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Variability and Asynchrony in Salmon Returns: Implications for Monitoring and Ecosystem Services

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Abstract

Variability and Asynchrony in Salmon Returns: Implications for Monitoring and Ecosystem Services

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Pacific salmon are well-known for their unique life-history characteristics, complex population structures, and the wide range of ecosystem services they provide. Variability in life-history characteristics across and within species, along with their tendency to return to their natal sites, leads to phenotypically distinct populations that create portfolios of populations within watersheds. Pacific salmon are important for supporting valuable fisheries and for supporting key ecosystem processes in the marine and freshwater environment. Alaskan sockeye salmon populations display overall population stability despite large commercial harvests, a characteristic that has been attributed to their intact population complexity. Those fish that are not captured by the commercial fishery support key ecosystem processes in freshwater environments. This yearly, pulsed, resource subsidy provides a reliable source of food and

nutrients to the watersheds where sockeye salmon spawn and die.

These complex populations may pose challenges for management due to difficulties separating the contributions of individual populations or habitats to the overall population complex (or portfolio). In Chapter 1 we used abundance data for sockeye salmon (*Oncorhynchus nerka*) spawning in a set of eight streams in the Wood River watershed, southwest Alaska, to demonstrate how natural patterns of variability affect the ability of fixed assessment windows to characterize the contribution of an individual spawning population to the entire portfolio. Additionally, simulated data are used to explore how different levels of synchrony and autocorrelation affect the ability of monitoring schemes to estimate the contributions of individual populations to a portfolio. We find that the ability of fixed assessment windows to characterize a population’s contribution to a portfolio is distinctly limited; asynchronous or independent dynamics among populations in a portfolio, and the presence of autocorrelation that creates slow changes in productivity, weaken the ability to characterize a stream's potential contribution to a portfolio. These results suggest that the structure of complex portfolios, and the presence of directional changes in productivity within individual populations, need to be taken into account when carrying out environmental risk assessments that aim to measure the contribution of an individual population or piece of habitat to dynamics observed at broader spatial and temporal scales.

The reliable yearly pulse of marine-derived nutrients, in the form of spawning salmon, provides inland freshwater habitats with food and nutrients in the form of live fish, their gametes, and their carcasses. The highest quality food is provided by live fish and their eggs, which are important food sources for resident fish, bears, and birds, are only available for a short period. While the effects of this specific resource pulse are widely appreciated, little attention has been paid to the role that timing plays in conferring benefits to consumers, and previous research has mainly focused on biomass as the main control on the magnitude of effects. In Chapter 2 we used multiple in-stream counts of adult sockeye salmon abundance within the spawning season, and tagging data to estimate in-stream life span, to estimate how the amount of time that consumers have access to live salmon as a food resource is related to the adult spawner density in an individual stream. Our results demonstrate that duration of salmon availability as a food source is non-linearly related to escapement; across 3 orders of magnitude of spawner abundance, salmon were available to predators from about 2 weeks to about 5 weeks. This saturating relationship indicates that higher escapement values may not translate to proportionally higher benefits for consumers when these benefits are available during a fleeting window of opportunity. This result demonstrates that ecosystem based fisheries management (EBFM) of anadromous salmon should assume that benefits inferred to consumers are inherently time-mediated, and the numerical benefits of increased salmon density will not be straight-forward to estimate. Conservation strategies to maintain a range of spawn timing across watersheds may be the most successful for maintaining the importance of salmon subsidies in watersheds.

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Chapter 1. The effects of variability and synchrony in assessing contributions of individual streams to habitat portfolios of river basins

1.1 Abstract

Despite complex population portfolios being identified as important sources of stability and resilience, the structure of such stock complexes is often not considered in monitoring schemes to inform environmental impact assessments. The use of “index” or “indicator” streams, and the use of short assessment windows to make broad claims about the relative importance of a piece of habitat or population within a portfolio, assume that regional populations are highly synchronous and that mean abundance is stable through time. The lack of synchrony among populations and changes in population productivity over time render these assumptions fundamentally flawed. In this study we used abundance data for sockeye salmon (*Oncorhynchus nerka*) spawning in a set of eight streams in the Wood River watershed, southwest Alaska, to demonstrate how natural patterns of variability affect the ability of fixed assessment windows to characterize the contribution of an individual spawning population to the entire portfolio. Additionally, simulated data are used to demonstrate how different levels of synchrony and autocorrelation affect the ability of monitoring schemes to estimate the contributions of individual populations to a portfolio. We find that the ability of fixed assessment windows to characterize a population’s contribution to a portfolio is distinctly limited; asynchronous or independent dynamics among populations in a portfolio, and the presence of autocorrelation that creates slow changes in productivity, weaken the ability to characterize a stream's potential contribution to a portfolio. These results suggest that the structure of complex portfolios, and the presence of directional changes in productivity within individual populations, need to be taken

into account when carrying out environmental risk assessments that aim to measure the contribution of an individual population or piece of habitat to overall dynamics. Typical risk assessments that depend on short monitoring periods are likely to vastly underestimate the potential long-term value of any specific habitat, and the population it supports, as a piece of a multi-population portfolio.

1.2 Introduction

A long-held theme in ecology has focused on how biological diversity may contribute to stable and resilient ecosystems (Peterson et al. 1998, Chapin et al. 2000, Loreau et al. 2001, Hooper et al. 2005). Complex communities are likely to display diverse reactions to environmental variation, resulting in independent dynamics of the species that comprise a community (Elmqvist et al. 2003). This asynchrony may lead to more temporally stable ecosystem functions and to more consistent delivery of ecosystem services that integrate across this response diversity. Such “portfolio effects” dampen community variance in a manner analogous to a diverse set of investments in financial portfolios (Figge 2004). Generally, when ecologists discuss the relationship between stability and diversity, they are referring to species diversity, though the phenomenon also operates among populations of the same species (Schindler et al. 2015). Pacific salmon (*Oncorhynchus spp*.) display extensive life history variability *within* species that has stabilizing effects on their populations, and to the ecosystems in which they play an important role (Hilborn et al. 2003, Schindler et al. 2010)

A primary life history characteristic that leads to this stabilizing complexity in Pacific salmon is their tendency to return to natal sites to spawn. These unique spawning sites are geomorphically and ecologically diverse, including rivers, lakes, and streams. Habitat complexity and reproductive isolation lead to individual spawning populations that have evolved distinct phenotypic variations among sites (Taylor 1991, Dittman and Quinn 1996). In watersheds with a diverse set of spawning habitats, and a diverse set of spawning populations, these traits lead to a *stock complex* of populations, which we refer to as a portfolio. In Bristol Bay, Alaska, the biocomplexity of sockeye salmon (*Oncorhynchus nerka*) in a heterogeneous landscape supports a sustainable and highly productive fishery (Hilborn et al. 2003). Here, locally adapted populations fluctuate somewhat independently, likely responding in different ways to prevailing environmental conditions, buffering the overall fishery from intense variability (Rogers and Schindler 2008, Schindler et al. 2009, 2010). This emergent temporal stability supports not only a multi-million dollar commercial fishery, but also the reliable upstream flow of marine-derived nutrients and energy that become important inputs to terrestrial and freshwater ecosystems (Naiman et al. 2002, Gende et al. 2002, Schindler et al. 2003). Spawning salmon provide an important food source for terrestrial and avian consumers such as bears and eagles, and their gametes an important food item for resident fish, like trout and grayling. These species provide important ecosystem services in the form of a valuable eco-tourism industry, for either fishing or wildlife viewing.

The biocomplexity that buffers the Bristol Bay sockeye salmon stock complex is maintained by a diverse set of spawning and rearing habitats and their associated locally-adapted populations. Maintaining this reliable production of sockeye each year should be an important goal for fisheries managers. Furthermore, Alaskan communities that rely heavily on fisheries or eco-tourism, which is supported indirectly by healthy spawning populations, have a vested interest in maintaining this diverse portfolio. Because the Bristol Bay Sockeye fishery continues to be well-managed, the largest threats to this biocomplexity are likely development and climate change. Expanding development into this area, as well as potential mining or hydro-electricity projects, could threaten some component habitats that support this population portfolio. Maintaining this functional landscape and the ecosystem services it supports into the future will require understanding of how individual streams contribute to the overall complexity of the stock, and ensuring conservation of key habitats in the face of development or other drivers of environmental change.

To properly characterize the contribution of individual habitats to overall biocomplexity, it is important to have monitoring and assessment programs that provide an accurate representation of not only a population’s numerical contribution to the stock complex, but perhaps more importantly, its potential relative contribution over the long-term. Within a set of asynchronously fluctuating populations, a population occupying a specific habitat that is, on average, a low contributor to the stock complex could be particularly important to the aggregate in years when returns to other, out-of-sync, spawning sites happen to be low. Even sites that, on average, provide habitat to a small fraction of total returning spawning adults can be critical buffers in years when returns to other high productivity streams are uncharacteristically low. In a case where consumers integrate across this complex set of populations, whether they be fishermen or bears (Schindler et al. 2010, 2013), the potential fractional contribution of an individual population to the stock complex may be the relevant metric to assess the potential long-term importance of an individual piece of habitat to the overall ecosystem.

Environmental impact assessments of new development activities in watersheds make critical assumptions about how short-term surveys of indicator habitat sites characterize the landscape at broader spatial scales. In general, it is assumed that indicator sites accurately reflect the dynamics of similar populations in a region (i.e., that populations are highly correlated within a region), and that short-term assessments of populations provide accurate estimates of the long-term contributions of any given site to a watershed over the long term (i.e. that populations tend to vary around a stationary mean over time). Both of these assumptions are rarely tested in field situations because of the extensive data sets required to properly challenge them.

If an assessment monitors multiple populations, in order to characterize the relative importance of each site to the portfolio, it is important to understand how proportional contribution might vary over time. Proportional contributions will only remain constant in the extreme case where all sites are 100% correlated; showing perfect synchrony. Alternatively, proportional contributions will remain near-constant when populations tend to have the close to the same returns each year — they vary closely around a mean that does not change over time. However, past work has shown that salmon populations in this area tend to vary on decadal, or even centennial, time-scales — and that these low frequency fluctuations in abundance tend to be asynchronous (Rogers et al. 2013). These long-term shifts in productivity that play out over time scales much longer than typical assessments, are unlikely to be detected.

Challenging assumptions about synchrony among sites, and the stationarity of population mean abundances, is crucial before decisions are made based on monitoring data. In this paper we will investigate the following two questions:

1) How well can we estimate the *potential* contribution of an individual habitat or population to a portfolio?
2) How wrong can we be about the contribution of an individual habitat or population given a fixed assessment window?

We confront these questions with 51 years of abundance data for sockeye salmon spawning in the Wood River system of southwest Alaska. Additionally, we simulate population portfolios with different levels of synchrony and differing tendencies to display low frequency fluctuations in abundance (measured as temporal autocorrelation) to investigate how these characteristics affect our ability to estimate 1) population potential and 2) our potential error in estimating the contribution of an individual population to the portfolio over the long-term.

1.3 Methods

1.3.1 *Case study system*

The Wood River lake system is characterized by a complex mosaic of predominantly pristine habitat for spawning Pacific salmon, the most abundant, and commercially valuable being sockeye salmon (*Oncorhynchus nerka*). From June through August adult sockeye salmon travel to their natal sites throughout the freshwater environment to spawn and die. Sockeye spawn either on lake beaches, in rivers, or in small tributary streams. Despite variability in spawn timing across populations, within a population, the timing of spawning is remarkably consistent across years (Moore and Schindler 2010, Lisi et al. 2013). Beginning in 1946, the University of Washington Alaska Salmon Program has been monitoring many of these populations over varying numbers of years. For stream populations, the timing of peak spawning was identified after several years where multiple stream counts were carried out within a season. For eight stream populations in tributaries of Lake Aleknagik and Lake Nerka, annual in-stream counts at the peak of the spawning season have been taken continuously since 1963 (Rogers and Schindler 2008). The sum of peak live salmon counted in stream, and the number of salmon carcasses is used as an indicator of the total number of salmon returning to spawn in a given stream, a reasonable approach based on comparisons to years when streams were surveyed multiple times over the spawning season (Davis et al. 2015 in Prep). Although these eight streams make up a small fraction of the total adult salmon returning to the Wood River lake system, they represent about one third of the populations spawning in second to fourth order streams, and provide a long-term sample of the level of variability and synchrony seen in a portfolio of populations within a stock complex (Schindler et al. 2010).

1.3.2 *Simulated data*

We used stochastic simulations to explore how changes in the degree of synchrony among populations in a stock complex, and the amount of temporal autocorrelation in individual population time series of abundance, affect the ability to properly characterize the potential contributions of a single spawning habitat to an aggregate portfolio. We simulated time series of population portfolios with similar dynamics to those in our case study system, and also across a range of autocorrelation, and correlation structures, which determine levels of synchrony/asynchrony among populations. Data were simulated by first assigning means and variances to populations within portfolios by sampling from distributions closely mimicking those distributions seen for means and variances in the case study populations. These base population portfolios were then assigned autocorrelation values (each population in the portfolio was assigned the same level of autocorrelation) ranging from near-zero to near-one.

We generated different levels of synchrony among populations by specifying correlation matrices with different values on the off-diagonals: either perfect correlation (all ones), positive correlation (positive numbers between 0 and 1), no correlation (zeros), or negative correlation (most values below zero). Because correlation and variance-covariance matrices need to be positive semi-definite we randomly sampled off-diagonal values and then discard those correlation and variance-covariance matrices that did not meet this requirement. To increase our rate of finding positive semi-definite correlation and variance-covariance matrices with negative correlations (or asynchronous dynamics) we also simulated data where populations were split into two groups, where populations in one group were positively correlated with each other, and very negatively correlated with populations in the other group.

From these base portfolios and correlation matrices we calculate the variance-covariance matrix for each combination of synchrony level and base population. We use these variance-covariance matrices to draw the "structured" part of the time series from a multivariate normal distribution. We then used the function arima.sim in R's base statistics library to add autocorrelated noise to the multivariate normal draws (R Core Team 2014). To keep simulated counts positive, time series were simulated in log space, and transformed back to normal space.

After time series were generated, we measured the observed level of autocorrelation by fitting an autoregressive (AR1) model to each population, and estimating the mean across component populations. We also measured the "community-wide synchrony" across populations in a portfolio as described by Loreau and de Mazencourt (2008) as:

$$\rho_x = \frac{\sigma_{x\,T}^2}{\left(\sum_i \sigma_{x_i}\right)^2}$$

where $\sigma_{x\,T}^2$ is the variance of the aggregate population and σ_{x_i} is the standard deviation of the ith component population. This index measures the level of correlation across a set of populations with a value of zero describing perfect asynchrony, and a value of one indicating perfect synchrony. A value of 0.5 indicates an approximate average correlation of 0.5 between populations. For plots we have shown $1 - \rho_x$ which indicates the level of asynchrony.

We simulated 10,300 fifty-year time series – each with ten populations. These populations had measured synchrony indices spanning from 0.03 to 1.00. Measured average autocorrelation values (AR1 coefficients) of populations within portfolios ranged from -0.27 to 1.00. Negative autocorrelation values indicate that subsequent year's observations tend to be divergent from each other; a lower than average observation is likely to be followed by a higher than average observation.

We use the metric of population variability to characterize variability in proportional contribution, as described by Heath (2006) which varies between zero (least variable) to one (most variable):

$$PV = \frac{\sum^{z} D(z)}{C}$$

Where z is the set of pairwise comparisons within a time series and C is the total number of these pairs in a time series of length n:

$$C = \frac{n(n-1)}{2}$$

$$D(z) = \frac{|z_i - z_j|}{\max(z_i, z_j)}$$

For illustrative purposes we simulated portfolios of four populations over 20 years with varying levels of asynchrony and autocorrelation (Figures 1.1 and 1.2). For these plots means and variances were chosen arbitrarily. Figure 1.1 shows a population with AR1 coefficient of 0.3, which is close to the mean of AR1 values for our study populations (0.279). Populations A through D have the same means and variances, the only component changing are the correlation matrices. The resulting synchrony indices measured for populations A-D were 1, 0.70, 0.39, and 0.17, respectively.

Figure 1.2 uses the same arbitrary means and variances as those shown in Figure 1.1, with low positive correlations between populations in a portfolio (correlation values of 0.1), resulting in synchrony values similar to our case study portfolio (0.37,0.18,0.28, respectively). To demonstrate the effect of low-frequency variability in population dynamics, we simulated portfolios with component population with increasing levels of positive autocorrelation. Populations within the three sample portfolios were simulated with autocorrelation values of 0, 0.5, and 0.95, respectively. The resulting simulated portfolios have estimated mean AR1 coefficients for component populations of 0.05, 0.45, and 0.67, respectively.

1.3.3 *Contributions to a portfolio*

We use two metrics to assess the ability of assessments with given monitoring windows to characterize the importance of an individual population within a portfolio of populations. The first aims to characterize the ability to observe the *maximum* potential of a population over relatively long time periods. For this metric we calculate the probability of observing the 75th percentile of proportional contribution within a given assessment window. This is calculated by scanning through each possible monitoring start date and seeing whether the highest observed proportional contribution is within the 75th percentile of values observed over the entire time series. This metric captures how often the population has a return year where its returns are substantially higher than usual, or other populations are lower, or both – and therefore may act as an important buffer site. These types of years are likely to be ones where the stream may act as a buffer for low-return populations, stabilizing the portfolio as a whole.

The second metric assesses how wrong one can be in assessing the potential contributions of an individual population to the overall population portfolio. For a given monitoring window, we identify the time windows with the highest and lowest average proportional contribution. The metric which we call “maximum error” is simply the difference between these two values. This metric indicates how widely proportional contribution can vary within a stream depending on when in the time series you monitor it.

For our sockeye salmon case study data we calculated these metrics for all monitored streams over the 51 years of the study. For the simulated data we calculated the averages of these metrics across populations within each simulated portfolio. Noise in average values from simulated data was reduced for visualization using localized polynomial regression (LOESS) using the function LOESS in the base R stats package (Team 2015).

1.4 Results

Our simplest simulated portfolios demonstrate that the proportional contribution of an individual stream to a habitat portfolio can vary substantially through time depending on the level of synchrony among populations, and the level of autocorrelation within populations (Figures 1.1 and 1.2). When populations are perfectly correlated, the proportional contribution of a single population is consistent across time (Figure 1.1a). However, when populations are not perfectly correlated, the contribution of an individual population to the portfolio can vary widely across years (Figure 1.1b). This variability in contribution of an individual site increases as asynchrony among population increases (Figures 1.1b-1.1d).

Low frequency variability in population abundance, produced by positive autocorrelation in individual populations, can further increase variability in proportional contribution by creating non-stationary dynamics. Figure 1.2 shows populations with low positive correlations *between* populations, and increasing levels of positive autocorrelation *within* each population. This figure demonstrates that increasingly high positive autocorrelation can lead to wide fluctuations in proportional contributions. In Figure 1.2a we observe proportional contributions that appear to fluctuate around a fixed mean over time, where Figure 1.2b shows how low-frequency variability (measured as high autocorrelation) can lead to wide swings in proportional contributions. This nonstationarity over time violates the oft-made assumption that the measured proportional contribution seen in a fixed assessment window predicts the long-term contribution of a given site or population. These long, slow, changes in mean abundance, measured and simulated as positive autocorrelation, more often lead to extreme values in both abundance and proportional contribution of a single site or population. Despite having the same simulated variance level as in Figure 1.1, the populations with higher autocorrelation levels plotted in Figure 1.2 generally led to more extreme values.

1.4.1 *Case study system*

Across eight populations of sockeye salmon we observed a low level of correlation between populations in the portfolio, with overall community-wide synchrony measured at 0.35 (or asynchrony of 0.65). The average level of autocorrelation for these eight populations over 51 years was 0.279, and ranged from 0.099 at Lynx Creek to 0.581 at Happy Creek. Proportional contribution values were quite variable for every stream, with PV values ranging between 0.332 and 0.556. The ability to identify potential contributions of individual streams, measured as probability of seeing values in the 75th percentile of historical values, increased with the length of the assessment window (Figure 1.3b). For streams with high positive autocorrelation, like Happy Creek; characterized by low frequency swings in abundance, even after monitoring for 10 years there is only a 64% chance of observing a proportional contribution value in the 75th percentile of historical values (Figure 1.3). For streams with low autocorrelation, like Lynx Creek which tends to fluctuate around a fixed mean over time, the probability of observing the 75th percentile of the maximum proportional abundance in 10 years was 97%, indicating that that stream's potential is more easily detected in a short assessment window.

The maximum error seen between the highest and lowest average historical window decreased with longer assessment windows (Figure 1.3c). Three-year assessments could produce estimates of proportional contribution that underestimate the true value by up to 34%. In this most extreme case, at Happy Creek, the lowest three-year window produced an average proportional contribution of 2.7%, and the highest window yielded an estimate of 36.8% — over a 10 fold difference in the estimated contribution of the stream to the portfolio. At this same site, even with a 10 year assessment window, potential contribution could still be underestimated by 25% (minimum estimate=4.2%, maximum estimate=29.4%). In Lynx Creek, the stream with the lowest level of autocorrelation, the maximum error seen over 10 years is drastically lower, at just 4%. The average maximum errors across streams with 3, 5, and 10 year windows are 20, 16, and 13% respectively.

These results highlight that for those streams characterized by low frequency variability; observed as long, slow changes in abundance over time, and measured as high positive autocorrelation, it is very hard to characterize their potential contribution to a habitat portfolio, even with an assessment window of 10 consecutive years. Happy Creek is one population where there is an obvious directional trend, or perhaps a regime shift, underlying the observed population numbers. This draws important attention to populations that may be undergoing directional changes, and our limited ability to characterize the importance of these populations over short periods of assessment.

1.4.2 *Simulated data*

We found that variability in the proportional contribution of an individual stream to a habitat portfolio increased with both temporal autocorrelation and asynchrony (Figures 1.1, 1.2, 1.4). Additionally, these simulations showed that our ability to characterize a stream's potential and average proportional contribution depended on both the level of asynchrony among populations and the level of autocorrelation within each population. Figure 1.5 shows that the probability of observing the 75th percentile of historical proportional contributions decreases with increasing autocorrelation in the abundance time series. We found that high levels of autocorrelation led to more extreme values, which create anomalies in proportional contribution that are not often observed during 3-10 year assessment windows. However, there was no apparent effect of the level of asynchrony on the probability of seeing the proportional contributions in the 75th percentile of values (Figure 1.4).

The maximum error between assessment windows increased with both autocorrelation and asynchrony (Figure 1.6). This is likely the combined effect of asynchronous dynamics leading to increasingly variable proportional contribution values, and autocorrelation leading to more extreme values and directional changes in mean contribution to the portfolio. This result demonstrates that even with long assessment windows (i.e. 10 years) when levels of asynchrony or autocorrelation are high, it is possible to grossly underestimate the potential of a stream as a proportion of the total portfolio.

1.5 Discussion

The common use of “index” or “indicator” sites for populations with complex population structures assumes that dynamics of individual populations are highly synchronous. These methods are still used despite growing appreciation that the independent or asynchronous population dynamics that tend to characterize these populations provide stability (Rogers and Schindler 2008, Schindler et al. 2010). When component populations are anything but highly synchronous, an “index” set will not indicate anything but that single population’s dynamics; and should not be used as an indicator for the dynamics of the overall population.

Furthermore, the use of an “index” site does not take into account that the contribution of a given piece of habitat or population to overall dynamics depends heavily on the relationships between the dynamics of all populations comprising an overall habitat complex. Although complexity has been identified as an important component of resilient and stable communities, most assessments are unable to characterize the contribution that an individual population makes to the overall stability of a system, due to limited assessment of select sites. If maintaining the stability of a portfolio is the overarching goal of an assessment project, the importance of individual populations to the overall complexity must be considered. By characterizing how much of the portfolio is contributed by a component population, or how many individuals a given piece of habitat supports, we can form a better understanding of how each piece of a portfolio makes up the whole. While characterizing sites or populations by their proportional contribution to the overall stock is an important step towards recognizing the importance of individual populations, it is not without pitfalls.

Our results demonstrate that when individual populations within a portfolio are anything but very highly correlated, their proportional contribution to the portfolio can fluctuate widely over time. Therefore, interpreting assessment schemes that assume observed proportional contributions are reliable indicators for importance to the overall portfolio is fraught with difficulty. Results from this study show that it may be very unlikely to estimate values anywhere near a population's *potential* contribution, and it is possible to severely underestimate a population's average contribution over time. Our case study system included a population where there was more than a 10-fold difference in proportional contribution between the highest and lowest abundances in 3-year assessment windows. Additionally, even with an assessment window of 10 years, the probability of seeing a proportional contribution in the 75th percentile was still below 65% for this site. Depending on when assessment takes place, these fixed-window glimpses can give drastically different indications as to how important a single population is to a stock complex. Therefore, assuming that the proportional contribution of a given population is consistent across time is fundamentally flawed in a system characterized by asynchrony and directional changes in the underlying productivity of any individual piece of habitat.

Furthermore, variability is often viewed as "white noise" (zero mean, constant variance) when it is well known that it is the structure of the variability in populations within a portfolio that define their dynamics and stability. This study sheds light on the importance of identifying "red noise" or temporal autocorrelation – which may indicate trends or regime shifts – in individual streams. Given the accumulating evidence that salmon stocks are often characterized by regime shifts (Hare & Manuta, 2009; Mantua et al. 1997; Rogers et al., 2013), our results suggest that nearly all short-term assessment studies will be likely to vastly underestimate the potential contribution of a given population to a portfolio. Recognizing that mean productivity of a given site or population may be changing over time is vital if management decisions are to be taken that are based on the value of that component of the habitat portfolio.

The largest challenges for characterizing the importance of a stream in our case study were found in streams with clear “red noise” which display distinct shifts in productivity part-way through the time series (e.g., in Happy Creek). Assessments before or after this shift gives completely different pictures of the importance of this stream. Furthermore, Happy Creek shows the highest level of autocorrelation across years, which means that the observations within a short assessment window are likely quite similar, so would appear to be stable within the assessment window. Short assessment windows in streams with such high autocorrelation can lead to the erroneous conclusion that the population contribution to the overall stock complex does not vary much over time.

Our simulations demonstrate the importance of synchrony among populations, and autocorrelation within populations, to our ability to measure the relative contribution of an individual population to a stock complex. Ecologists have identified asynchrony among populations as an important attribute of stable communities, but have been slow to consider this in assessment schemes. The use of “index” or “indicator” streams in ecological studies, especially those for Pacific salmon, or other species with high temporal autocorrelation and asynchronous regional population dynamics, fail to characterize the important variance structure among populations that we promote as increasingly important to maintain in the face of climate change and threats of development. Additionally, assuming that observed variability is simply “white noise” may lead us to miss important long-term shifts in underlying productivity that we have found to be very important in determining our ability to characterize an individual population's relative importance.

Future assessment projects for the purpose of environmental impact assessments should validate assumptions about the structure of complex populations. Maintaining a diverse portfolio of populations has been highlighted as a key strategy for maintaining ecosystem resilience, yet impact assessments rarely take this into account. In Bristol Bay, Alaska, the diversity of Sockeye spawning stocks across nine river populations and a diverse set of habitats, has enabled the reliable delivery of ecosystem services in the form of a sustainable fishery, and marine-derived subsidies to watersheds (Hilborn et al. 2003, Schindler et al. 2010). This diversity not only ensures reliable delivery of a major food subsidy to consumers, it also increases the window of availability and the benefits conferred to consumers (Schindler et al. 2013). Risk assessments cannot ignore the complexity of such systems by using "index" sites, or by assuming that proportional contribution is consistent across time – as complexity itself is the attribute that needs to be preserved. One reasonable approach to maintaining functioning landscapes might then be to focus on maintaining the processes that generate diversity in the first place (Beechie et al. 2010). At the very least, it should be properly acknowledged that any short term assessment of a populations contribution to an overall portfolio be considered as a highly conservative estimate of its long-term contribution.

In the face of development and climate change, decisions will need to be made about where development will be allowed to take place, and which habitats and their dependent populations will be preserved. In the case of species, like sockeye salmon, which are characterized by a complex set of component populations, these decisions will be especially complicated. A typical assessment would likely survey threatened habitats for a given window of years, estimate the number of salmon that use that habitat to spawn, and decisions will be made based on the perceived loss to the overall population if that habitat were altered. This type of assessment assumes that the contribution of a given site to the overall portfolio of populations in that window is representative of its long-term average contribution. This type of assessment does not take into account that independent or asynchronous dynamics or low-frequency swings in abundance, may result in high variability in proportional contributions over time. It is also important to consider that these portfolios are comprised of distinct genetic populations, and the loss of any spawning habitat, will inherently reduce the genetic complexity of the portfolio. While recognizing that the numerical contribution of an individual habitat or population to an overall portfolio can drastically change over time, as we have shown in this paper, the loss in terms of habitat or genetic complexity still stand to degrade the stability of such populations.

1.6 Figures

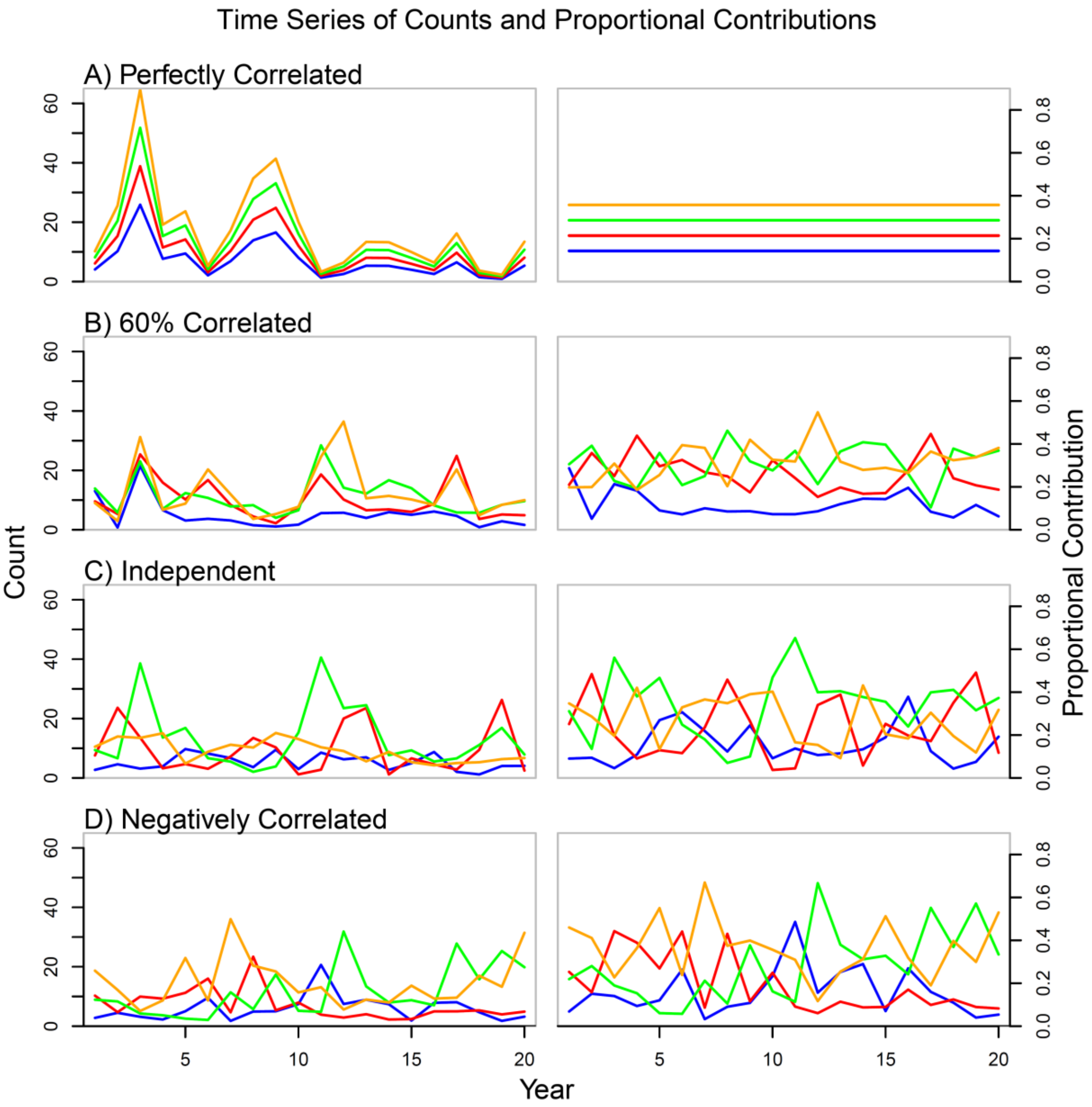

Figure 1.1. Simulated portfolio of four populations for 20 years (left) and proportional contributions for each individual population over same time window (right). Time series are simulated with lag-one correlation coefficient of 0.3. Levels of synchrony decrease from A) perfect synchrony, to D) which is highly asynchronous. Measured community-wide synchrony values for these simulated portfolios are 1, 0.70, 0.39, and 0.17, respectively.

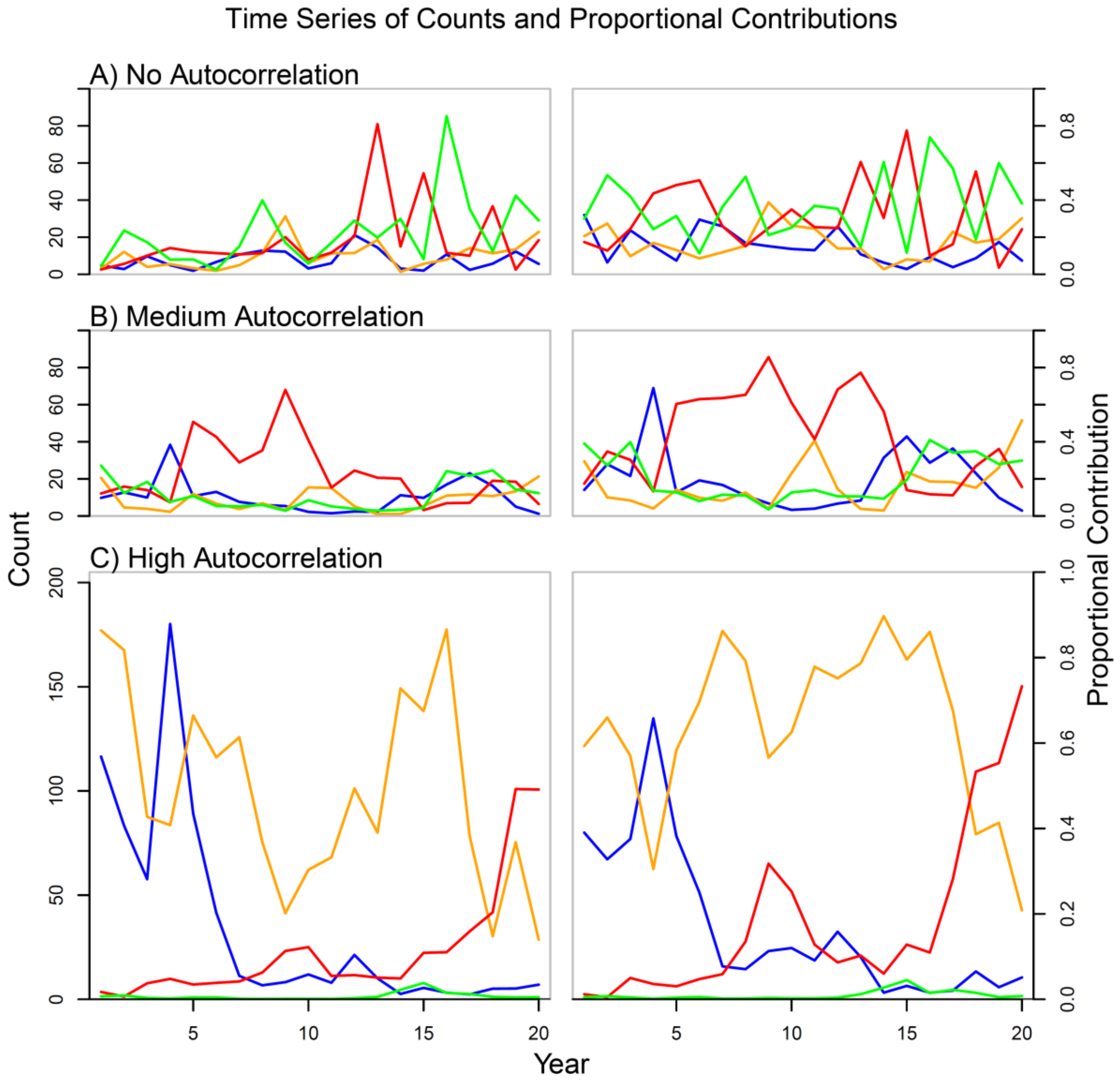

Figure 1.2. Simulated portfolio of four populations for 20 years (left) and proportional contributions for each individual population over same time window (right). Time series are simulated with correlations of 0.1 between populations, resulting in synchrony values of 0.37, 0.54, and 0.56, respectively. Measured average lag-one correlation coefficients within portfolios were 0.05, 0.45, and 0.67, respectively.

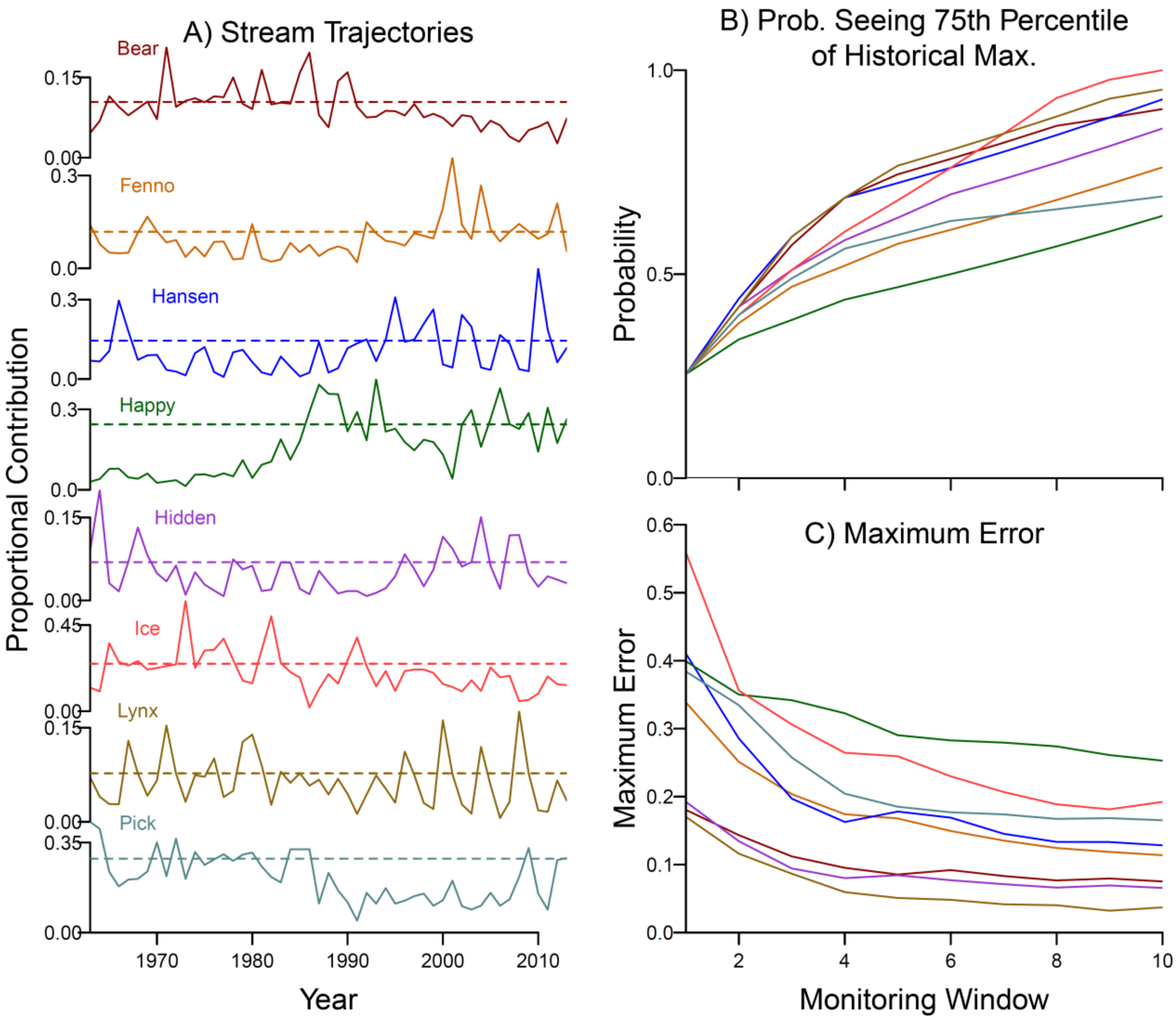

Figure 1.3. Time series of proportional contributions for 8 streams in the Wood River watershed, southwest Alaska (A). Dashed lines show 75th percentile of values over the entire time series. Probability of observing a value in the 75th percentile (B), and the maximum error, across different assessment windows (C).

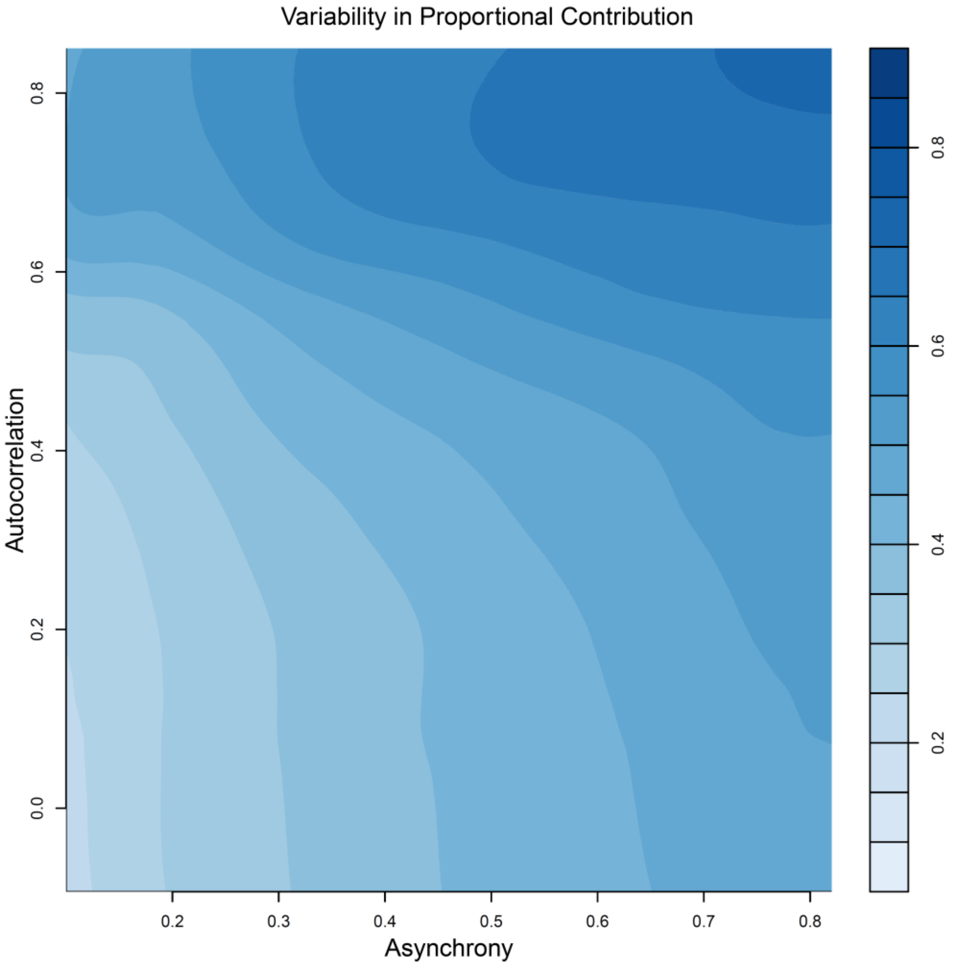

Figure 1.4. Population variability (PV) values for proportional contributions of simulated populations portfolio with increasing autocorrelation (y-axis) and decreasing correlation between populations expressed as 1 minus the synchrony index (x-axis).

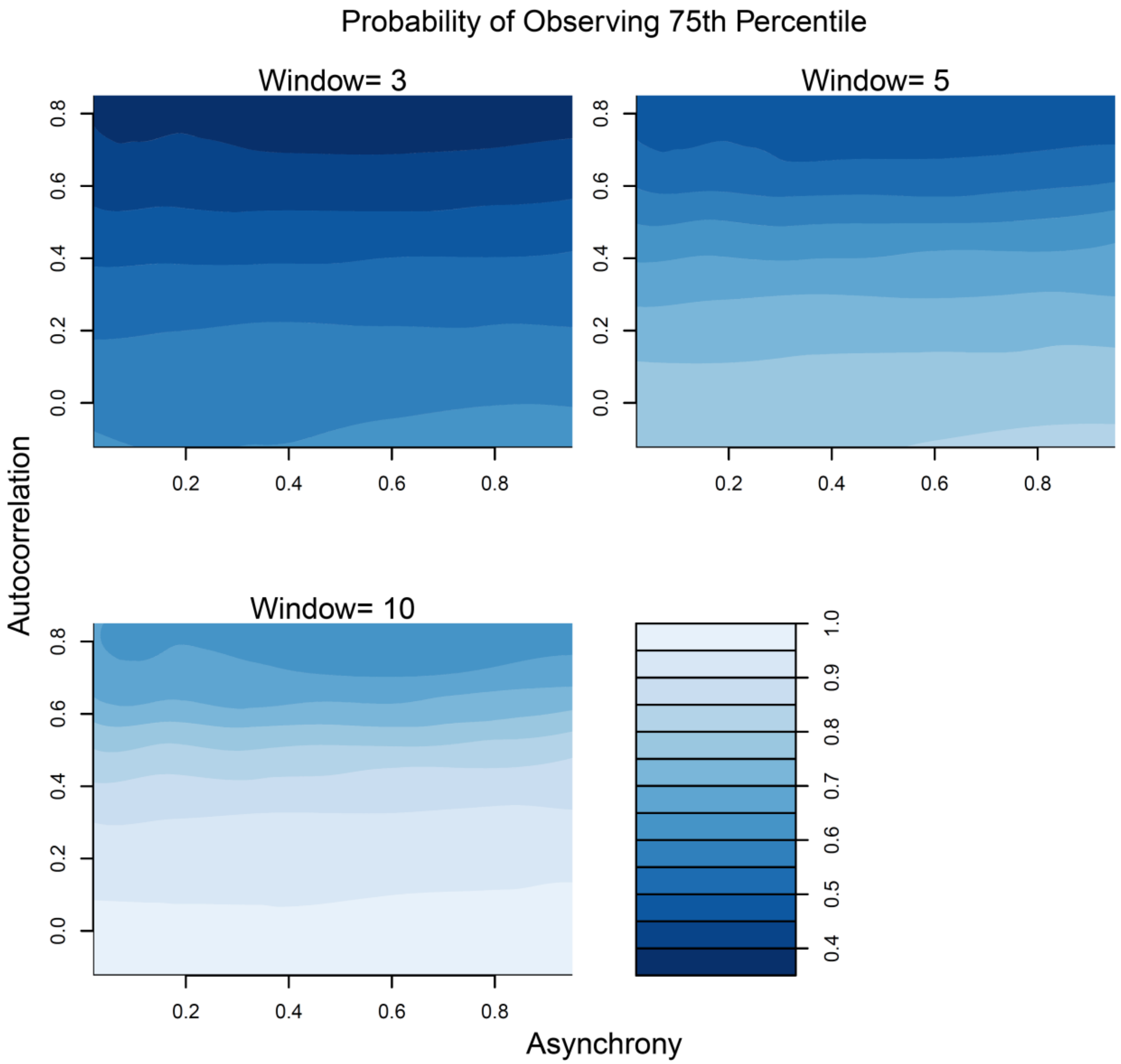

Figure 1.5. Probability of seeing value in 75th percentile of historical values for assessment windows of 3, 5, and 10 years, across levels of asynchrony and autocorrelation.

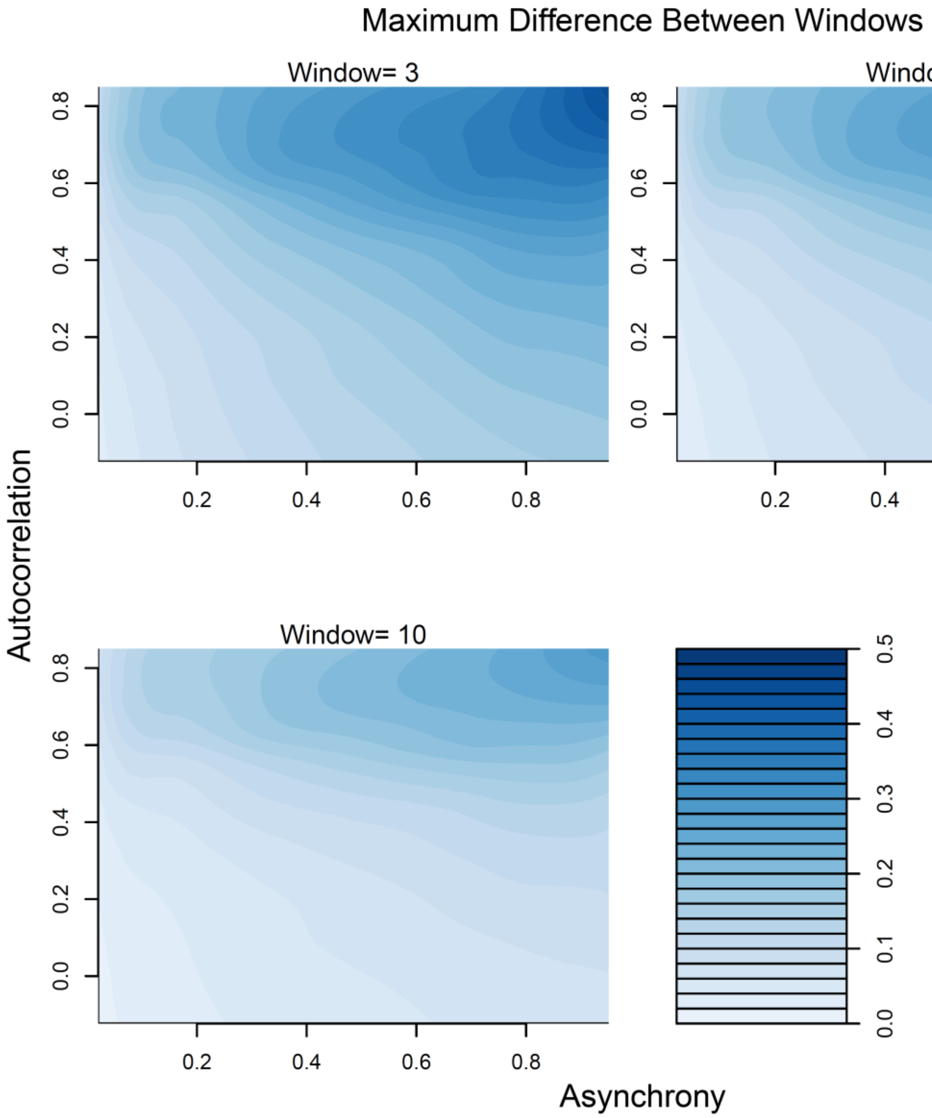

Figure 1.6. Maximum error measured as difference between mean of the highest and lowest average historical windows, for assessment windows of 3, 5, and 10 years, across levels of asynchrony and autocorrelation.

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Chapter 2. Linking sockeye escapement to resource accessibility for consumers

2.1 Abstract

In many ecosystems, important resource subsidies arrive as a pronounced pulse — creating a short window of hyper-abundance in productivity or food availability. In the case of Pacific salmon, a yearly pulse of marine-derived resources, in the form of spawning anadromous fish, inundates inland freshwater habitats with food and nutrients in the form of live fish, their gametes, and their carcasses. The highest quality food is provided by live fish and their eggs, which are important food sources for resident fish, bears, and birds, but are only available for a short period. While the effects of this specific resource pulse are widely appreciated, little attention has been paid to the role that timing plays in conferring benefits to consumers, and studies have mainly focused on biomass as the main control on the magnitude of effects. In this study we used multiple in-stream counts of adult sockeye salmon abundance within the spawning season, and tagging data to estimate in-stream life span, to explore how escapement to individual streams is related to the amount of time that consumers have access to live salmon as a food resource. Our results demonstrate that duration of salmon availability as a food source is non-linearly related to escapement; across 3 orders of magnitude of spawner abundance, salmon were available to predators from about 2 weeks to about 5 weeks per year at any given site. This saturating relationship indicates that higher escapement values may not translate to proportionally higher benefits for consumers when these benefits are mediated by a fleeting window of opportunity. This result demonstrates that ecosystem based fisheries management (EBFM)

of anadromous salmon should assume that benefits inferred to consumers are inherently time-mediated, and the numerical benefits of increased salmon density will not be straight-forward to estimate.

2.2 Introduction

An important development in ecology has been the widespread recognition of the importance of resource subsidies for supporting ecosystem production and structuring communities (Polis et al. 1997b, 2004). However, understanding of how recipient ecosystems respond to changes in the magnitude of subsidies remains weak. The effects of subsidies are likely context dependent; depending on the background productivity of recipient ecosystems and constraints on the abilities of consumers to benefit from resource subsidies. An important but relatively unexplored characteristic of subsidies is that they often occur as low frequency, large magnitude, and short duration events of resource hyper-abundance (Yang et al. 2008). Such resource pulses have been explored theoretically (Holt 2008) and identified in communities across vast ranges and scales (Yang et al. 2010). Combined, the spatial process of resource subsidies, the magnitude of resource increase, and the time scale over which this flux occurs — can all be important factors determining the effects of such material inputs to ecosystems.

How resource pulses are distributed across space and time, and how the distribution of pulses interacts with their magnitude, likely mediate their effects on recipient ecosystems; however, these relationships remain poorly described in nearly all systems subject to resource pulses. Many cases of resource pulses and their effects on community structure have been observed, including rapid plant growth triggered by El

Nino rain events (Polis et al. 1997a) or floods (Nakamura et al. 2005), mast seeding events (Kelly 1994), seaweed deposition on beaches following storms (Spiller et al. 2010), and many more (see Yang et al. 2010). Many of these events are triggered by rare and extreme weather events; others, while equally ephemeral, occur with predictable periodicity due to hardwired life histories. For example, periodic 17-year cicadas (*Magicicada spp.*) have been shown to directly but temporarily increase microbial biomass and nutrient availability in forest soils, resulting in cascading effects on forest plants (Yang 2004) and even longer lasting effects for stream and pond communities (Nowlin et al. 2007). Most of these studies focus on the immediate effects to primary producers and primary consumers which tend to have short enough lifespans that numerical responses are seen in a matter of days or weeks. The effects of pulses with different magnitudes, durations, and intervals, to organisms with longer lifespans are less well understood.

In ecosystems that support Pacific salmon, the yearly transport of a large marine subsidy of nutrients and energy, in the form of terminal spawners returning from sea, represents an important pulse of resources for freshwater and riparian ecosystems. These marine-derived inputs of nutrients and energy are either integrated into freshwater and riparian nutrient cycles following decomposition of carcasses, or are consumed directly by a diverse array of predators and scavengers (Naiman et al. 2002, Gende et al. 2002, Schindler et al. 2003). Despite wide recognition of situations where marine derived subsidies are incorporated into inland ecosystems, little is known about how changes in the magnitude of salmon resources translate into changes in the dynamics of recipient ecosystems (but see Moore and Schindler 2010, Verspoor et al. 2010, 2011, Bentley et al. 2012).

Salmon provide a high quality food source to terrestrial predators (i.e. bears, wolves) and other consumers (i.e. resident fish) while they are actively spawning during a short time period of the year (Schindler et al. 2010, 2013). This ephemeral availability of live, spawning salmon and their eggs suggests that the duration of time that consumers have access to spawning salmon may control the extent to which consumers benefit from salmon resources. For example, brown bears (*Ursus arctos)* are highly selective on high quality tissues of spawning salmon (Gende et al. 2004), suggesting that they are limited by their digestive capacity to consume and metabolize salmon resources over a short period of time, rather than limited by the number of salmon *per se*. Growth of resident fish such as rainbow trout (*Oncorhynchus mykiss*) and arctic grayling (*Thymallus arcticus*) which rely heavily on salmon resources during a short period of time each year (Scheuerell et al. 2007) becomes saturated at high abundances of spawning sockeye salmon (*O. nerka*) in watersheds, and is mediated by the productivity of the stream outside of the spawning season (Bentley et al. 2012). Further, Ruff et al. (2011) showed that rainbow trout that were able to move among sockeye salmon populations that had different spawn timing had higher seasonal growth rates than individuals that remained stationary and only consumed sockeye salmon eggs from a single population. Together, these findings suggest that the magnitude of the salmon resource pulse is unlikely the only factor determining the effect on consumers, and imply that factors that control the period of time over which consumers can feed on salmon may regulate how these marine resources affect benefit consumers.

The duration and seasonality of salmon presence in spawning habitats is dependent on a combination of the timing of when they enter spawning habitat, their rates of senescence, and the rate at which predators (particularly brown bears) kill them (Quinn et al. 2001, 2003, Carlson et al. 2007). After death, the scavenger community, ranging from mammals, birds, invertebrates and bacteria rapidly assimilate these marine-derived nutrients into the ecosystem (Schindler et al. 2003). Because predation rates are modified by stream geomorphic characteristics (Quinn et al. 2001, Carlson et al. 2007) the duration of this resource pulse is likely controlled both by the number of fish at a spawning location and by bear predation as regulated by stream geomorphic characteristics.

In many locations, the magnitude of the pulsed marine subsidy provided by spawning Pacific salmon is partially controlled by human activities. Most Pacific salmon fisheries intercept adults as they travel shoreward, just before entering the freshwater environment. Fisheries managed for escapement prescribe the number of fish to be allowed to enter the spawning grounds, the goal being to catch the remainder of the inshore run. In most ecosystems, these escapement goals are generally based on the density of spawning salmon that will lead to maximum sustainable yield (MSY), which maximizes production for the next generation of fish. Despite a large body of literature describing the importance of spawning Pacific salmon to freshwater and riparian ecosystems, there are few examples where quantification of these benefits enters into decisions about the allocation of these resources to upstream ecosystems. Furthermore, no previous studies have quantified how changes in salmon escapement might control resource flows to consumers through effects on the period of time over which salmon are available to those consumers.

Initial attempts to examine trade-offs between allocation of salmon to fisheries versus watersheds have assumed that benefits to consumers scale with the abundance of returning salmon; the *magnitude* of the resource pulse (Darimont et al. 2010, Levi et al.

2012). This assumption fails to consider that the timing of salmon availability, or the *duration* of the resource pulse, may be an important mediating factor. In Levi et al. (2012) the assumed numerical response of brown bears to increased salmon density depended on two parts: 1) a relationship between salmon density and percent salmon in diet, based on stable isotopes, and 2) a weak linear relationship between percent meat in diet (assumed here to be only provided by spawning salmon) and bear population density (Hilderbrand et al. 1999, Levi et al. 2012). These studies ignore the possibility that attributes of the pulsed-subsidy, besides magnitude, may modulate the effects of salmon resources on consumer populations. Relationships between dietary meat (which has been shown to be comprised of mainly salmon in coastal populations) and increased female body mass and litter size in coastal brown bears provide compelling evidence of the importance of spawning salmon in their diets (Hilderbrand et al. 1999, Mowat and Heard 2006). However, studies have yet to link increased salmon density, at a given site, to increased bear density – a causal link that has been assumed in studies assessing trade-offs between the fishery and coastal bear populations. In order to assess these trade-offs, it needs to be fully understood how changes in spawning salmon densities affect bear populations, and whether the main mediator of this effect is abundance or timing.

The goal of this study was to quantify the duration of the live-salmon resource pulse in individual stream habitats across a range of escapement densities (i.e. magnitudes of the resource subsidy). We used data from 10 streams in the Wood River system, southeast Alaska, to quantify the relationship between spawning population size and the duration of time that live, spawning sockeye are present in spawning streams — which is when they are available as a high quality food source for consumers.

2.3 Methods

2.3.1 *Study site*

Sockeye salmon return to the rivers, lakes, and streams of Bristol Bay, Alaska from June to August each year. Fish queue at the mouths of their natal streams, where they reach full reproductive maturity before entering the spawning streams. Bristol Bay sockeye return times are predictable, falling within the same short time window each year (Moore and Schindler 2010, Lisi et al. 2013). This entry into spawning streams generally marks the beginning of their availability as a food source for consumers such as bears and gulls; and also the availability of their eggs as a food source for resident fish (Scheuerell et al. 2007).

2.3.2 *Stream surveys*

Stream surveys of the number of live and dead salmon have been carried out for over 50 years in the study area by the University of Washington's Alaska Salmon Program. For this study we use counts from streams draining into two of five lakes that comprise the Wood River Lake system: Lake Aleknagik and Lake Nerka. Salmon count data in streams were included for those stream/year combinations in which more than one count was taken in a spawning season. We were able to use data from 10 streams (seven draining into Lake Aleknagik, three into Lake Nerka) for varying numbers of years. Data quality ranged from 23 years of near-daily counts for Hansen Creek, to five years of two to seven counts per season over five years for Pick Creek. In addition to these counts, for several streams, yearly observations of stream entry date were available – the date that the first "push" of mature salmon entered the stream. Using these observations and the fact that entry date is consistent from year to year, at least five zero counts were added to the beginning of each year’s data set for consecutive days ending in the first day of entry to the streams. Because we know that fish tend to enter in a coherent “push” upstream (Doctor and Quinn 2009), zeroes were added up to the observed entry date where available, and added up to the earliest known entry date for a given stream where no observations had been made in that year.

2.3.3 *In-stream lifespan data*

Dates of stream entry and death for individual fish were estimated at four of our study sites, using tagged fish data available over varying time periods (n=2, 2, 4, 16 years) and for varying numbers of fish (757-3102 individuals). Fish were intercepted shortly before, or immediately after (within one day of) entry to the individual stream. Fish were tagged with external disk tags with codes that were easily observed from above the surface of these shallow streams (Carlson et al. 2007). Streams were surveyed visually on foot each day (with some exception) to determine date of death for each tagged fish. When a fish disappeared from the stream, or if a survey day was missed and a fish was found dead the next day, it was assumed to have died the day after its last live sighting. This tagging method has been shown to have no measurable effects on survival or reproductive success (McPhee and Quinn 1998, Hendry et al. 1999, Baker and Schindler 2009). Stream life is defined as the number of days a fish is alive on the spawning grounds, including the day of death. For our data analyses, we pooled one and two day lifespans to reduce ambiguity due to sampling inconsistencies. Thus, a fish discovered dead on first in-stream observation, a fish that disappears after one live observation, and a fish that is found dead the day after its first in-stream observation, were all assigned stream lives of two days. This definition means that each fish is in stream and available to predators for at least one day; the day that it entered the spawning habitat. This pooling substantially improved convergence of our mortality model, and had little effect on estimates of stream duration and escapement.

2.3.4 *Modelling duration of spawning activity*

To estimate the seasonal duration of salmon availability to predators, we needed to interpolate between surveys to estimate the number of fish on the spawning grounds each day. We simultaneously estimated in-stream numbers and total escapement for the year by modeling entry and mortality using an altered form of the Bayesian hierarchical model presented in Su et al. (2001). This model was built to estimate historical pink salmon (*Oncorynchus gorbuscha*) escapement to individual streams in Southeast Alaska, as an alternative to area under the curve and maximum likelihood methods previously used (see Hilborn, Bue, & Sharr, 1999).

In this model we estimate the number of fish present (η), entering (x), and dying (d) for each day of the spawning season, and also the total escapement to the stream (E). Here, η_t represents the number of fish in stream at the beginning of day t, x_t is the number of fish that enter during day t, and d_t is the number of fish that die on day t. The model is being fit to observations of the number of fish in stream, η_t.

$$\begin{aligned}\eta_{t+1} &= \eta_t + x_t - d_t \\ &= \sum_{k=1}^{t} x_k - \sum_{k=1}^{t} d_k\end{aligned}$$

2.3.5 *Salmon entry date*

We assume that the number of fish that enter on a given day (x_t), of the total number of fish that will enter that year (E_y), is determined by a normal distribution with estimated year-specific mean M_y and standard deviation S_y.

$$x_t = {E_y e^{-(t-M_y)^2/(2S_y^2)}}\Big/{\psi}$$

A normalizing constant (ψ) is required to ensure that the total number of fish entering adds to the total escapement (E_y). We bounded the model between days T_1 and T_2 chosen far from the known approximate entry dates and end of run date, and initiated the model with $T_1 = 0$.

$$\psi = \sum_{t=T_1}^{T_2} e^{-(t-M_y)^2/(2S_y^2)}$$

2.3.6 *In-stream lifespan*

In order to estimate the number of fish dying on each day (d_t) we assign an in-stream stream life, and therefore a “death date”, to each entering fish. The number of fish dying on given day is then the sum of all fish that have entered, and been assigned that death date.

An extension to the original model was made in order to account for observed high variability in stream life in this system. In Su et al. (2001) an exponentially decreasing curve was fit to explain the relationship between entry date (in terms of deviation from mean entry date) and stream life. In their formulation, the same in-stream lifespan is assigned to all fish that enter on a given day, according to this curve. In our formulation, fish entering on the each day will be assigned “death dates” according to an estimated probability distribution, and can therefore have different in-stream lifespans.

While the relationship between entry date and life-span was generally decreasing (Figure 2.1), we found that even for fish that enter on the same day, stream life can be highly variable — likely due to individual variation in spawn timing and senescence and the high rates of bear predation in some streams (Figure 2.2). It has been estimated that predation rates for these study streams vary between 19 and 49% (Quinn et al. 2003). In-stream lifespan decreases as fish enter spawning grounds later in the season, and the risk of bear predation changes over time, with the direction and magnitude of this change variable across streams with different attributes (Carlson et al. 2007). In shallow streams where fish can be easily caught, bears are able to fulfill their preference for younger fish, and the risk of predation by bears decreases the longer a fish has been present in the stream (Carlson et al. 2007). These dynamics result in the patterns seen in Hansen creek (Figure 2.2) where death rates are very high for the first two days after entry, and those fish that survive the initial days of high predation risk, generally live until senescence. This results in a flat or arc-shaped relationship between entry date and average stream life, with fish dying much earlier than expected — due to predation by bears that prefer “fresh” fish that have only recently matured and entered. In large streams, or those with refugia from predation (such as deep pools or undercut banks), bears are not able to catch young, fast fish and tend to kill older, slower individuals nearing senescence. This process results in increasingly short stream lives for late entering fish due to a combination of predation and quickly occurring natural senescence. To accommodate the two processes: predation, or, more generally, premature death (which could also be due to stranding in shallow areas or other predators) and natural death due to senescence, we developed a two-source mortality model to be fit to tagging data.

Predation risk is modeled as a function of in-stream age (amount of time since stream entry). In order to accommodate differing relationships between days in stream or "stream life" (t_{SL}) and predation risk (M_p), we used a flexible inverse logit function which can be either monotonically increasing or decreasing, and both linear and non-linear, depending on two estimated parameters, α and β.

$$M_p\,(t_{SL}) = e^{\,(\alpha t_{SL}+\beta)} \Big/ 1 + e^{(\alpha t_{SL}+\beta)}$$

Senescence was modeled using a logistic function where the mean date until senescence (μ_{t_E}) changed linearly (became shorter) the later that fish entered (t_E), depending on parameter σ.

$$M_S(t_{SL},\ t_E) = \ 1 \Big/ 1 + e^{(-\frac{t_E-\mu_{t_E}}{\sigma})}$$

$$\mu_{t_E} \ = ct_E + d$$

Therefore the total risk of predation given an entry date and in-stream age is estimated as:

$$M_{total}\big(t_{SL},\ t_E\big) = M_p\,(t_{SL}) + M_s(t_{SL}, t_E) - \ M_p\,(t_{SL}) * M_s(t_{SL}, t_E)$$

We fit this model to tagging data in a maximum likelihood framework. Tagging data are fed into a likelihood function as entry dates (t_E) and either death dates (t_D) or last date of observation (t_{LO}) for those fish that lived past the last survey date (t_{SL}). This results in the following two likelihood functions for those fish with observed death dates (1), and those fish that are still alive at the survey's end (2):

1) $\mathrm{L}\big(\mathrm{Die\ day\ t_D}\ \big|\ \mathrm{Entered\ day\ t_E}\big)\ = \prod_{\mathrm{i<t_D}} \Big(1 - \mathrm{M_{total}}\big(\mathrm{t_i},\ \mathrm{t_E}\big)\Big)\ *\ \mathrm{M_{total}}\big(\mathrm{t_D},\ \mathrm{t_E}\big)$

2) $\mathrm{L(Survive\ until\ day\ t_{LO}\ |\ Entered\ day\ t_E)}\ = \prod_{\mathrm{i}<LO}\left(1-\mathrm{M_{total}}(\mathrm{t_i},\ \mathrm{t_E})\right)$

The outputs of this model are estimates of parameters $\alpha, \beta, c, d, \sigma$ for each stream, from which we can estimate the probability distributions of death dates for fish entering on each day during the spawning season. We then generate an upper-diagonal matrix (L) where each row is comprised of the probability distribution for death dates for that row's entry date.

$$L(i,j) = \Pr(Die\ on\ day\ j, given\ entered\ day\ i)$$

From this matrix, L, and a column vector X which contains the number of fish entering each day (x_t) we can get a matrix D which indicates the number of fish dying on each day. Where $D(i,j)$ is the number of fish that entered on day i, that die on day j. In Matrix notation:

$$X\ \cdot L = D$$

Finally, the number of fish that die on each day (d_t) can be estimated by taking the sum of row t:

$$d_t = \sum^{i} D(i,t)$$

Since tagging data were only available for four of the 10 streams for which we had multiple in-stream count data, we split streams into three categories, based on stream depth and width, to account for differences in susceptibility to bear predation (Quinn et al. 2003). Small, high predation streams, where all fish are easily caught and therefore younger, fresher fish are preferentially caught; medium size streams with intermediate levels of predation, where older slower moving fish are much easier to catch, and more often targeted; and large, low predation streams, where bear predation is consistently low regardless of in-stream age. We have tagging data from one stream each in the small and large categories, Hansen Creek and Pick Creek, and two streams in the intermediate category: Bear Creek and Yako Creek. For streams without tagging data in the intermediate category, we used a stream life model fit from tagging observations from both Bear and Yako creeks, adjusted such that average entry dates aligned. For those streams with tagging data from multiple years, all years were pooled together and modeled based on calendar day, since entry dates were so consistent from year to year, and multiple years of tagging data were required to get enough representation across possible entry dates. Stream life matrices were adjusted such that the average entry date seen over time for the population without tagging data would be aligned with the average entry date for salmon in the stream for which the model was fit.

2.3.7 *Hierarchical structure*

The hierarchical structure of the model is based on the knowledge that entry timing is very consistent from year to year, within a stream. We assumed that both M and S varies annually according to stream-specific normal and lognormal distributions, respectively.

$$M_y \mid \mu_m, \tau_m^2 \sim N(\mu_m, \tau_m^2)$$

$$\ln\left(S_y\right) \mid \mu_s,\ \tau_s^2 \sim N(\mu_s, \tau_s^2)$$

Because escapement is highly variable from year to year, within a given stream, we did not place a hierarchy on E. Uninformative uniform and inverse-gamma priors were put on hyper-parameters μ_m, μ_s (~unif(T_1,T_2)) and τ_s, τ_M (~IG(0.001,0.001)). An uninformative uniform prior was used for logged annual total escapement, E (log(E)~unif(0,13). Observation errors on in-stream counts were assumed to be Poisson distributed.

2.3.8 *Model implementation*

The in-stream lifespan model was fit to tagging data using maximum likelihood estimation in ADMB (Fournier et al. 2012), and the L matrix was used as an input for the Bayesian hierarchical model estimating presence, entries, and deaths on each day, as well as total escapement for each year. The hierarchical model was fit using MCMC sampling carried out in JAGS, implemented in R using the package "R2jags" (R Core Team 2014, Yu-Sung Su and Masanao Yajima 2014). Year-stream combinations with convergence issues indicated by diagnostic checks, or with poor fit indicated by modeled peaks substantially higher than observed peaks, were excluded from further analysis, removing 18 out of the total 102 stream-year combinations. The final model outputs were posterior distributions for escapement, E, and a measure for fish availability: the number of days in which >100 fish were present on spawning grounds. Although the number 100 was chosen somewhat arbitrarily (Quinn et al. (2003) estimated an average of 100-130 fish killed per day in these streams), our results were similar when using number of days with more than 50 and 200 fish.

Model fits were generally very good, with well-defined posterior distributions for Escapement and number of days salmon were available to consumers (figures 2.3-2.5 show 95% CI, figures A.2-A.11). To objectively investigate the nature of the relationship between escapement and number of days of salmon availability, we fit a set of post hoc linear models to determine if the relationship between escapement and the duration of salmon availability was similar between streams, and see if it was affected by stream size. Models covered all combinations of fixed and random intercepts and slopes across streams, as well as the same combinations with size categories (S, M, L as described in tagging data) instead of Site as a predictor and grouping factor. Models were compared using Akaike Information Criterion adjusted for small sample size (AICc), which ranks the most parsimonious model as the one with the lowest AICc value (Burnham and Anderson 2002). Note that these models aren't being fit to draw numerical, statistical inference, simply to explore the model outputs.

Because the mortality model was estimated outside of the Bayesian hierarchical model, the error in these mortality distributions was not propagated through to escapement estimates, and therefore credible intervals are conditional on our estimated mortality schedules. Therefore, our posterior densities are likely over-confident, and may not include the real escapement value. Due to this fact we also inspected the relationship between the estimated duration of salmon availability and peak counts of live and dead salmon, which are available for almost all stream/year combinations, and often used as minimum estimate of escapement to a stream.

2.4 Results

The two-source mortality model effectively captured the dynamics of predation and senescence for our four streams with tagging data (Figure 2.2). Escapement was highly variable across streams and years, with the lowest escapement year estimated at 131 (95% CI 103, 163) at Mission Creek in 2009, and highest observed escapement of 9.98 x 10^4 (95% CI 9.94 x 10^4, 1.00 x 10^4) at Hansen Creek in 2014. The number of days with more than 100 fish in the stream varied from a minimum of 0, associated with the lowest observed escapement mentioned previously, to 64 days in Lynx creek in 2008, associated with an estimated escapement of 2.69 x 10^4 (95% CI 2.65 x 10^4,2.72 x 10^4). Mean entry date

(M) was fairly consistent from year to year, within streams, with estimated standard deviation of mean entry date (τ_M) ranging from 2.02(95% CI 1.28, 3.71) to 8.9 (95% CI 4.34, 27.9) days. The spread of entry timing across the spawning season, within a stream (S) ranged from 0.68 (95% 0.0389, 2.03) to 2.23(95% CI 1.78, 2.70) and was also quite consistent — with standard deviations (τ_S) within a stream, across years, estimated between 0.14 (95% CI 0.0460, 0.721) and 1.58 (95% CI 0.870, 3.595). Model fits of daily in-stream abundance fit to survey for all stream-year combinations can be seen in supplemental Figures A.2-A.11.

Across all streams, there was a positive relationship between estimated escapement and the duration of salmon availability (Figures 2.3-2.5). This relationship appeared to be saturating for most streams (Figure 2.4), and was linear when plotted against escapement on a (natural) log scale. (Figures 2.3 and 2.4). This pattern was also consistent when comparing duration of salmon availability to our model-independent index of escapement; peak count of live and dead salmon (Figure 2.3). Two linear mixed effects models examining stream-specific relationships between the log of escapement and the duration of salmon availability tied as the most parsimonious (Table 2.1, Figure 2.5). Both of these models had separate, fixed intercepts for each streams, and random slopes for each site or stream size grouping. The model with slopes grouped by stream size showed that the relationship between logged escapement and salmon availability tended to be steeper for large streams compared to small streams (Figure 2.5). These results demonstrate that while streams have distinct intercepts for this escapement – availability relationships, slopes are fairly similar across sites, and also similar across size categories. This indicates that across streams, the total escapement level needed to have fish more than one day with more than 100 fish varies. However, as escapement increases, the number of days with more than 100 fish in stream increases at similar rates across sites.

Although a simple linear model describing the relationship between logged escapement and number of days with more than 100 fish, with all data pooled, ignores the underlying structure of the data, it explained 62% of the variability in the data (int=-31.7, slope=7.49). The same model fit with peak counts, which are generally much more widely available, in the place of escapement explained 52% of the variability in the data (int=19.19, slope=6.35). This indicates that the relationship between salmon abundance and availability is quite consistent across sites. Furthermore, it indicates that there may be some predictive potential for using widely-available peak count data to infer salmon availability in sites outside of these study sites.

2.5 Discussion

2.5.1 *Model considerations*

These results demonstrate that there is a saturating relationship between escapement and duration of time that salmon are active in spawning habitat; as escapement increases there are diminishing returns in terms of availability to consumers. This relationship was consistent among streams, with a simple linear model of estimated logged abundances explaining more than 65% of the estimated variation in run duration among streams and years. Further analysis showed that the slope of this relationship was best described as a random draw from a shared distribution for all stream slopes (stream as a random effect) rather than distinguishably different for each stream. There is also evidence that stream size might moderate the relationship between escapement and availability with smaller streams showing slower increases in available as escapement increases (ie. shallower slopes) (Fig 2.5).

The resulting shallower slopes (for the relationship between logged escapement and run duration) for smaller streams could be at least partially an artifact of an assumption made in the stream life model. Due to tagging data constraints, we assumed that the risk of predation was only dependent on in-stream life, and not on density. It has been found at these sites that in small streams with high predation rates, the proportion of fish killed by bears can be much higher in low return years than in high return years (Quinn et al. 2003). This is likely due to consumption limits of nearby bears that consume a fairly constant *number* of fish each year – since there are generally enough fish available for them to reach their daily consumptive limits during the spawning period. It has also been found that as salmon density increases, bears preferentially select pre-spawn individuals and focus primarily on consuming energy rich body parts such as brains and gonads (Gende et al. 2001). In this model, using average predation rates across densities would result in longer in-stream lifespans than expected in low return years, and shorter than expected in-stream life spans in high return years. This would likely have little effect on timing/availability estimates, since the shape of the curve expressing number of fish in stream is directly informed by in-stream counts. However, the predicted stream lives would be much more likely to affect our escapement estimates. In a small stream we would then underestimate escapement in low return years, since we don't account for extra predation that occurs at low densities, and probably over-estimate in-stream life. Conversely, in high return years we would overestimate predation rates, and therefore estimate in-stream lives that are shorter than reality – causing us to overestimate escapement. Underestimating low escapement and overestimating high escapement would lead to more “spread out” escapement estimates associated with the same change in availability; and therefore a lower magnitude effect of escapement (and shallower slope)

For one stream in our system (Hansen Creek), we can directly estimate availability and escapement due to some years of daily in-stream counts that spanned the entire run, and yearly total counts of all observed dead salmon, which is a minimum estimate of total escapement. This data allows us to explore the relationship between escapement and availability without the use of the models described above, for one small stream. Comparing observed minimum escapement estimates (from summing all dead salmon), to our model’s escapement estimates, we see the expected pattern described above of over-estimating escapement in high years, and underestimating in low years. However, the pattern of saturating availability with escapement remains (figure A.1). When we underestimate low years and overestimate high years we essentially expand the observed escapements, and end up with an underestimated slope for the relationship between escapement and availability. This would mean that, perhaps, the relationship between logged escapement and availability is more consistent across streams than suggested by our results, since we are likely predicting a shallower slope than reality for small streams with high predation. Despite this fact, the daily counts and escapement estimates based on dead counts for Hansen creek verify the saturating relationship between escapement and availability.

The observed phenomenon of distinct intercepts across sites, even within a size group, may have been influenced by limited data within sites – which captures streams at different stages of this saturating relationship. Some streams seem to have been observed on the lower end of their escapements, with availability increasing substantially with escapement, while others may have been observed on the flatter "plateau" of this relationship. Only a few streams (see Hansen, Yako, and Ice; Figure 2.5) have enough observations that span over a range of escapement values to really see the full saturating relationship.

2.5.2 *Implications for ecosystem-based fisheries management (EBFM)*

Calls for marine ecosystem-based fisheries management have increased over the past 20 years, recognizing that single species management may not adequately maintain ecosystem structure and function (Christensen et al. 1996, McLeod et al. 2005). Calls for ecosystem based management for Pacific salmon have been made to help restore protected riparian areas, and to benefit brown bear populations (Darimont et al. 2010, Levi et al. 2012). So far these studies have focused on increasing total numbers of salmon allowed to enter the spawning grounds, and have not considered how time might mediate benefits to consumers. For example, it has been found in a system with high runs of pink (*O. gorbuscha*) and chum (*0. keta*) salmon, that the increase of in-stream nutrients and biofilm closely tracks *live* salmon abundance, and is increased very little by the presence of senescent carcasses (Tiegs et al. 2011). Additionally, the quality of salmon as a food source decreases rapidly with maturity, as salmon stop feeding upon entering the freshwater environment (Quinn 2005). Eggs are also an ephemeral resource since those eggs that are disturbed by nesting activity are primarily available to resident fish, although higher spawner densities have been shown to increase nest disturbance, and accelerate egg availability (Moore et al. 2008). Additionally, salmon carcasses are rapidly consumed by invertebrate scavengers and microbial decomposers that functionally compete with vertebrate consumers for this resource subsidy (Rüegg et al. 2014). Drawing from these examples, it is likely that benefits delivered to terrestrial and freshwater ecosystems in the form of nutrients from excretion and carcasses, and the presence of live salmon and their eggs as a high quality food source for large predators and scavengers are fundamentally time-dependent.

In order to make the link between salmon escapement and benefits delivered to terrestrial and aquatic consumers, it is imperative to understand how numerical escapement and run duration affect survival and reproduction of the consumers. A positive relationship between percent meat in diet and both female body size and litter size is especially compelling, but how escapement might alter the amount of meat in a bear's diet is not well understood (Hilderbrand et al. 1999). For bears living amongst salmon spawning streams the percent meat in diet would likely be consistently high when salmon are present, regardless of actual salmon density. Percent meat in diet over a wider time-frame, including those times outside of the salmon spawning season, is probably much more variable. A bear's ability to integrate over a variety of spawning populations and increase the total duration of salmon availability might be more of a limiting factor than the total number of fish on the landscape (Schindler et al. 2013). In this study we have shown that the relationship between numerical abundance and duration of live salmon presence is non-linear, and that predicting the benefits to consumers, like bears, from increased escapement will not be straight-forward to calculate.

At a wider, landscape-level scale, mobile consumers, such as bears, gulls, and resident fish, are able to take advantage of phenotypically and phenologically distinct populations that spawn in streams, rivers, or lake shores at different times throughout the spring and summer. Another artifact of this ecological and genetic differentiation between spawning populations is their (somewhat) independent or asynchronous dynamics (Rogers and Schindler 2008, Rogers et al. 2013). While this characteristic has been shown to afford stability to the sockeye populations of Bristol Bay and the resulting fishery, it also complicates the relationship between escapement and availability at the watershed level. Due to these independent, or asynchronous dynamics between spawning populations, it is hard to predict how total escapement is distributed across the watershed. Therefore, it is hard to predict how a given escapement at the watershed level will translate into total salmon availability for mobile consumers. Identifying the “local relationship” between escapement and duration, as we have in this study, is the first step towards being able to allocate salmon to the watershed that takes into account the benefits delivered to consumers.

While our study shows how the magnitude of the salmon resource pulse affects its duration at the stream level, it is important to note that management does not occur at this fine scale. Further, mobile predators can integrate across landscape variation in run size and timing as they move to track the availability of salmon resources. The next step towards ecosystem-based management in this system will be identifying management practices where the fishing level experienced by specific fish populations can be controlled. There is evidence that the timing of migration into the freshwater environment (and thereby passage through the area where fishing is focused) is related to spawn timing for sockeye salmon in another Alaska system (Boatright et al. 2004). If the timing of individual groups through the fishery could be estimated, the level of escapement across different groups (whether segregated by spawning habitat, or timing) could be regulated. If this were possible, management decisions could be made that distribute the total catch more evenly across different spawn timings, and help to maximize the amount of time terrestrial consumers have to benefit from the presence of live, spawning salmon. In turn, such an approach would reduce unnecessary catch restrictions for systems when additional escapement is not likely to benefit salmon predators.

Our results demonstrate that despite high harvest rates, many streams in the Wood River often achieve densities that saturate the duration of time they are available to consumers. Thus, high escapements may not necessarily translate into proportionally higher marine resource subsidies to watershed consumers. Whether this relationship occurs in other watersheds is not known, but will likely depend on the system as affected by geomorphology, climate, and the consumer community.

Although pulsed resource subsidies have been identified across a wide range of ecosystems, and their effects on productivity and consumers acknowledged, there has been little work to investigate how the effects of these pulses are mediated by their magnitude and duration. In the case of Pacific salmon, the annual pulse of marine resources carried by spawning salmon has been described across a wide selection of literature. Additionally, there have been calls for management to recognize the importance of this resource subsidy, and incorporate the value of these fish to upstream ecosystems into allocation decisions (Darimont et al. 2010). So far, little attention has been paid to the effect that the duration of this resource pulse might have on the benefits to an ecosystem. In this study we have demonstrated that the relationship between this resource pulse's magnitude (measured in total number of fish escaping to a given stream) and its duration is linear on a log scale.

With plenty of evidence indicating that benefits conferred to consumers by live salmon are likely time-limited rather than escapement-limited, this result demonstrates that the benefits delivered to consumers, at the stream level, saturate as escapement increases. Further research needs to be done to see how this relationship might play out at the landscape level; the level at which both management and roving consumers act. This work is a first step towards understanding how ecosystem-based fisheries management might be able to regulate time-limited benefits to watersheds.

2.6 Tables and Figures

	MODEL EQUATION	**AICC**
MODEL 1	$y = \alpha_0 + \alpha_1 S_1 + \cdots + \alpha_{n-1} S_{n-1} + \beta_1 E + Z_{site} E + \epsilon$ $Z \sim N(0, \sigma_E^2), \epsilon \sim N(0, \sigma^2)$	504.5
MODEL 2	$y = \alpha_0 + \alpha_1 S_1 + \cdots + \alpha_{n-1} S_{n-1} + \beta_1 E + Z_{size} E + \epsilon$ $Z \sim N(0, \sigma_E^2), \epsilon \sim N(0, \sigma^2)$	505.3

Table 2.1. Top two models to explain relationship between logged escapement (x) and salmon availability measured in number of days with 100 fish or more in stream (y).

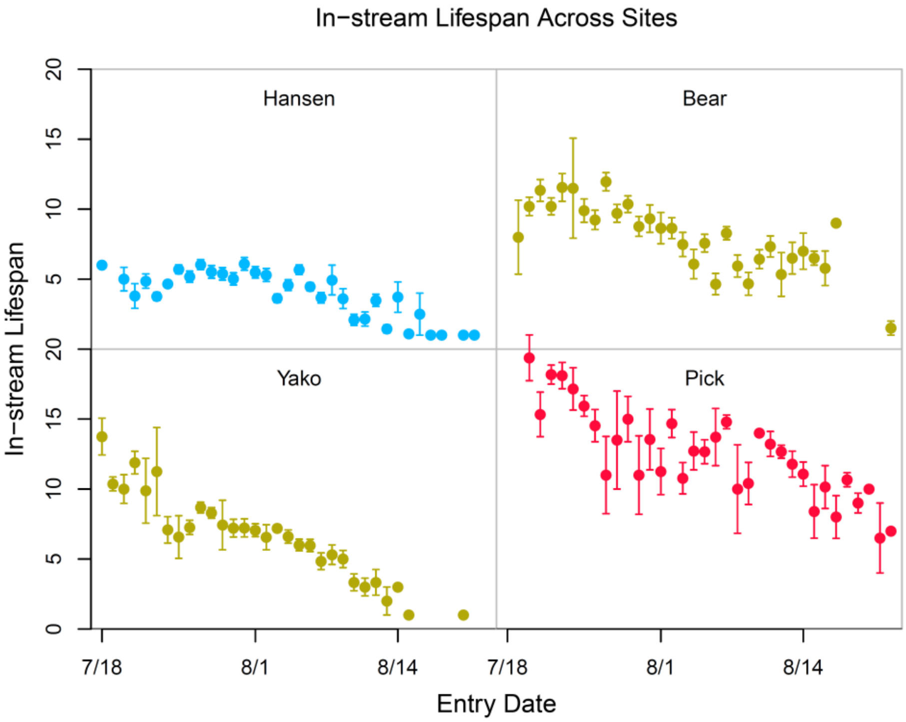

Figure 2.1. In-stream life span across entry dates for four streams. Colors indicate stream size categorized as small (blue), medium (yellow), and large (red). Error bars indicate standard errors where multiple tagged fish were observed entering on the same date. Number of fish tagged (n) and number of years tagging was carried out (m) for Hansen, Bear, Yako, Pick creek respectively: n=3102, 924, 964, 757; m=16, 2, 2, 4.

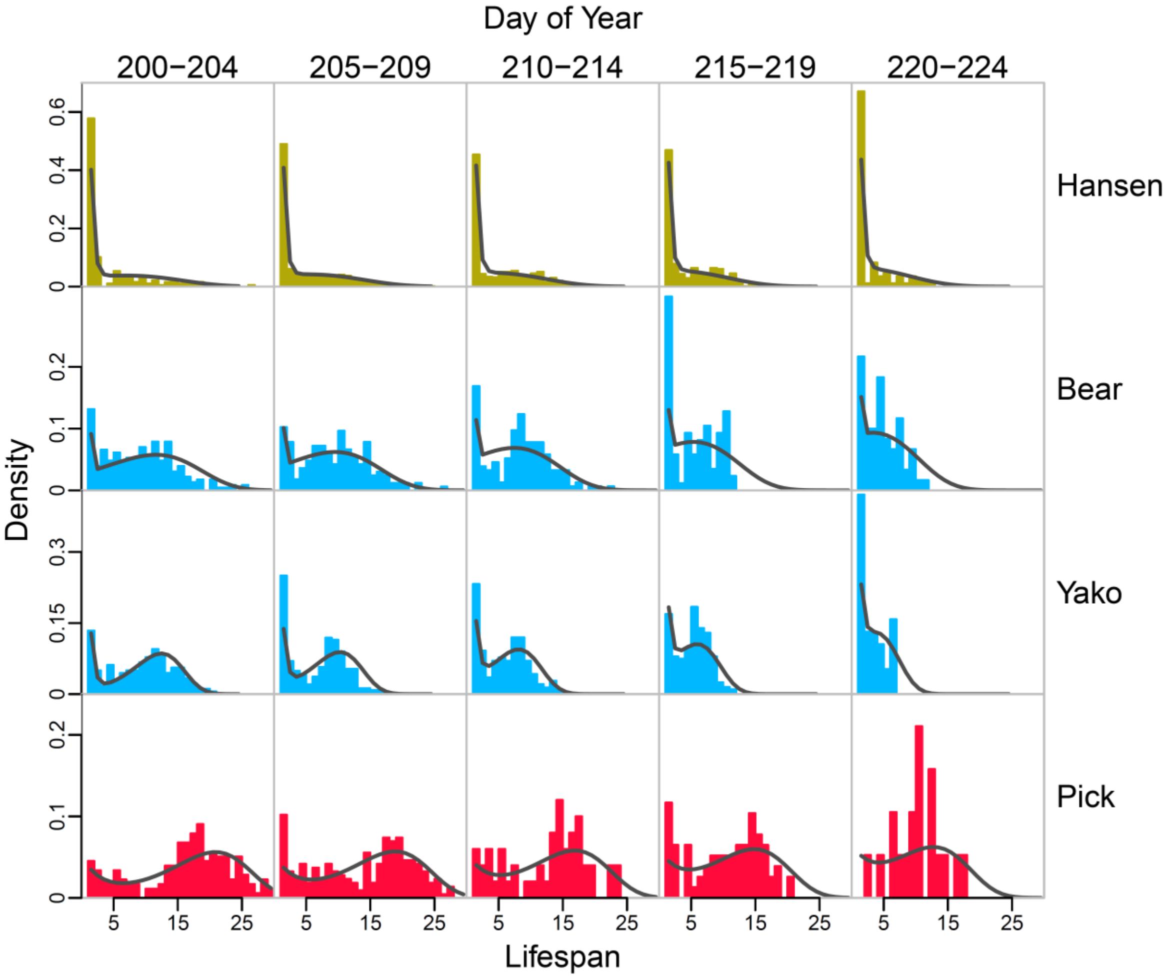

Figure 2.2. Lifespan over the spawning season (in 5 day intervals) for four streams with tagging data. Colors indicate stream size categorized as small (blue), medium (yellow), and large (red). Grey lines show mortality model fits to data at midpoint of each 5-day interval.

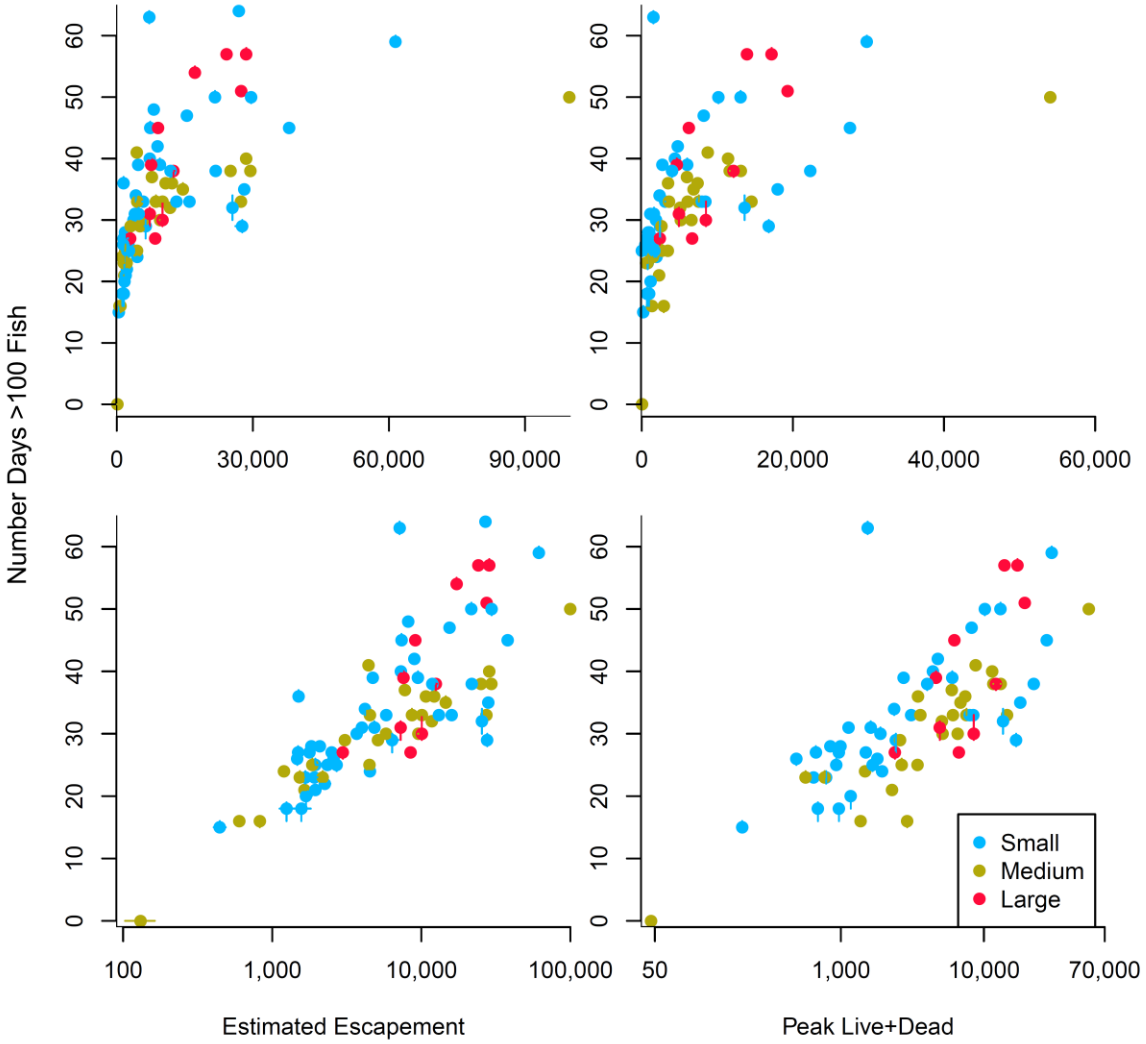

Figure 2.3. Estimated escapement and peak live plus dead counts versus salmon availability (measured as number of days with more than 100 fish in-stream), shown on regular (top) and log (bottom) scales. Error bars indicate 95% posterior densities, which are conditional on mortality model fits.

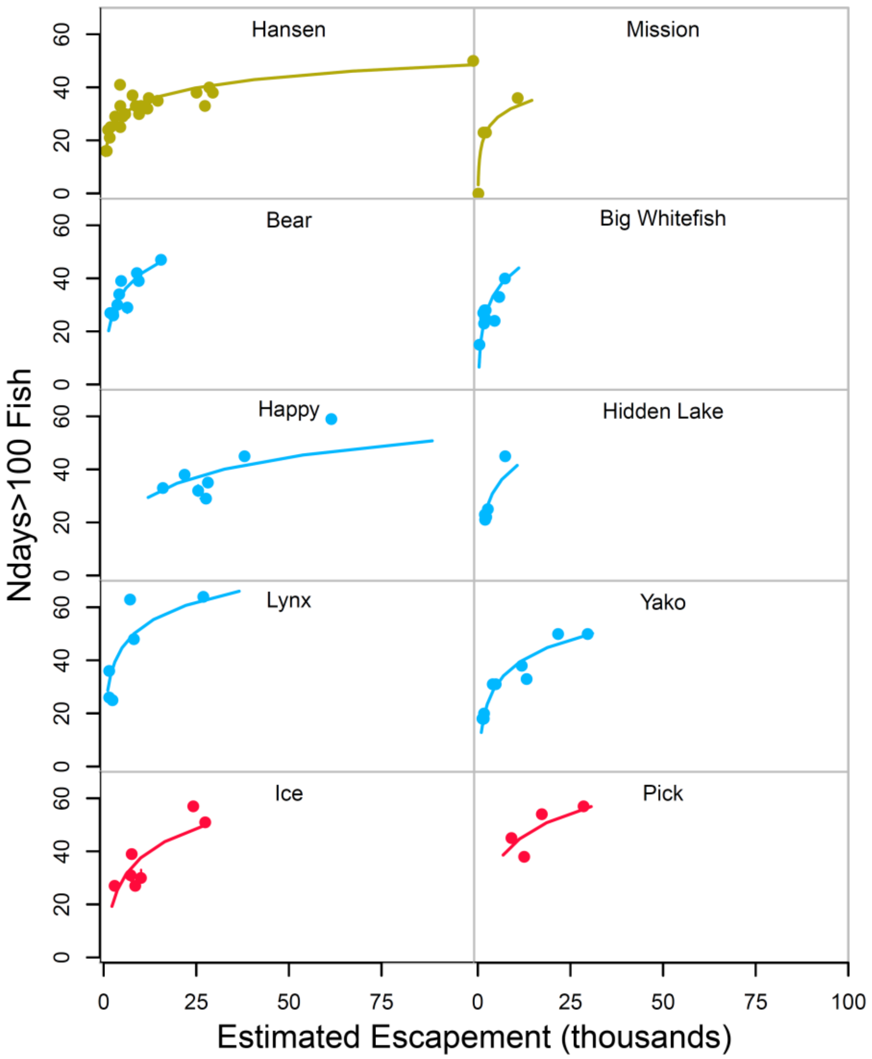

Figure 2.4. Model estimated escapements versus salmon availability measured in number of days with 100 fish or more in stream. Lines fit are for model 2 (Table 2.1) with individual intercepts for each streams, and random slopes within size groupings.

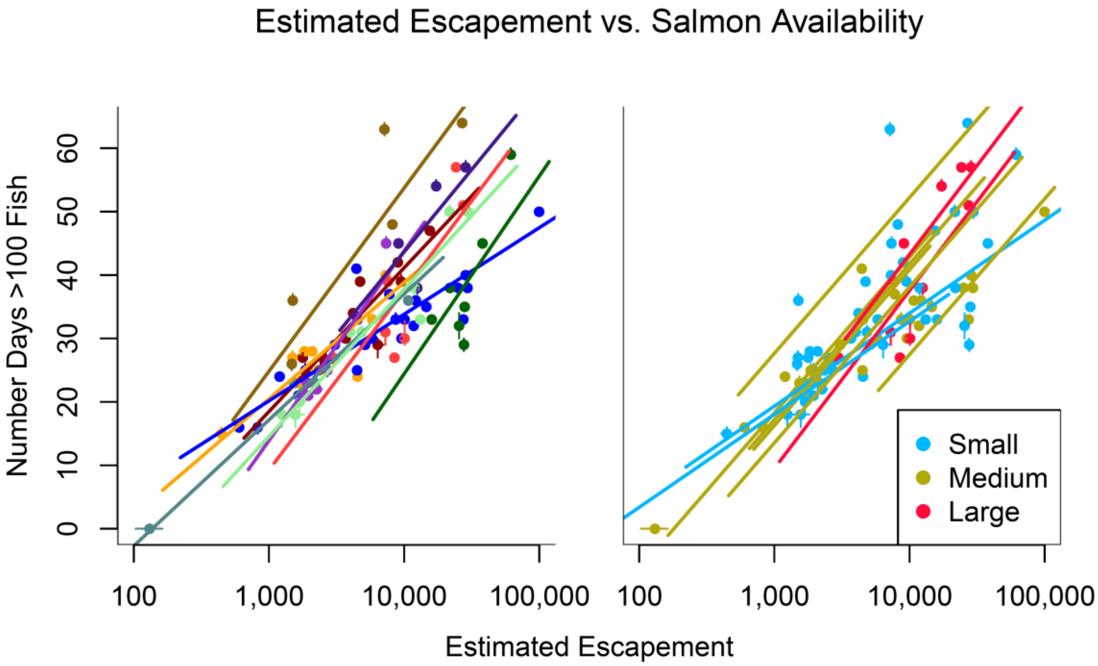

Figure 2.5. Model estimated escapements versus salmon availability measured in number of days with 100 fish or more in stream, shown on a log scale. Left plot shows fits for model 1 (Table 2.1) with fixed, individual intercepts for each stream, and random slopes for each stream. Right plot shows fits for model 1 (Table 2.1) with fixed, individual intercepts for each stream, and random slopes for each size grouping.

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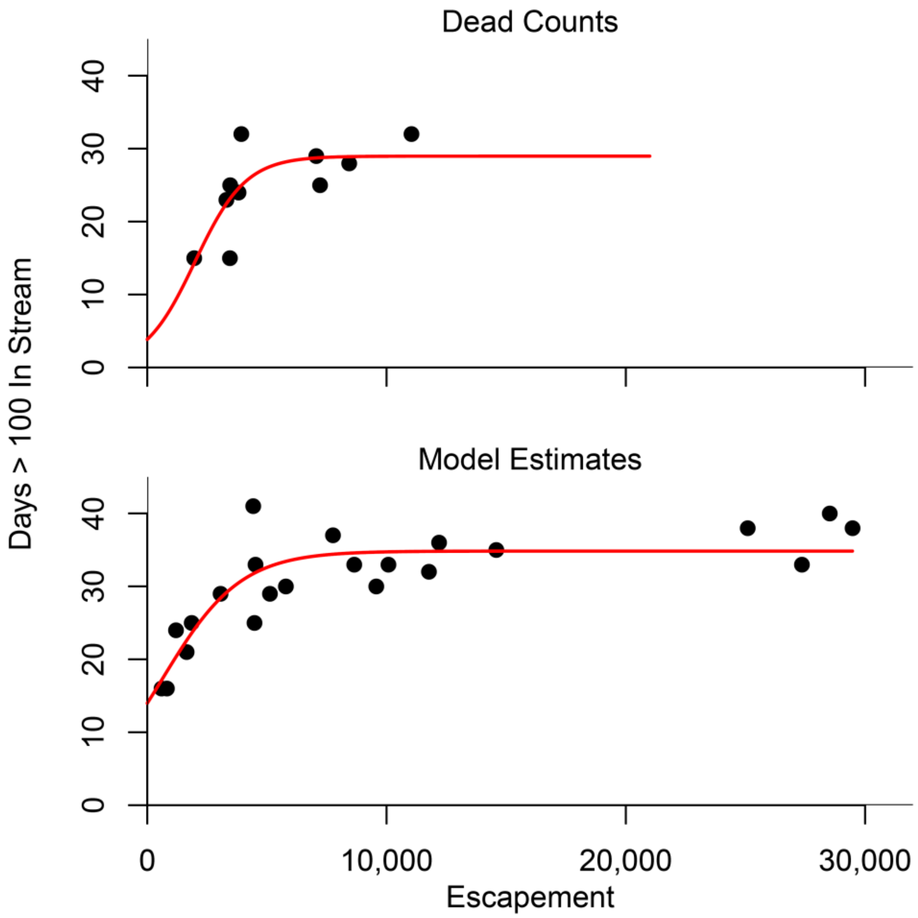
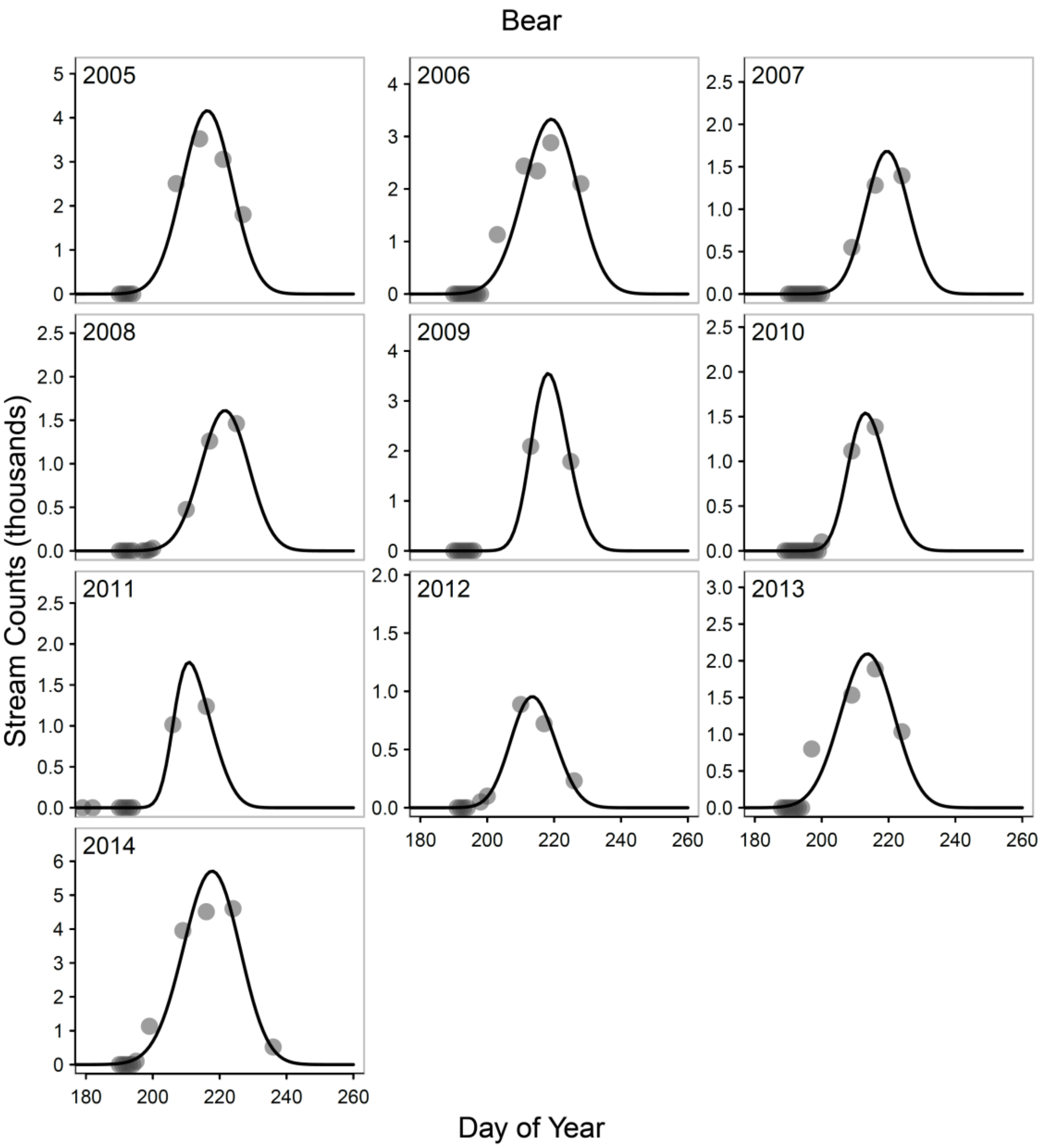
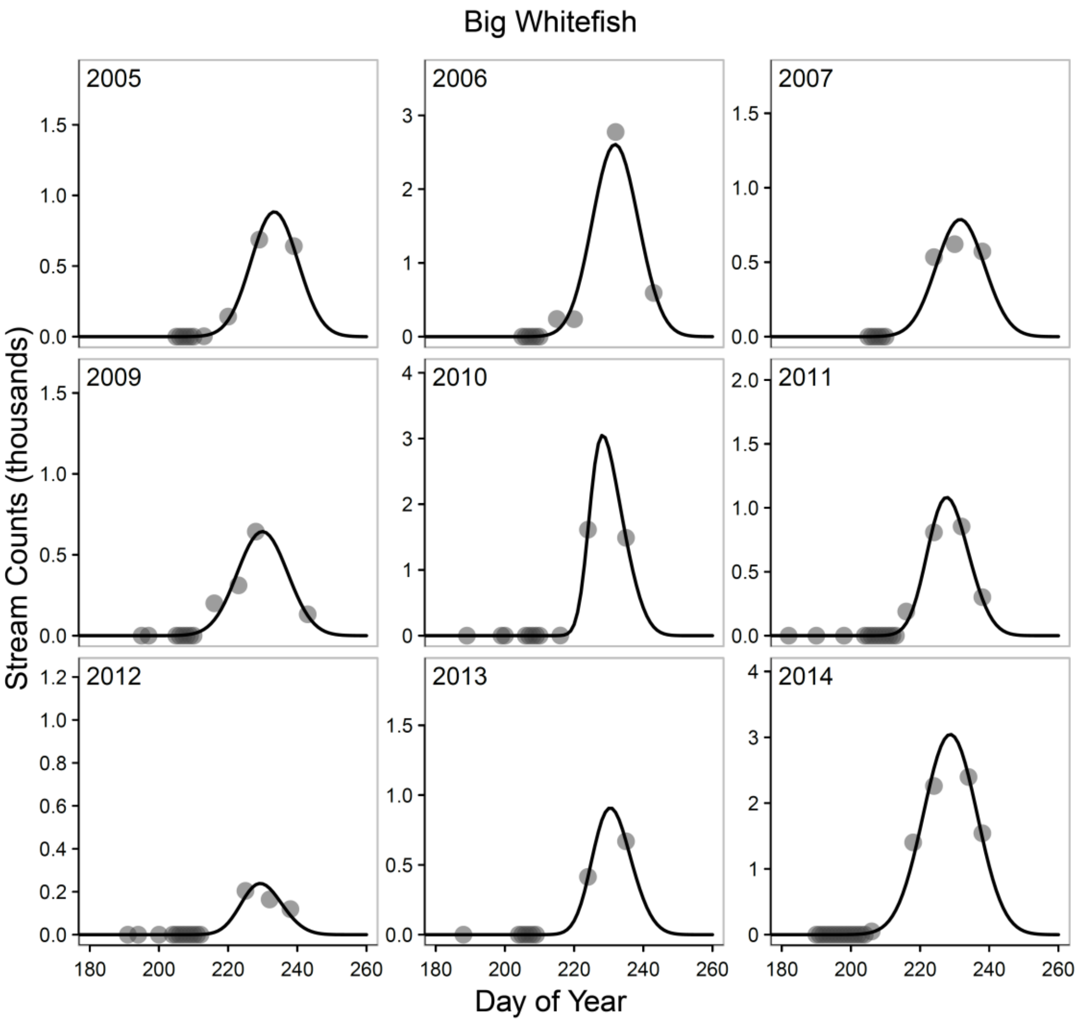
Appendix



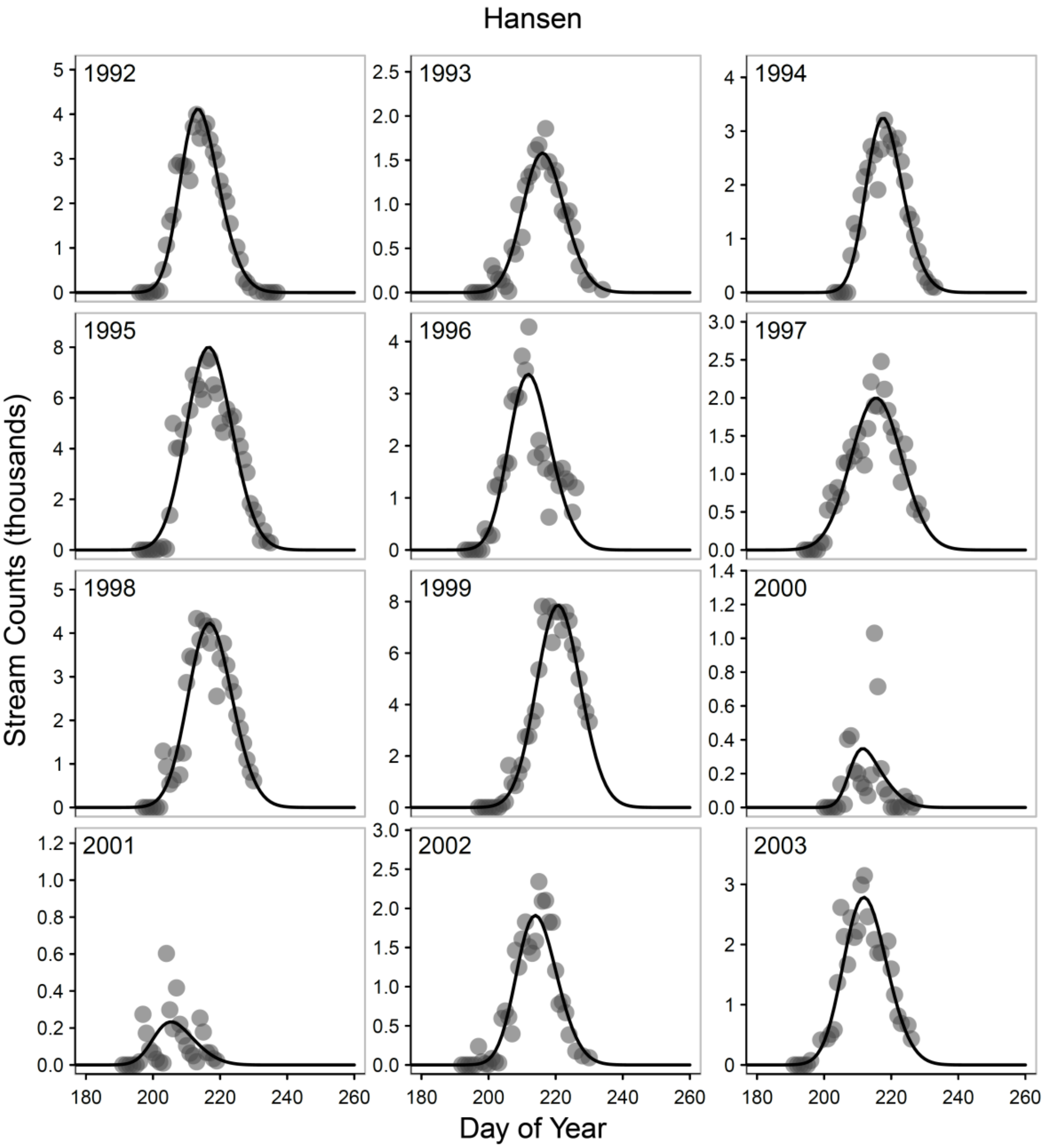
A.1. Estimated escapement versus salmon availability measured as number of days with more than 100 fish in stream. Top plot shows escapement estimates based on total dead fish counted, and number of days with more than 100 fish measured from daily counts (only select years had daily counts up until less than 100 fish were present). Bottom plot shows the same but model estimated escapement and availability. Bottom plot excludes 2014 data point which had an estimated escapement near 100,000 – with number of days with more than 100 fish estimated at 50.



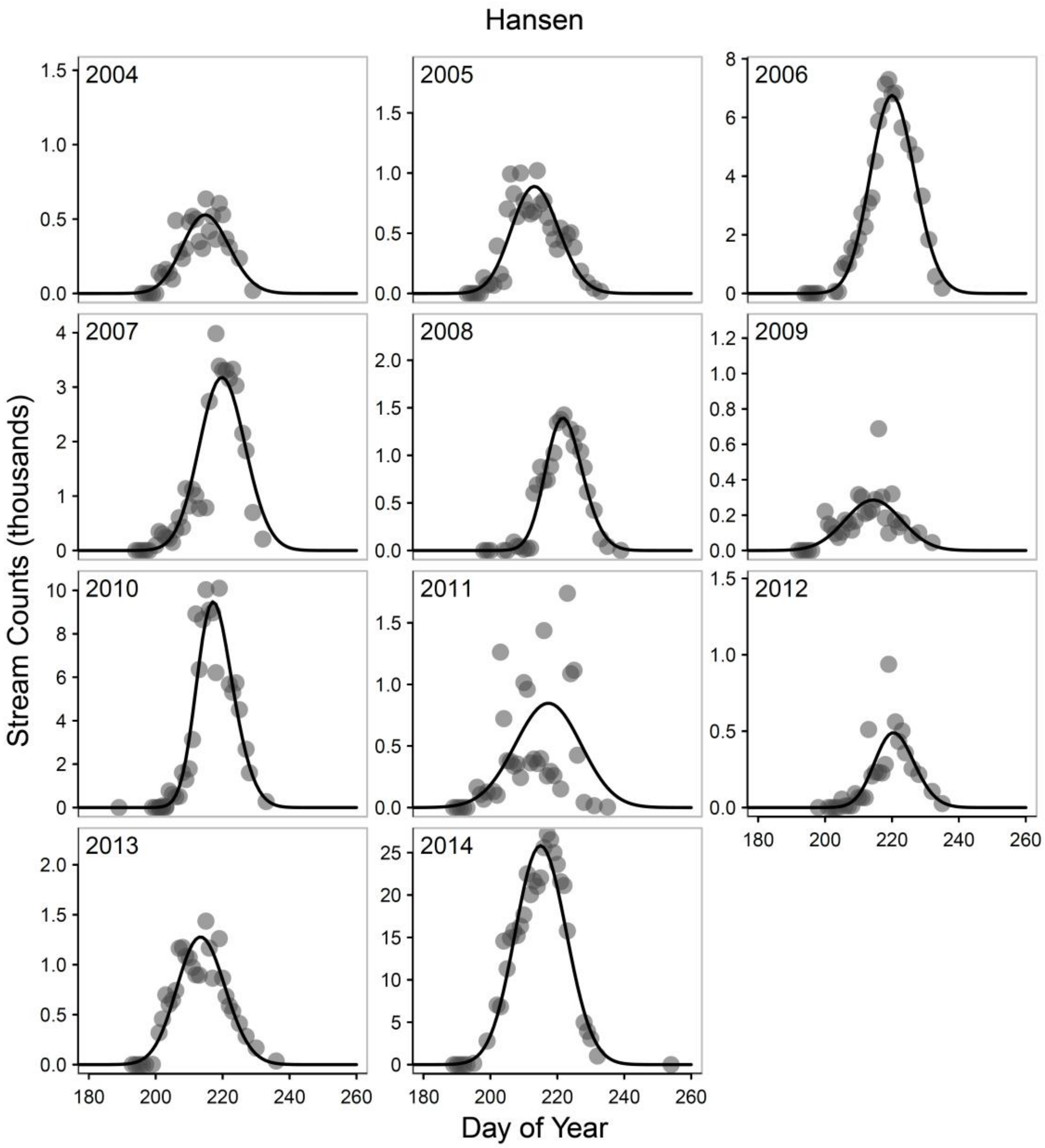
A.2. Data and model fits for number of fish instream over the spawning season at Bear creek, which is characterizes as a medium-sized stream in our analysis.



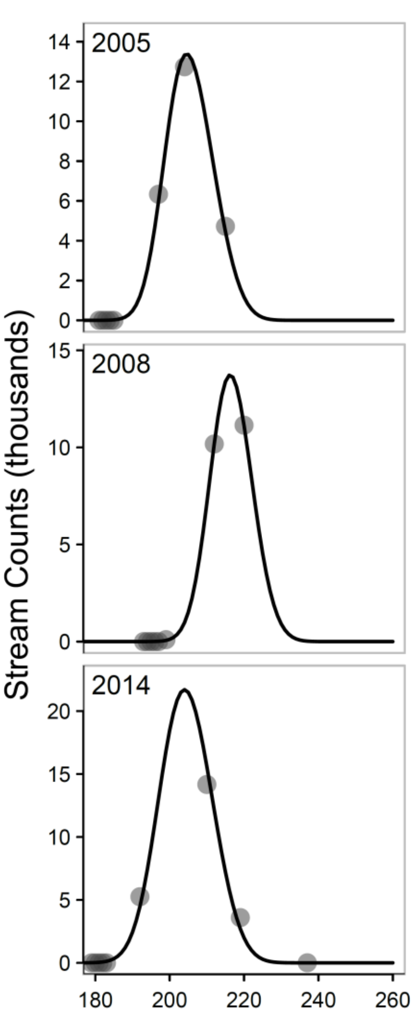
A.3. Data and model fits for number of fish instream over the spawning season at Big Whitefish creek, which is characterizes as a medium-sized stream in our analysis.



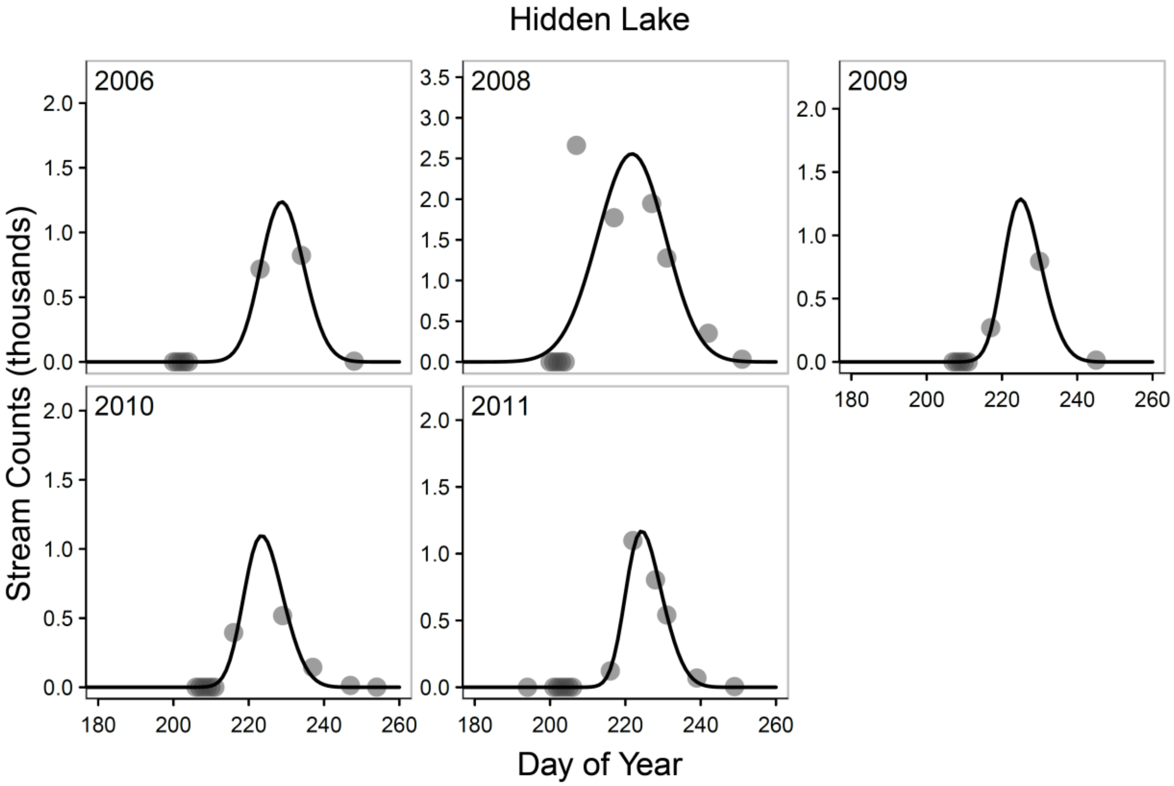
A.4.1 Data and model fits for number of fish instream over the spawning season at Hansen creek, which is characterizes as a small-sized, high predation stream in our analysis.



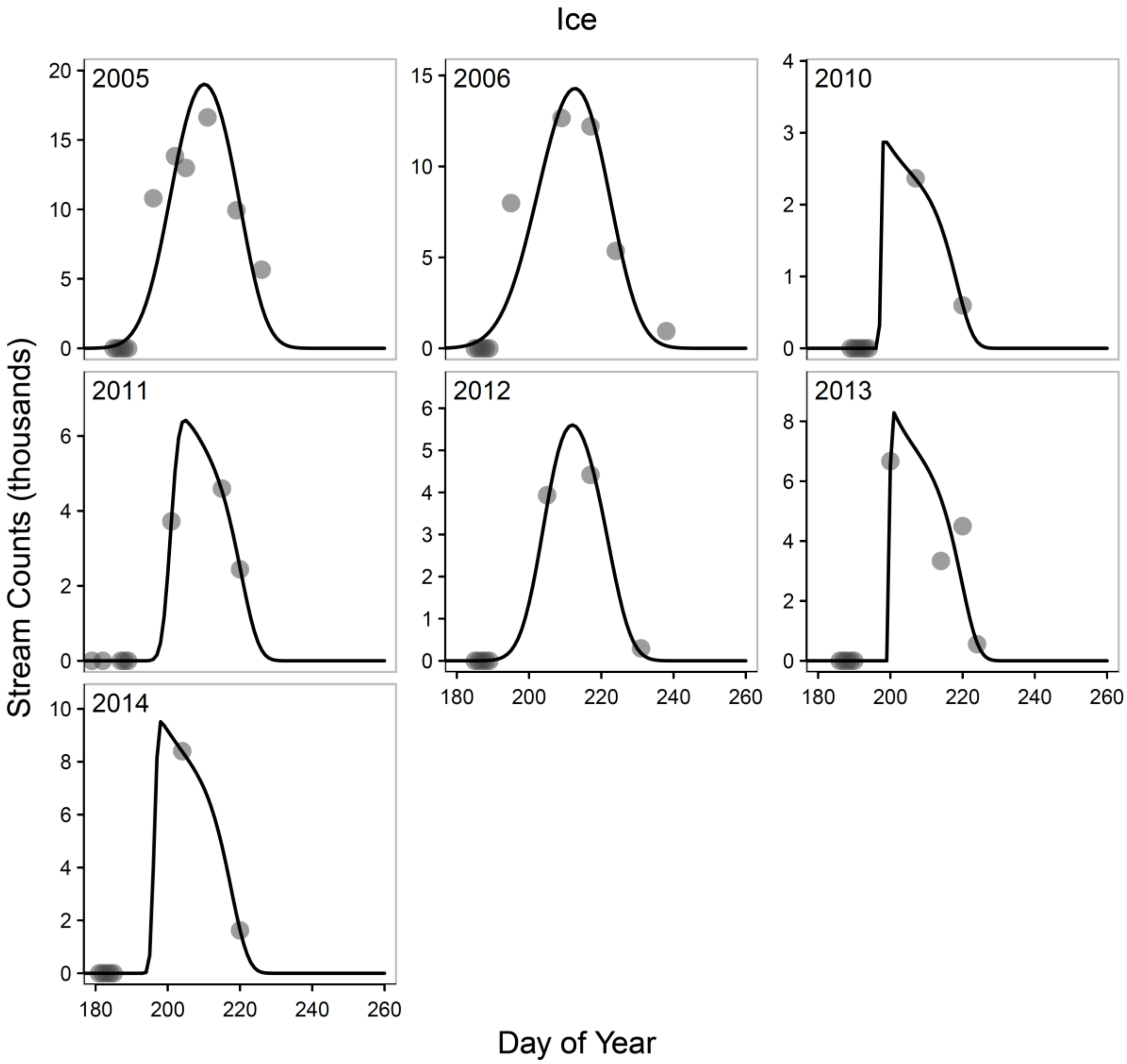
A.4.2 Data and model fits for number of fish instream over the spawning season at Hansen creek, which is characterizes as a small-sized, high predation stream in our analysis.



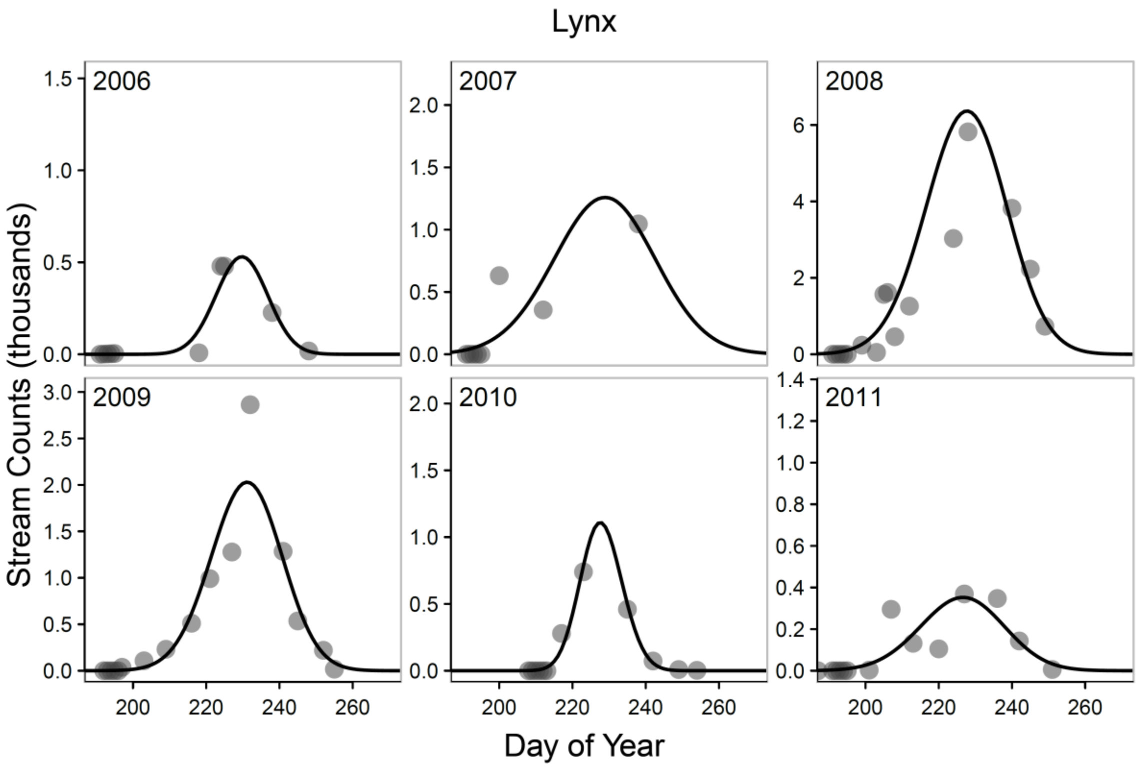
A.5. Data and model fits for number of fish instream over the spawning season at Happy creek, which is characterizes as a medium-sized stream in our analysis.



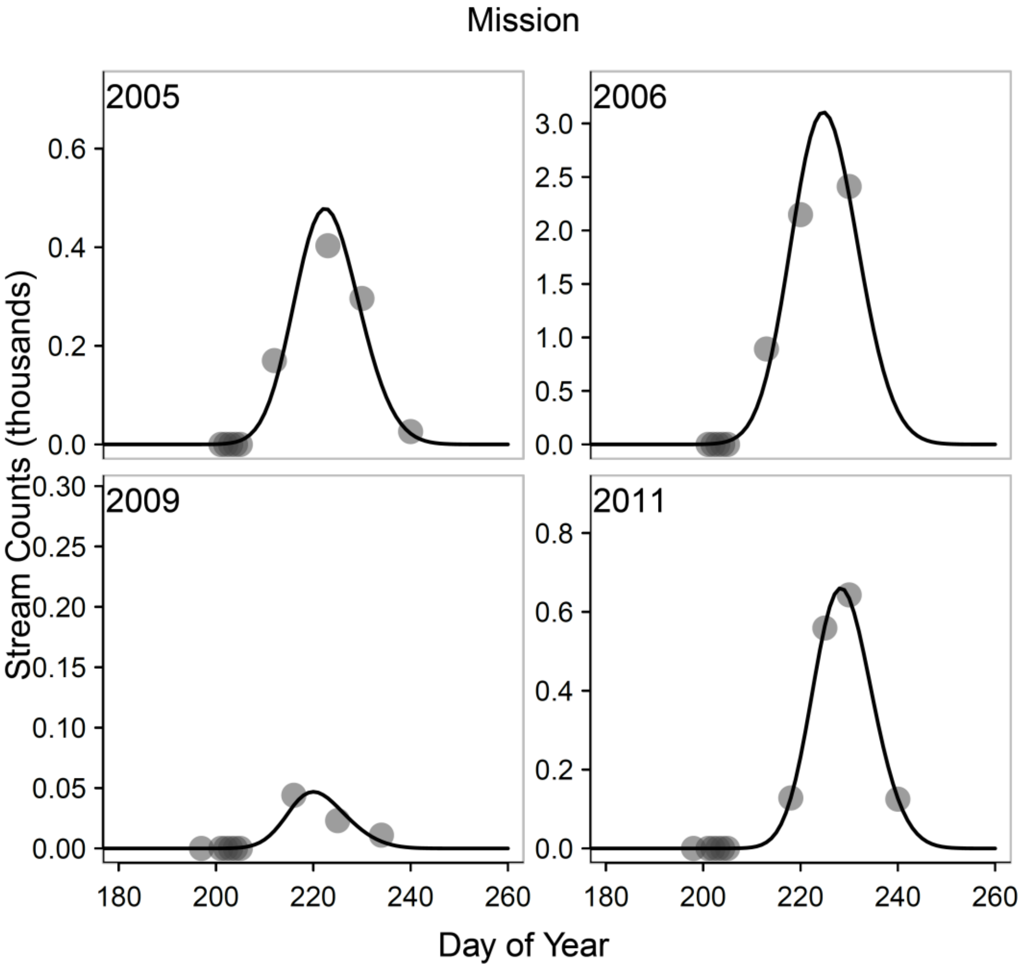
A.6. Data and model fits for number of fish instream over the spawning season at Hidden creek, which is characterizes as a medium-sized stream in our analysis.



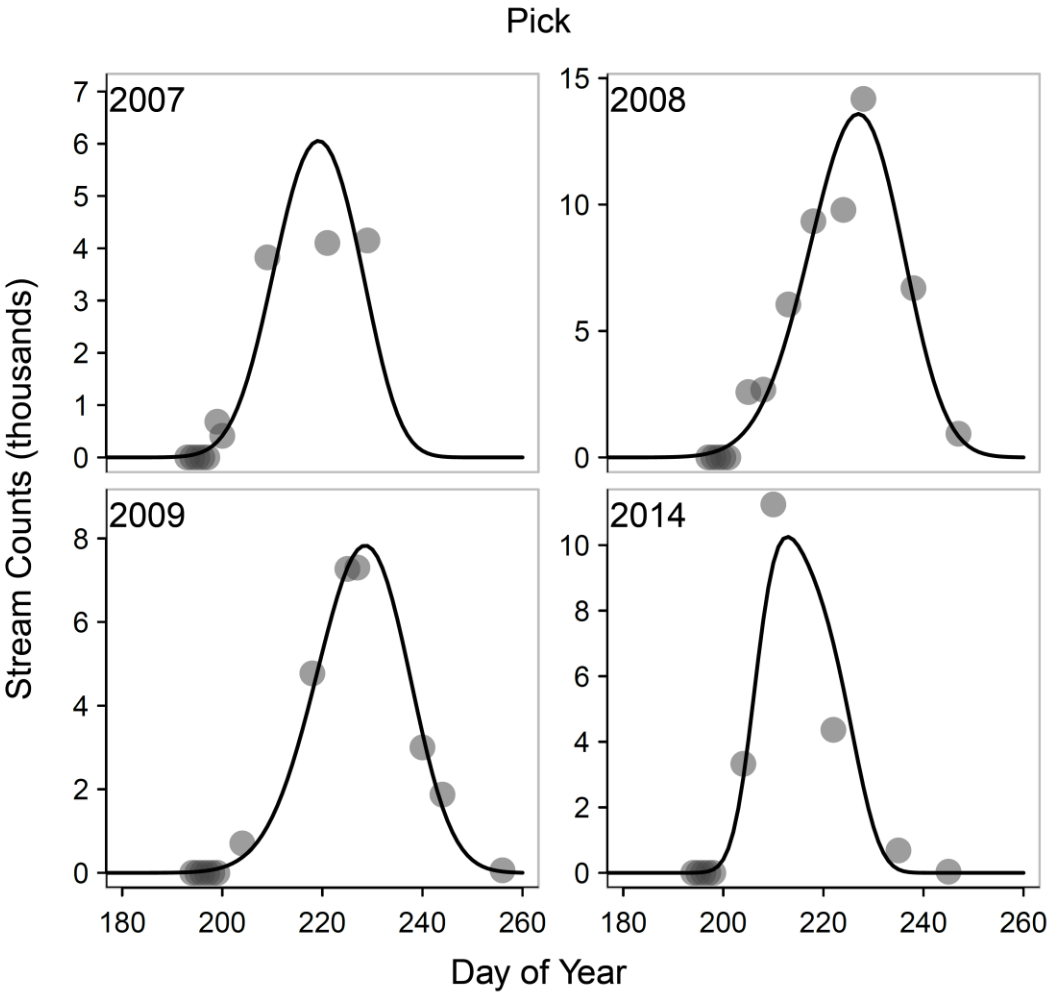
A.7. Data and model fits for number of fish instream over the spawning season at Ice creek, which is characterizes as a large-sized, low predation stream in our analysis.



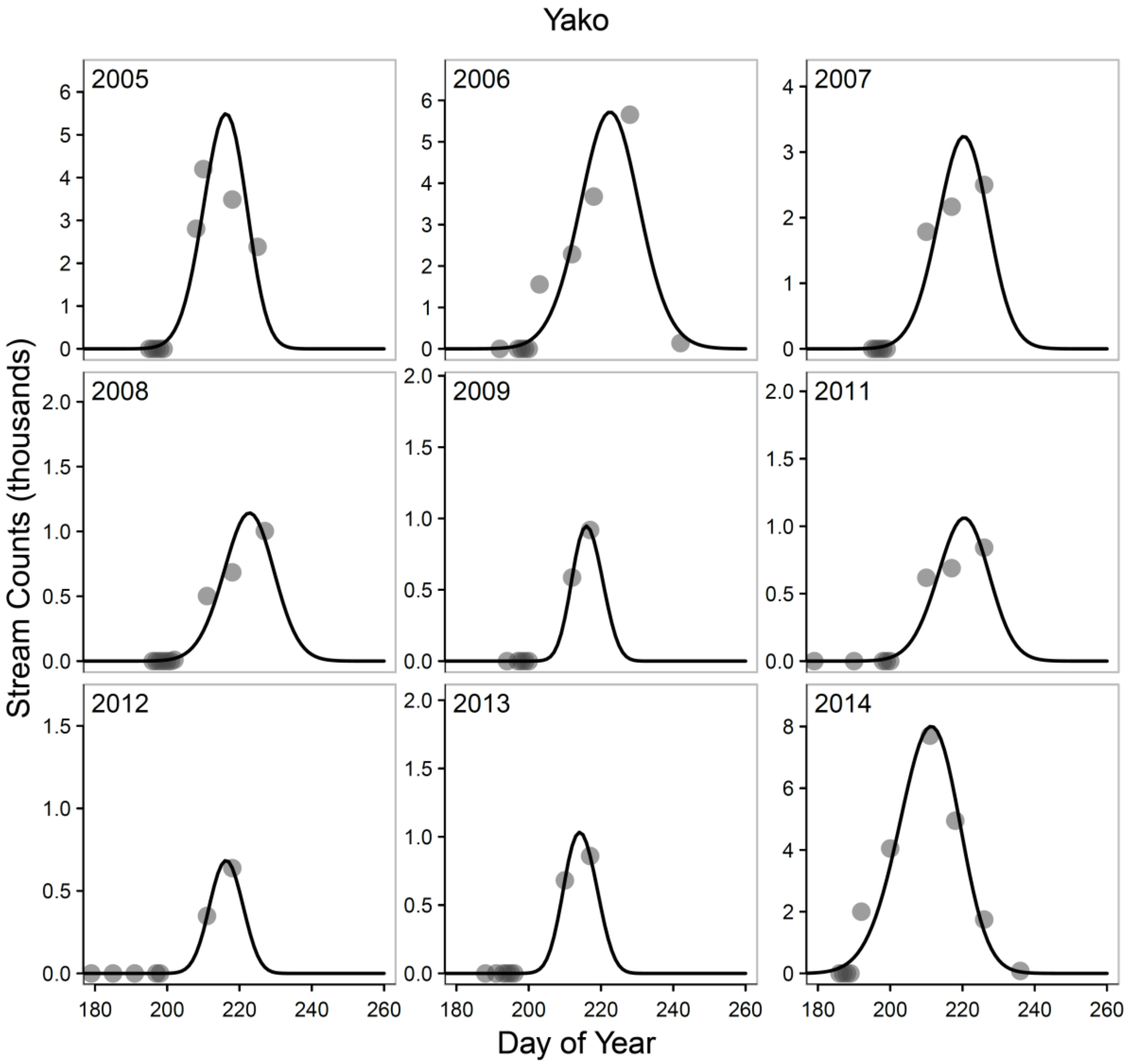
A.8. Data and model fits for number of fish instream over the spawning season at Lynx creek, which is characterizes as a medium-sized stream in our analysis.



A.9. Data and model fits for number of fish instream over the spawning season at Mission creek, which is characterizes as a small-sized, high predation stream in our analysis.



A.10. Data and model fits for number of fish instream over the spawning season at Pick creek, which is characterizes as a large-sized, low predation stream in our analysis.



A.11. Data and model fits for number of fish instream over the spawning season at Yako creek, which is characterizes as a medium-sized stream in our analysis.