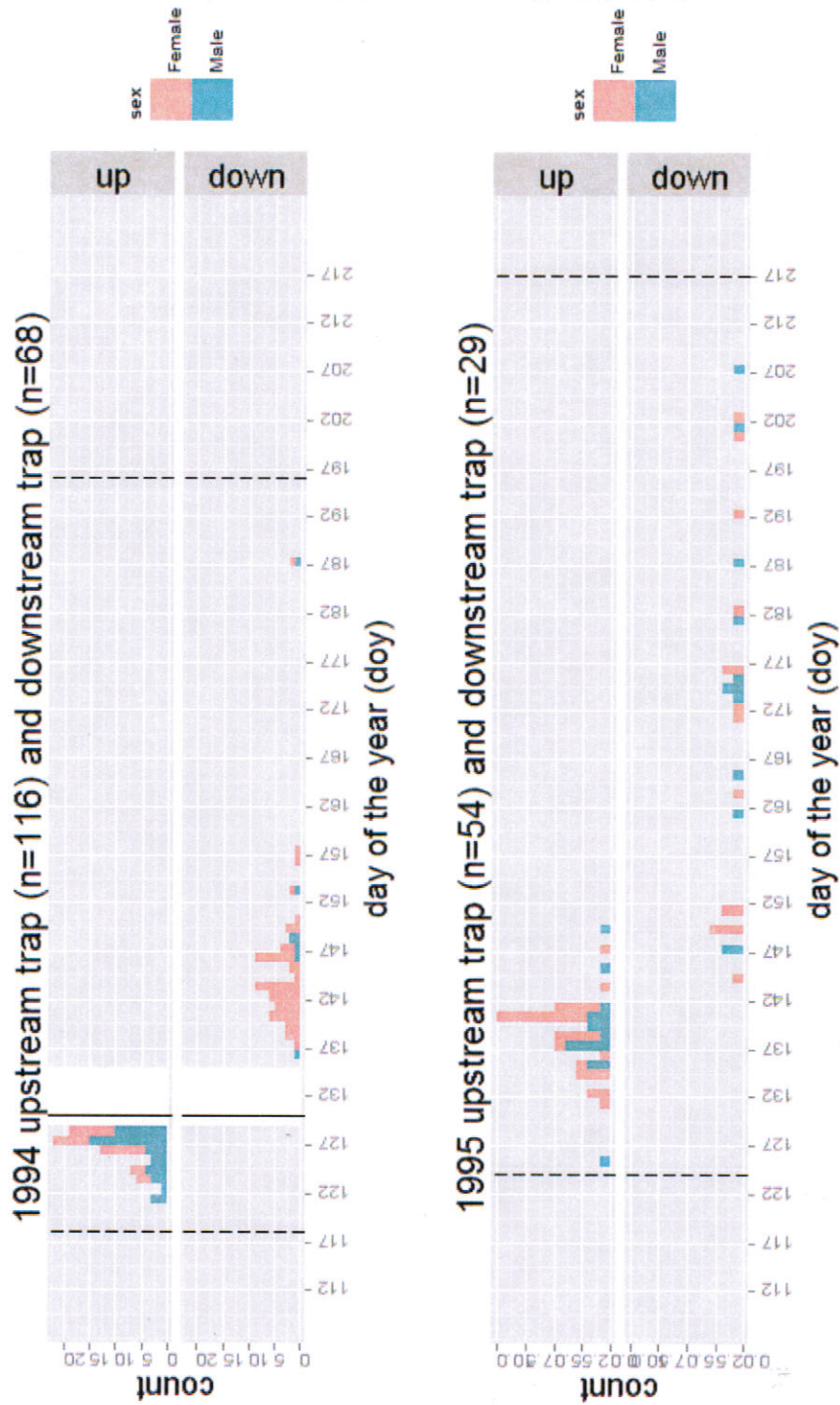


Figure 9. Counts of fish in the traps by day of the year (doy), segregated trap and sex. Dotted lines bracket the installation and removal of the trap. Solid line indicates the day of an electrofishing transect. White areas indicate periods in which the trap was blown out due to high water, removed or in some way compromised.

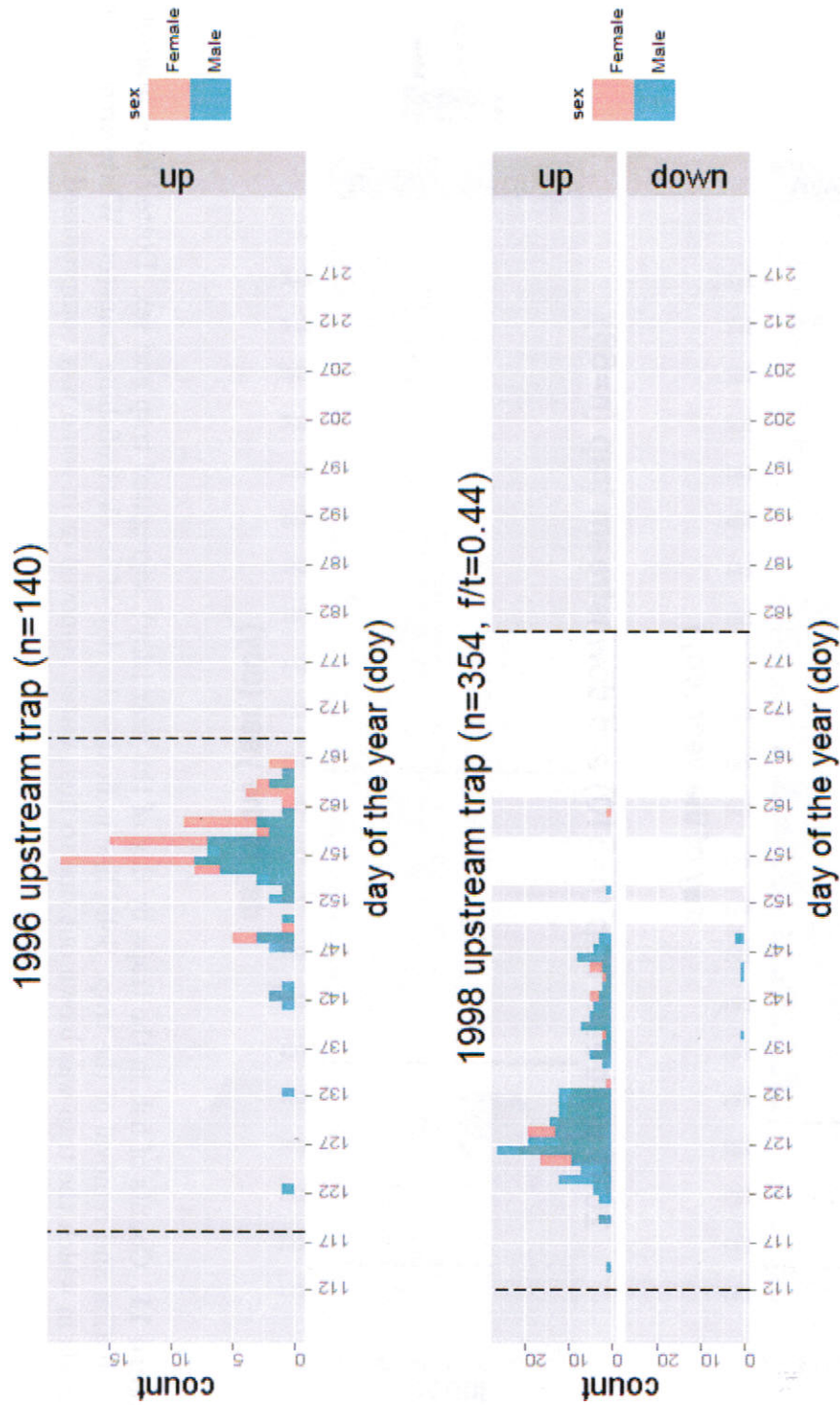


Figure 10. Counts of fish in the traps by day of the year (doy), segregated trap and sex. Dotted lines bracket the installation and removal of the trap. Solid line indicates the day of an electrofishing transect. White areas indicate periods in which the trap was blown out due to high water, removed or in some way compromised.

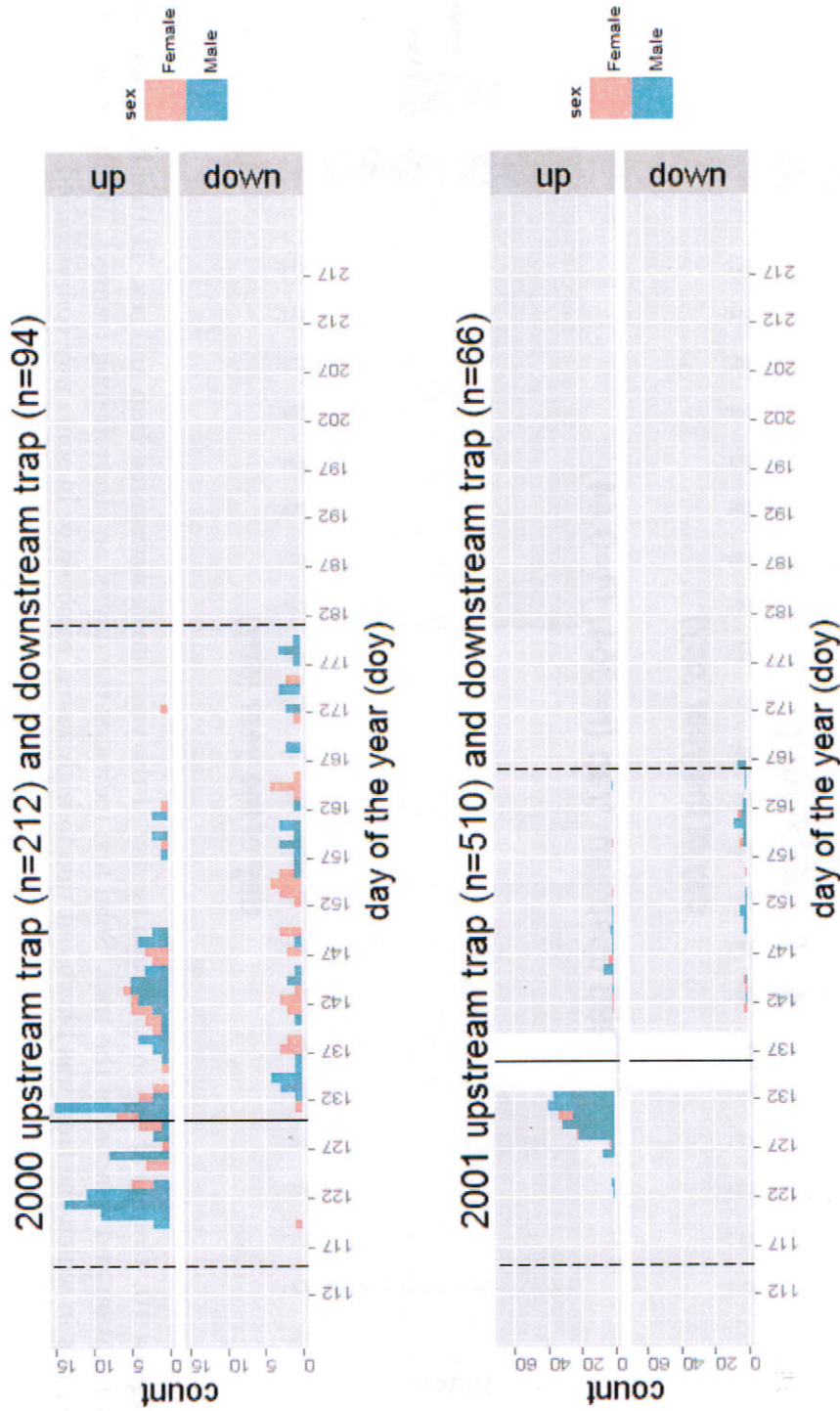


Figure 11. Counts of fish in the traps by day of the year (doy), segregated trap and sex. Dotted lines bracket the installation and removal of the trap. Solid line indicates the day of an electrofishing transect. White areas indicate periods in which the trap was blown out due to high water, removed or in some way compromised.

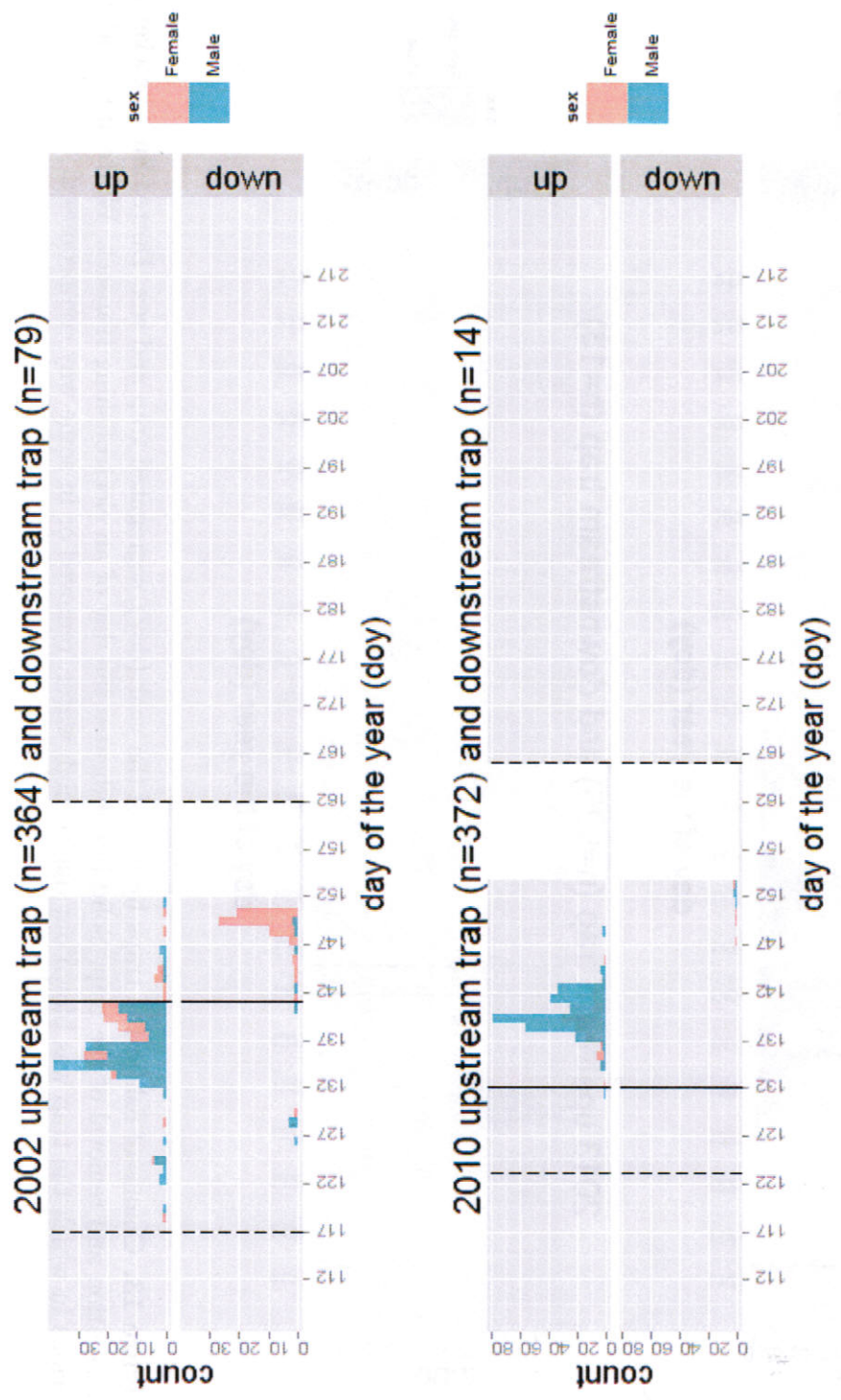


Figure 12. Counts of fish in the traps by day of the year (doy), segregated trap and sex. Dotted lines bracket the installation and removal of the trap. Solid line indicates the day of an electrofishing transect. White areas indicate periods in which the trap was blown out due to high water, removed or in some way compromised.

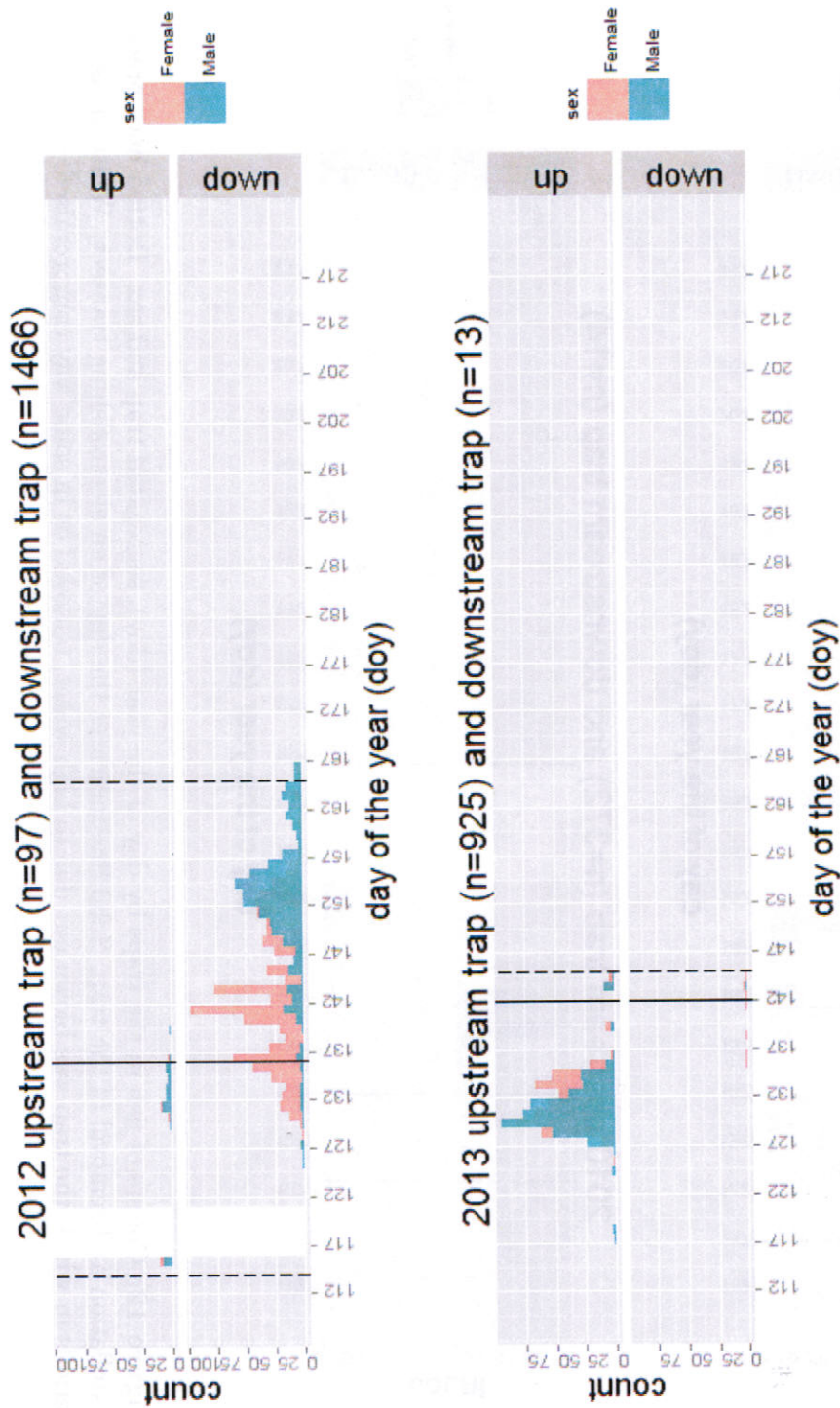


Figure 13. Counts of fish in the traps by day of the year (doy), segregated trap and sex. Dotted lines bracket the installation and removal of the trap. Solid line indicates the day of an electrofishing transect. White areas indicate periods in which the trap was blown out due to high water, removed or in some way compromised.