Received: 20 February 2018 | Accepted: 3 August 2018
DOI: 10.1111/1365-2664.13286

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Trophic implications of a phenological paradigm shift: Bald eagles and salmon in a changing climate

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Abstract

1. Climate change influences apex predators in complex ways, due to their important trophic position, capacity for resource plasticity, and sensitivity to numerous anthropogenic stressors. Bald eagles, an ecologically and culturally significant apex predator, congregate seasonally in high densities on salmon spawning rivers across the Pacific Northwest. One of the largest eagle concentrations is in the Skagit River watershed, which connects the montane wilderness of North Cascades National Park to the Puget Sound.
2. Using multiple long-term datasets, we evaluated local bald eagle abundance in relation to chum and coho salmon availability; salmon phenology; and the number and timing of flood events in the Skagit. We analysed changes over time as a reflection of climate change impacts, as well as differences between managed and unmanaged portions of the river.
3. We found that peaks in chum salmon and bald eagle presence have advanced at remarkably similar rates (*c.* 0.45 days/year), suggesting synchronous phenological responses within this trophic relationship.
4. Yet the temporal relationship between chum salmon spawning and flood events, which remove salmon carcasses from the system, has not remained constant. This has resulted in a paradigm shift whereby the peak of chum spawning now occurs before the first flood event of the season rather than after.
5. The interval between peak chum and first flood event was a significant predictor of bald eagle presence: as this interval grew over time (by nearly one day per year), bald eagle counts declined, with a steady decrease in bald eagle observations since 2002. River section was also an important factor, with fewer flood events, and more eagle observations occurring in the river section experiencing direct hydroelectric flow management.
6. *Synthesis and applications*. The effects of climate change and hydroelectric management contribute to a complex human footprint in the North Cascades National Park, an otherwise largely natural ecosystem. By accounting for the differential phenological impacts of climate change on bald eagles, salmon, and flood events, Park managers and the operators of the hydroelectric system can more effectively ensure the resilience of the eagle–salmon relationship along the Skagit River.

KEYWORDS
bald eagle, climate change, flood, *Haliaeetus leucocephalus*, hydroelectric management, phenology, salmon, trophic interactions

1 | INTRODUCTION

Wildlife in both protected and human-dominated landscapes face uncertain futures as Earth's climate changes (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Groffman et al., 2014). While some of these changes are readily observable and represent dramatic shifts, other changes to species' ranges, abundances, and phenology reflect varied and complex responses to changing environmental conditions (Pacifici et al., 2017). The implications of climate change vary across species and regions, and interact with other anthropogenic stressors on landscapes, such as those occurring from hydroelectric dams, resource extraction, and commercial harvest (Crain, Kroeker, & Halpern, 2008; Mantyka-pringle, Martin, & Rhodes, 2012). Furthermore, the effects of climate change are not limited to direct impacts on a single species, but will also impact interspecific and trophic interactions, thereby increasing the uncertainty of long-term climate change effects on ecological communities (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010).

Some of the most remote areas of wilderness in the continental United States are found in the transboundary region of the Canadian-United States border of the Pacific Northwest (Figure 1). This area includes the North Cascades National Park Service Complex (NOCA), which provides valuable habitat for a number of species in an otherwise rapidly developing region (Gray, Azuma, Lettman, Thompson, & Mckay, 2013; Yeakley, Maas-Hebner, & Hughes, 2014). The Skagit River is a key geographic and ecological feature in the western portion of the Park, connecting remote montane ecosystems to the Puget Sound and serving as a key wintering site for bald eagles (*Haliaeetus leucocephalus*), an apex predator that feeds in high densities on spawning of chum (*Oncorhynchus keta*), and coho (*Oncorhynchus kisutch*) salmon.

As a National Park Service Complex, NOCA embodies both traditional and more contemporary models of conservation: in the classical model of the U.S. National Park System, NOCA includes vast areas of officially designated wilderness with limitations on backcountry use and permitted activities, as well as two National Recreation Areas that permit hunting, fishing, and recreational watercraft. Yet along the Skagit River, NOCA also houses some of the region's largest hydroelectric dam infrastructure, which has resulted in substantial changes to the hydro-ecology of the system and reflects a more modern vision of achieving conservation within mixed-use landscapes (U.S. National Park Service, 2012). These co-existing models of conservation are both being challenged by climate change, a distinctly modern threat which recognises no park boundary and which impacts ecosystems in multiple, interacting ways (Carroll, Dunk, & Moilanen, 2010). Indeed, climate change has compelled the broader natural resource management community to seek management practices which can accommodate species' shifting spatial distributions, abundances, and phenology as they adapt to a changing climate (Monzón, Moyer-Horner, & Palamar, 2011; Rannow et al., 2014; Welling, 2011). In this endeavour, long-term datasets are particularly valuable as a means of understanding long-term trends in species distributions, habitat use, and phenology, and to distinguish natural variability from climate-driven, directional changes.

In this study, we use over 30 years of data and build on previous analyses (Dunwiddie & Kuntz, 2001) to evaluate the relationship between bald eagle habitat use; chum and coho salmon availability and phenology; and the number and timing of flood events in the Skagit. Although it is well established that bald eagles respond readily to spawning salmon availability (Restani, Harmata, & Madden, 2000; Stinson, Watson, & McAllister, 2001), we examine the particular dynamics of this relationship within the context of climate change and the effects of hydroelectric dam management by comparing

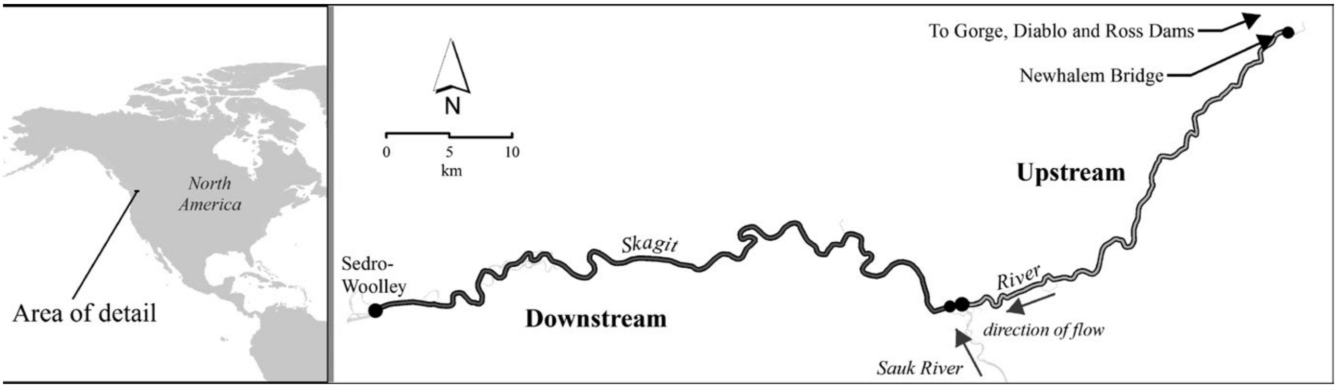

FIGURE 1 Map of the Skagit River Study Area. Map of the Skagit River (Washington, USA), showing both the upstream section (grey) where flow is highly managed by three hydroelectric dams, and the downstream section (black) where flow is less managed due to additional inputs from unregulated tributaries

sections of the river with primarily controlled vs. uncontrolled flows. Building upon previous analyses, we assess trends in eagle habitat use, salmon escapement, number of flood events, and examine the role of climate change as a driver of phenological relationships between these interacting components of the ecosystem.

2 | MATERIALS AND METHODS

For all analyses, we divided the Skagit into two sections: the upstream section (river mile 67.2 to 93.3), which is dominated by flow regulation from the Ross, Diablo, and Gorge hydroelectric dams. The downstream section (river mile 24–67.2) includes the confluence of the unmanaged Sauk River, which contributes an average of 2,740 cubic feet per second (CFS) (U.S. Geological Survey, 2018) to the main stem of the Skagit, resulting in significant uncontrolled flows as compared to the upstream portion of the Skagit (Figure 1). Data on eagles, salmon, and flood events were collected in different years depending on the source and location, resulting in asymmetrical data availability across years for different components of the system (Supporting Information Table S1). Whenever possible, we conducted our statistical analyses using data from all available years.

2.1 | Eagles

Eagle counts were collected weekly by biologists from the National Park Service (NPS), the US Forest Service (USFS), and The Nature Conservancy (TNC), with assistance from citizen science volunteers. Eagles were counted from 1982 to 2016 in the upstream portion, and from 1990 to 2016 in the downstream section (Supporting Information Table S1). Observations were conducted as described in Dunwiddie and Kuntz (2001): one or two observers counted each eagle, noting the time, location, and, in some instances, weather conditions and whether the individual was an adult (fully white head) or a subadult (brown or mottled head). For these analyses, detection bias could not be quantified across the entire study; however, we assumed such bias was negligible because overwintering bald eagles in this system are easily detectable to even casual observers by their contrasting color and form against defoliated deciduous trees, high perches atop conifer crowns, and flying and foraging behaviour. At least one experienced observer conducted each survey and was typically supported by at least one additional observer.

Observers counted from a slow-moving vehicle on State Route 20 (north side of Skagit), and on foot from fixed vantage points where Route 20 did not allow for direct view of the river. Much of the upstream data (from Rockport to Marblemount, 1982–2000) were collected by the same individual, but counts in the downstream portion were conducted by numerous volunteers through time. Counts were conducted between 9:00 and 10:00 a.m. local time, and duration depended primarily on observed eagle density, visibility, and weather conditions. Although an effort was made to maintain the same observational sites from year to year, the long duration of this study resulted in new tree growth which blocked visibility of the river at some locations. In these cases, new fixed observation points were established or slightly relocated to maintain consistency of the observational area through time.

Although portions of the datasets include observations ranging from November to March, most years included observations only from December to January; therefore, we focused our analysis for eagles, salmon, and flood events on this period of 7 weeks (calendar weeks 49-3; average dates: Dec 7–Jan 21) (Supporting Information Table S2). Eagle phenology was derived from this dataset of observational counts by identifying the week of the year in which maximum eagle observations were made.

Eagle count data were assimilated and analysed by combining datasets from the three sources (NOCA, USFS, and TNC). We used NOCA data on eagle counts whenever available since these data had more detail (i.e., adult:subadult ratio) and were more complete. In weeks where NOCA data were not available, we substituted analogous eagle count data from the USFS and TNC datasets. Because surveys were conducted roughly every Wednesday, weekly survey dates from year to year were not necessarily consistent; we therefore compared weekly totals and analysed inter-annual trends based on the week of the year in which the data were collected, rather than on calendar date (Supporting Information Table S2). We express this as "season week," whereby the first week of December (calendar week 49) is the first week of the observation season (week 1). When calculating annual totals, we summed all available counts; when calculating weekly averages, we ignored any missing weeks (i.e., missing values were treated as NA).

2.2 | Salmon

Escapement describes the annual number of salmon which escape mortality and return back to their spawning groups (Nehlsen, Williams, & Lichatowich, 1991). Escapement represents the spawning population, and is an important measure of salmon availability for predators such as bald eagles (Dunwiddie & Kuntz, 2001). Escapement data were obtained from publicly available datasets from Washington Department of Fish and Wildlife (WDFW, 2018). For chum, escapement data were available for 1968–2015; coho escapement data were available from 1983 to 2015 (Supporting Information Table S1). We examined only fall chum and coho runs in the main stem of the Skagit (population names *Mainstem Skagit Fall Chum* and *Skagit Coho*). Salmon escapement phenology data for the Skagit River and associated tributaries were provided for 1981–2015 by WDFW (WDFW, unpublished data), based on live surveys of chum and coho at 34 distinct survey locations in the downstream section and 37 locations in the upstream section. Survey efforts at specific river miles and tributaries varied across years in effort and timing, but the large number of surveys each year provided substantial data to generate an annual mean date of peak run for both river sections.

To assess trends in salmon escapement, we used a robust regression methodology described by Geiger and Zhang (2002), which estimates annual changes in salmon escapement and contextualises the biological significance of these changes based on estimated escapement levels in a "year-zero" reference year. In contrast to standard regression, which is sensitive to outliers and data series length, this methodology was designed to estimate changes in escapement despite high inter-annual variability (Geiger & Zhang, 2002). We divided the data into chronological thirds and calculated a robust estimate of the slope across all years as:

$$s = \frac{m_1 - m_3}{\text{years}}$$

where s is the slope, m_1 is median escapement in the first third, m_3 is median escapement in the last third, and *years* is the number of years between the middle of the first and last thirds. We then used resistant regression to back-cast to a year-zero reference point (i.e., to estimate the escapement level in the year before the first observation was made) and applied the robust slope derived above to the median escapement level in each third. We then calculated and averaged the three y-intercepts to find the robust estimate of the year-zero escapement level, and used this average as the reference escapement level. The y-intercept in each third is calculated as:

$$y_0 = s(years) + m_i$$

where y_0 is the y-intercept in period i, s is the robust estimated slope (as calculated above), *years* is the number of years between the beginning of the series and the midpoint of period i, and m_i is the median in period i. Using this methodology, a stock is considered to be in decline if it meets the following criteria: the stock experienced a 50% decline from the reference level over 15 years (i.e., the median escapement level in the last third of data is less than half of the reference level); or if the robust estimate of annual decline (i.e., the slope) exceeds 5% of the reference level.

Salmon phenology was determined by identifying the day of year in which peak salmon counts occurred, as averaged across multiple survey sites in a river section. When examining the phenological relationship between salmon and eagle peaks, we use salmon day of peak to calculate the associated week of peak, which we then compared to eagle phenology at a weekly scale. Because bald eagles feed principally on salmon carcasses, we expect peak salmon availability for eagles to occur slightly after live salmon peaks. Although we considered coho salmon, the abundance of chum in the Skagit and the preference of bald eagle for chum over coho led us to focus much of our later analysis on chum–eagle–flood relationships (Dunwiddie & Kuntz, 2001; Stinson et al., 2001; B. Barkdull, pers. comm., WDFW, May 02, 2017). When comparing salmon phenology to flood timing, we compared salmon day of peak and day of first flood event.

2.3 | Flood events

Flood events were derived from publicly available USGS gage data (U.S. Geological Survey, 2018). We used stream flow data from two stations in the upstream (Newhalem, Station ID: 12178000) and downstream (Concrete, Station ID: 12193000) sections of the river. Using the raw flow data, available in 15-min increments from 1987 to 2016, we identified the daily maximum flow rate and calculated the number of flood events per season. We then derived phenological data (i.e., date of first flood event) from this flow dataset (Supporting Information Table S1).

We counted flood events per season by defining a minimum threshold at each gage: if water levels reached or exceeded that threshold at any point during a given 24-hr period, we counted one flood event. We used two different thresholds to define flood events at the different stations, identifying water levels that would result in gravel beds being covered by water and therefore washing out salmon carcasses. Based on consultations with WDFW fisheries biologists, we set the flood stage level at 8,000 CFS and 24,000 CFS at Newhalem and Concrete, respectively. In order to identify discreet flood events (i.e., to distinguish a multi-day flood from distinct flood events occurring in short succession), we considered any consecutive days above the flood threshold to be part of a single flood event; a subsequent event was not counted unless there was at least one 24-hr period where water levels fell below the threshold.

2.4 | Statistical methods

When comparing counts across river section, we used ANOVA to assess significance. We used multiple linear regression with year as one of several potential regressors to assess trends in counts or phenology over time, using forward stepwise regression and adjusted R^2 to select the final model. We used quadratic terms when appropriate to model trends over time, and transformed the response variable and/or modelled variance separately (i.e., through a generalised linear model with a power variance function) when needed to account for unequal variance. We defined a significance level of $\alpha = 0.1$ for the purposes of this analysis. All analyses were conducted in R (Version 1.0.136).

3 | RESULTS

3.1 | Bald eagle counts and phenology

We analysed trends in total annual eagle observations and mean weekly observations in upstream and downstream sections (Supporting Information Table S3). Eagle observations were higher upstream than downstream (Figure 2) ($p < 0.001$). In the upstream section, total annual eagle counts averaged 1,210.4 (309 – 2,599, ±532.5), with an average weekly count of 179.9. Downstream, annual eagle counts averaged 616.7 (254 – 1,259, ±270.3), with an average weekly count of 92.6. Average weekly eagle counts were used to examine inter-annual trends in eagle observations, rather than annual totals, to account for years with incomplete survey weeks. Over the study period, mean weekly eagle counts declined overall (Figure 2), although the trend displayed a quadratic pattern: initially, mean weekly eagle counts increased (13.8, $p < 0.001$) until peaking in 1997 (upstream) and 2002 (downstream). After this peak, weekly eagle counts declined along the entire river (−0.003, $p < 0.001$). To contextualise possible population trends, we used the subset of eagle data including adult/subadult notation to examine changes in the adult:subadult

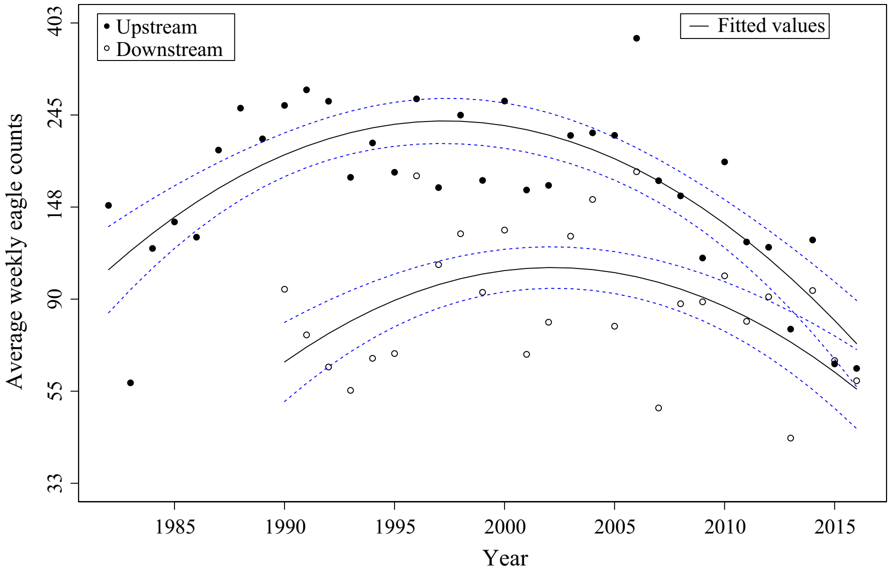

FIGURE 2 Average weekly eagle counts. Average weekly eagle counts in the Skagit River Study Area fit with regression lines after natural log transformation. *Y* axis has been back-transformed to show units as untransformed eagle observations

ratio (Supporting Information Table S4). Age class observations were available for only a portion of all the eagle observations (those made by NPS rather than TNC or USFS) and were only taken in some years in limited parts of the river (miles 24–74). In all years (*n* = 34, excluding one outlier; Supporting Information Table S4), adults uniformly outnumbered subadults (average ratio: 2.61), We found, however, no discernible trend in this ratio over time (0.004, *p*-value = 0.658).

Week of peak eagle detections occurred in season week 4.3 (Dec. 23–30) upstream (range: Dec. 9–Jan 21), and season week 4.2 (Dec. 23–30) downstream (range: Dec 01–Jan 21). The timing of peak eagle detections became significantly earlier during the study period: across both river sections, week of peak eagle count advanced an average of 0.065 weeks (equivalent to 0.45 days) per year (*p* = 0.001) (Figure 3a). Phenological differences in peak between river sections was not significant, nor was the interaction term between river section and year, indicating that eagle phenological shifts did not differ between river section.

3.2 | Salmon escapement and phenology

We compared escapement levels for chum and coho and analysed trends in salmon escapement over time. Chum are generally more abundant in the Skagit than coho (61,810.2; range: 3,193 to −209,478; Figure 4), particularly in even years when mean chum escapement is over three times higher than odd-year escapement. Annual coho escapement in the Skagit averaged 52,971.9 (range: 5,476–136,054).

We found mixed evidence of decline in salmon escapement in the Skagit: while our analyses found that one of the significance thresholds laid out by Geiger and Zhang (2002) was generally met (median stocks in the last third less than or equal to 50% of the reference level), annual declines were consistently below the significance threshold (−5% per year) (Supporting Information Table S5). For coho (1983–2015), median escapement in the last third was only 42.4% of the reference level, indicating a decline. However, the annual rate of decline was <5% (1.9%), falling short of the threshold (Figure 4). For chum across both even and odd years (1968–2015), we similarly found that the annual rate of decline was <5% (.95% per year); median escapement in the last third of the data was 56.4% of the reference level. In even years, however, when chum are highly abundant, stocks have declined by 3.8% per year, and the median escapement in the last third of even years was only 32.4% of the even-year reference period (Figure 4), reflecting a potentially more significant decline.

Peak chum generally occurred earlier (day 305–352; Nov.1–Dec. 18) than peak coho (day 332–56; Nov. 28–Feb 25). As with eagles, salmon peaks in the upstream section generally occurred after the downstream peak (12 days later for chum, and nearly 3 days later for coho). Salmon phenology also advanced over the study period: when considered across the entire river, chum peak date advanced by nearly half a day per year (0.43 days, *p* = 0.002; Figure 3a), while coho advanced by over 0.8 days per year (*p* < 0.001). In the downstream section, chum day of peak became earlier from 1982 until 2000, at which point the trend reversed through 2016.

3.3 | Flood events and timing

Upstream, there was an average of 1.1 flood events per season (range: 0–5); downstream, there was an average of 3.7 floods per season (range: 0–7). This corresponds with our expectation of more common flood events in the downstream section, given that the flow is only partially regulated in this river section. Using a Poisson regression, we analysed trends in the number of floods per season and found that across both river sections, there is limited evidence that flood events increased slightly over time (0.01 flood events/season, *p* = 0.07). When we consider the upstream section alone, however, we see that there was a significant increase in flood events per year (0.05, *p* = 0.008).

On average, the date of first flood event of the observational season was day 347.8 (Dec 13; range: Nov. 23–Feb. 23); there was no significant difference in average date of first flood in the upstream/downstream

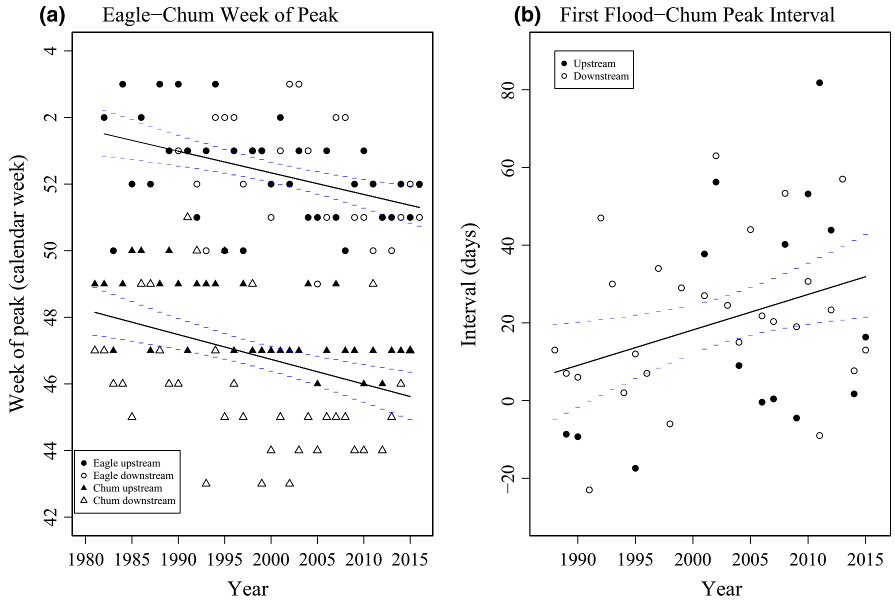

FIGURE 3 Eagle–chum–flood phenological relationship. Phenological relationships between the week of peak eagle observations; week of peak chum escapement; and the interval between first flood event of the season and peak chum observations in the Skagit River. Week of peak chum salmon and eagle observations (1982–2015) have advanced at similar rates, resulting in synchronous phenological shifts within this trophic relationship (a). In contrast, the interval (measured in days) between the first flood event of the season and peak of chum observations (1988–2015) has increased significantly, reflecting asynchronous temporal changes between flood events and chum (b). Weeks are expressed as calendar week of the year (see Supporting Information Table S2 for corresponding week of observational season). River sections are distinguished by closed symbols (upstream) and open symbols (downstream). Trend lines in (a) represent linear regressions for chum (dashed) and eagle (solid) as a function of year across both river section. Negative intervals in (b) indicate that the first flood of the season occurred before peak chum observations; positive intervals indicate that peak chum occurred before the first flood event

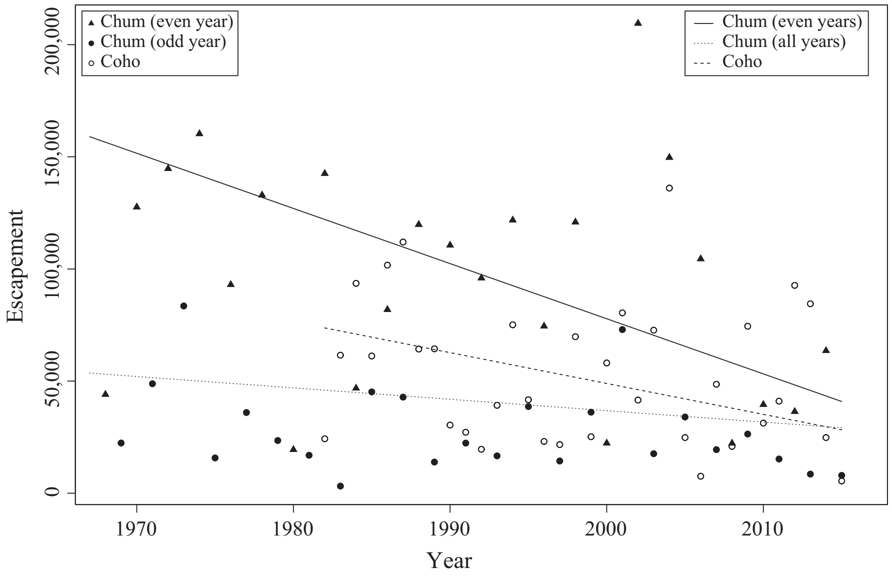

FIGURE 4 Salmon Escapement in the Skagit. Annual escapement for coho and chum salmon in the Skagit River over the study period (1968–2015). Regression lines reflect slope and reference year level as calculated through robust regression analysis (see Supporting Information Table S5); earliest values of the regression lines reflect the back-cast estimate of escapement in the reference year. Robust regression lines are shown for chum (even years; solid line); chum (all years; dashed line); and coho (all years; dotted line)

sections. The date of first flood event has grown slightly later over time: using a generalised linear model fit with power variance function such that variance is proportional to year, we found limited evidence that the date of first flood in the season has grown later by 0.66 days per year ($p = 0.07$). Variability in day of first flood, however, also increased markedly over time: across all years (1987–2016), the *SE* was 0.36, while from 2007 to 2016 it increased more than sixfold to 2.28.

3.4 | Eagle–salmon–flood relationships

We found several notable relationships between the counts and phenology of eagles, salmon, and flood events. Using Pearson's product-moment correlation coefficient, we assessed the degree of correlation between chum escapement and eagle detections (1982–2015), and found a strong positive correlation between chum escapement and eagle detections across the entire river ($r = 0.292$, $p = 0.02$). There was no significant correlation between coho salmon escapement and bald eagle counts ($r = -0.02$, $p = 0.85$). Floods were a significantly predictor of eagle counts (121 fewer eagles observed per flood event, $p < 0.001$). In years with the most floods (5–7 floods/year), the average annual eagle count was 512.6 eagles/year ($n = 8$); in years with the fewest floods (0–2 floods/year), the average eagle count was significantly higher (1,178 eagles/year, $n = 31$).

We examined phenological relationships between eagle, salmon, and flood event timing. Bald eagles and chum salmon have experienced similar phenological shifts: eagles advanced their peak by 0.065 weeks/year (*c.* 0.45 days/year), while chum salmon advanced their peak by nearly the same amount (0.43 days/year) (Figure 3a). To address whether the phenology of salmon and flood events interacted to affect bald eagles, we looked at the interval (in days) between the first flood event of the season and peak chum escapement. We found that this interval has been increasing steadily and significantly (0.91 days/year, p-value = 0.03) (Figure 3b).

Finally, we developed a linear model to describe average weekly eagle counts, taking into consideration the effects of salmon availability, salmon phenology, and the timing and number of flood events. Our final model of log-transformed average weekly eagle counts included the following regressors: year (12.5, $p < 0.001$), including a quadratic term (−0.003, $p < 0.001$); river section (upstream, 0.6, $p < 0.001$); even/odd year, which functions as an effective indicator of chum escapement (even, 0.3, $p < 0.001$); and the interval between first flood event and peak chum (−0.006, $p = 0.008$, adjusted $r^2 = 0.66$). The interval between peak chum and peak eagle observations, as well as the interval between peak coho and peak eagle observations, were not significant and were therefore excluded from the final model.

4 | DISCUSSION

Our analysis demonstrates the strong links between local bald eagle abundance, the timing and abundance of salmon runs, and the number and timing of flood events in the Skagit. We found strong evidence that phenological shifts have occurred in both bald eagle and salmon populations, and that the temporal relationship between chum peaks and flood events has changed in ways that are affecting the local abundance of bald eagles.

The number of eagles using the Skagit increased dramatically in the early part of our study period, although we detected a decreasing trend in recent years. This may reflect a spatial shift in resource use or could be a reflection of regional density-dependent declines in reproduction as populations recover from pesticide pollution and direct mortality experienced during the early and mid-20th century and reach regional carrying capacity (Elliott, Elliott, Wilson, Jones, & Stenerson, 2011; Stinson et al., 2001). Our data, however, only portray trends in local abundance and resource selection, rather than true population size; in fact, bald eagle populations have increased nationally (FWS, 2016). Because most overwintering eagles in this region migrate from Canada and Alaska, numerous drivers outside this study area could explain observed population trends (Stinson et al., 2001).

We found mixed evidence that chum and coho salmon escapement levels have decreased over time. Regionally, coho is considered to be a “species of concern” in the Puget Sound/Strait of Georgia region (an ecological unit which contains the Skagit River), indicating that this stock is thought to be stressed but that there is insufficient information to assess its status (NOAA National Marine Fisheries Service, 2009). In the neighbouring Nooksack River, wild strains of coho are thought to have gone extinct in 1991 (Nehlsen et al., 1991). Although we found relatively strong declines in chum escapement levels in even years, analyses of chum escapement trends at a regional scale indicate that the fish is doing relatively well: in 1997, a NOAA Stock Status report finds that there has been a 6.1% increase in Mainstream Skagit Chum (Johnson et al., 1997). More recent analyses have found that although broad declines in chum productivity have been observed since the early 2000s in the Pacific Northwest region, chum productivity inside Washington State has in fact increased (Malick & Cox, 2016).

As expected, we found a strong positive relationship between chum escapement and eagle counts, a strong negative relationship between flood events and eagle counts, and a non-significant relationship between coho escapement and eagle counts. We found mixed evidence for an increase in the number of flood events per year, although high variability made it difficult to draw firm conclusions about trends in flood events over time. Of particular interest was the significant negative relationship between the flood-chum interval (i.e., the interval between day of first flood event and chum peak) and weekly eagle counts: as the interval between the day of first flood and the day of peak chum escapement grew, average weekly eagle counts declined. This interval grew larger and more positive over time, with early years tending to demonstrate flood peaks before chum peaks (i.e., a negative interval) and later years demonstrating first floods after chum peaks (i.e., a positive interval) (Figure 3b). The negative effect of this changing interval on eagles was small but significant (−0.006, $p < 0.001$), demonstrating that the local abundance of eagles in this region is sensitive to the temporal relationship between salmon availability and flood events. In addition, the negative sign of this interval suggests that such asynchronous changes may have negative impacts for bald eagles if further changes continue.

4.1 | Effects of climate change

Climate change is affecting the phenology of nearly all terrestrial and aquatic systems at global and regional scales (Thackeray et al., 2016), and we see strong evidence for this particular dimension of climate change in the Skagit: both eagles and salmon have advanced their phenology significantly over the course of the study period. The rate of phenological change between interacting species is critical in determining the ecological consequences of phenological shifts, and our analysis found that eagles and chum salmon in the Skagit have advanced their phenology at remarkably similar rates (*c*. 0.45 days/year). This suggests a synchronous phenological response to climate change within this trophic relationship. Although higher trophic levels often display slower phenological responses than their prey (Thackeray et al., 2010), the synchronous relationship observed here is likely a reflection of eagles' ability to rapidly respond to patchy, ephemeral resources across the landscape (Knight & Knight, 1983). In contrast, we found an asynchronous temporal relationship between chum peaks and flood events: the interval between chum peak and first flood event increased significantly over the study period, growing by nearly 1 day per year. As this interval grew over time, a phenological paradigm shift occurred: historically, the earliest flood events occurred while chum were still alive and swimming, whereas increasingly floods begin after chum have peaked, spawn, and are on gravel banks in the form of carrion for eagles. While it is beyond the scope of this study to fully address the ecological implications of this shift, such a change is likely to have important impacts on eagles and the Skagit ecosystem more broadly: although eagles exhibit considerable plasticity in their ability to exploit resources, the limits of this adaptive plasticity in the face of rapid environmental change are poorly characterised (Reed, Schindler, & Waples, 2011). In addition, changes in salmon mortality and consumption could have wide-ranging consequences for components of the riparian ecosystem that are affected by transfer of nutrients from marine to freshwater systems facilitated by salmon migration (Schindler et al., 2003).

The phenological shifts documented in this study are not occurring in isolation, but instead interact with multiple other climate change impacts. Changes in temperature and the type, timing, and amount of precipitation are driving declines in snowpack and altering associated hydrological dynamics in the region (i.e., the timing and intensity of flood events and warm season flow levels) (Adam, Hamlet, & Lettenmaier, 2009; Mote, Hamlet, Clark, & Lettenmaier, 2005). Although warming in the winter and spring may benefit the freshwater life-cycle stage of some salmon, overall reproductive success for salmon is expected to decline in Washington State (Grah & Beaulieu, 2014) as a result of increased winter flows and scour events, earlier snowmelt, decreased base-flows in summer, and increasing water temperatures (Mantua, Tohver, & Hamlet, 2010). Salmonids are generally stressed by rising thermal water temperatures, which is predicted to become severe in the later part of the 21st century under A1B and B1 greenhouse gas scenarios (Mantua et al., 2010). Finally, bioenergetic models of climate change impacts to bald eagles suggest that while overall food requirements will decline only slightly by 2050, higher temperatures will cause salmon carcasses to decompose more rapidly, potentially forcing bald eagles to seek alternative prey or feeding grounds in the region (Harvey, Moriarty, & Salathé, 2012).

Our findings demonstrate the complex impacts of climate change on this system, although we acknowledge a number of limitations to our analysis. Data were collected over decades by multiple observers and at multiple temporal scales (weekly, daily, annually), resulting in a fairly coarse scale of measure and inconsistent resolutions. Although the data collection methods were not originally designed to answer phenological questions, such long-term datasets are undoubtedly useful for investigating emergent phenomenon and underscore the need to develop flexible analytical methods to take advantage of existing datasets for novel scientific questions.

Finally, our analysis touches on questions of hydro-power management and its implications for the broader eagle–salmon–flood relationship. Current hydroelectric flow management practices aim to promote, among other things, salmon spawning and redd protection, with increased flow resuming immediately following salmon spawning. Although these objectives clearly have an important trophic impact on eagles, eagle resource use and the interaction between salmon-eagle flood phenology in this system are not currently explicitly considered in flow management. The ability of hydroelectric infrastructure to manage flow, and the demonstrated importance of flow regimes for both salmon and eagles, therefore provides an adaptive management opportunity to consider trophic levels in flow management plans, broadening the traditional focus on salmon spawning to a more comprehensive consideration of the critical eagle use period.

5 | CONCLUSIONS

In this system with both wild and heavily managed components, alternative visions for protected area management are being tested: while the Park Service was designed to address traditional conservation challenges, like the pollution, overharvesting, and habitat loss which dogged bald eagles and salmon during the 20th century, climate change poses a novel challenge to conventional management strategies. Eagles are adaptive, vagile creatures, capable of tracking salmon as they spawn in rivers across the Pacific Northwest, suggesting that they could continue to thrive with effective climate-informed management. While our work has shown that eagles respond to phenological changes in the salmon–flood relationships, additional research can help to further clarify the degree to which changes in the hydrology of this system determine local eagle abundance, and could point to potential management actions to maintain desired eagle and salmon abundance. Ultimately, balancing anthropogenic infrastructure, such as hydroelectric infrastructure, with sufficient protections for natural systems can provide a range of resource conditions that may result in increased resilience for eagles and salmon in the face of changing climate.

ACKNOWLEDGEMENTS

We would like to thank those who assisted in data collection, including Tanya Kitterman (U.S. Forest Service), biologists from NOCA, TNC, and USFS, and citizen science volunteers. Special thanks to Bob Kuntz (former NPS biologist), who facilitated data collection for decades, and to the Washington Department of Fish and Wildlife for making their data available. In particular, we thank Brett Barkdull for sharing his expertise on the ecology of salmon in the Skagit.

AUTHORS' CONTRIBUTIONS

J.I.R. and R.C. contributed to data collection. M.A.R. conducted the data analysis, with assistance from J.I.R. M.A.R. led the development of the manuscript, with assistance from J.I.R. and R.C. All authors provided final approval for publication.

DATA ACCESSIBILITY

All data and metadata are available via USGS Science Base https://doi.org/10.5066/p91vexew (Rubenstein, Christophersen, & Ransom, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Rubenstein MA, Christophersen R, Ransom JI. Trophic implications of a phenological paradigm shift: Bald eagles and salmon in a changing climate. *J Appl Ecol*. 2019;56:769–778. https://doi.org/10.1111/1365-2664.13286

Supporting Information

Table S1. Description of Datasets Used: Availability, Scope, and Scale

Data	Years Available	Temporal Scale	Source
Eagle Counts, Upstream	1982-2016	Weekly, (Dec.-Jan.)	NOCA, TNC, USFS
Eagle Counts, Downstream	1990-2016	Weekly (Dec.-Jan.)	NOCA, TNC
Eagle Adult:Subadult	1983-2016	Weekly (Dec.-Jan.)	NOCA
Chum Escapement (entire river)	1968-2015	Annual	WDFG
Coho Escapement (entire river)	1983-2015	Annual	WDFG
Eagle Phenology, Upstream	1982-2016	Annual (derived)	NOCA, TNC, USFS
Eagle Phenology, Downstream	1990-2016	Annual (derived)	TNC
Chum Phenology, Upstream	1981-2015	Annual	WDFW
Chum Phenology, Downstream	1981-2015	Annual	WDFW
Coho Phenology, Upstream	1981-2015	Annual	WDFW
Coho Phenology, Downstream	1981-2014	Annual	WDFW
Flood Events, Upstream	1987-2016	15-minute increments	USGS
Flood Events, Downstream	1987-2016	15-minute increments	USGS
Flood Timing, Upstream	1987-2016	Annual (derived)	USGS
Flood Timing, Downstream	1987-2016	Annual (derived)	USGS

Description of data used in analysis, along with relevant years available, temporal scale (resolution), and data source. “Derived” indicates where phenological data were derived from count data.

Table S2. Seasonal data availability of eagle surveys in the Skagit River Study Area (Washington, USA)

Range of Survey Dates[1]	Equivalent Day of the Year[2]	Equivalent Calendar Week[3]	Equivalent Week of Study Season
Dec 01-Dec 8	335-342	49	1
Dec 09-Dec 17	343-351	50	2
Dec 16-Dec 23	350-357	51	3
Dec 23-Dec 30	357-364	52	4
Dec 30-Jan 02	364-2	1	5
Jan 06-Jan 14	6-14	2	6
Jan 14-Jan 21	14-21	3	7

[1] There is some overlap of between dates, due to surveys occasionally being conducted either close to the end or beginning of a season week (i.e., Friday or Monday).
[2] Expressed as ordinal day of the year for *non-leap* years.
[3] Calendar dates were converted to week of year using R’s *strptime* function; the first week in January with four or more days in the new year is considered the first week of the year.

Table S3. Annual and Average Weekly Eagle Counts by River Section

Year	River Section	Total Annual Eagle Counts	Average Weekly Eagle Counts
1982	Upstream	1044	149.81
1983	Upstream	400	57.14
1984	Upstream	830	118.57
1985	Upstream	834	136.93
1986	Upstream	763	126.05
1987	Upstream	1416	202.29
1988	Upstream	1778	254.00
1989	Upstream	1505	215.00
1990	Upstream	1784	257.81
1991	Upstream	1964	280.57
1992	Upstream	1846	263.71
1993	Upstream	1221	174.43
1994	Upstream	1456	210.26
1995	Upstream	1200	179.29
1996	Upstream	1870	267.14
1997	Upstream	1155	165.00
1998	Upstream	1712	244.57
1999	Upstream	1201	171.57
2000	Upstream	1848	264.00
2001	Upstream	1140	162.86
2002	Upstream	1169	167.00
2003	Upstream	1533	219.00
2004	Upstream	1555	222.14
2005	Upstream	1534	219.14
2006	Upstream	2599	371.29
2007	Upstream	1199	171.29
2008	Upstream	878	157.75
2009	Upstream	694	112.57
2010	Upstream	1014	189.70
2011	Upstream	614	122.80
2012	Upstream	716	119.33
2013	Upstream	459	76.50
2014	Upstream	745	124.17
2015	Upstream	380	63.33
2016	Upstream	309	61.80
1990	Downstream	665	95.00
1991	Downstream	519	74.14
1992	Downstream	436	62.29
1993	Downstream	384	54.86
1994	Downstream	457	65.29
1995	Downstream	469	67.00
1996	Downstream	1231	175.86
1997	Downstream	760	108.57

1998	Downstream	899	128.43
1999	Downstream	654	93.43
2000	Downstream	917	131.00
2001	Downstream	467	66.71
2002	Downstream	556	79.43
2003	Downstream	887	126.71
2004	Downstream	1083	154.71
2005	Downstream	544	77.71
2006	Downstream	1259	179.86
2007	Downstream	349	49.86
2008	Downstream	439	87.80
2009	Downstream	621	88.71
2010	Downstream	613	102.17
2011	Downstream	399	79.80
2012	Downstream	547	91.17
2013	Downstream	254	42.33
2014	Downstream	566	94.33
2015	Downstream	387	64.50
2016	Downstream	289	57.80

Total annual observed eagle counts and average weekly eagle counts along the Skagit River, distinguished by river section.

Table S4. Adult:Subadult Ratio

Year	**Adult**	**Subadult**	**Ratio**
1982	29	1	29.00
1983	39	11	3.55
1984	32	11	2.91
1985	55	29	1.90
1986	31	15	2.07
1987	63	43	1.47
1988	84	43	1.95
1989	81	43	1.88
1990	964	475	2.03
1991	1150	498	2.31
1992	1269	477	2.66
1993	827	278	2.97
1994	924	256	3.61
1995	672	216	3.11
1996	1675	691	2.42
1997	1239	476	2.60
1998	1747	493	3.54
1999	704	167	4.22
2000	974	313	3.11
2001	107	50	2.14
2002	398	127	3.13
2003	1158	563	2.06
2004	1580	777	2.03
2005	633	253	2.50
2006	1457	622	2.34
2007	417	139	3.00
2008	460	146	3.15
2009	591	196	3.02
2010	1133	469	2.42
2011	728	260	2.80
2012	797	438	1.82
2013	522	179	2.92
2014	915	379	2.41
2015	530	221	2.40
2016	426	167	2.55

Observations of adult and subadult eagles. Only a subset of all eagle observations (Table S3) included information about the age of observed individuals; therefore, total sum of adult/subadult observations will not always equal total observed eagles in a given year. These data should be considered a general indicator of population ratios, rather than a comprehensive assessment of demographic change. When calculating average adult:subadult ratio and trends over time, we excluded the first year (1982) as an outlier.

Table S5. Chum and Coho Escapement Trends (Robust Regression)

Stock	Reference Year	Estimated Escapement in Reference Year	Estimated Annual Decline (%)	Estimated Annual Decline (Fish/year)	Median Escapement in Last Third (% of Reference Level)
Coho	1982	73,703.1	-1.9%	-1,376.04	42.4%
Chum (even years)	1967	158,954.7	-3.8%	-4,918.59	32.4%
Chum (all years)	1967	53,567.6	-0.95%	-507.52	56.4%

Estimates for reference year escapement levels and annul rates of decline for coho and chum salmon in the Skagit (based on Geiger & Zhang (2002)). According to this method, a stock is considered to be in decline if it meets the following criteria: the stock experienced a 50% decline from the reference level over 15 years (i.e., the median escapement level in the last third of data is less than half of the reference level); or if the robust estimate of annual decline (i.e., the slope) exceeds 5% of the reference level.