Measuring the additive effects of predation on prey survival across spatial scales

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Abstract. The degree to which predation is an additive vs. compensatory source of mortality is fundamental to understanding the effects of predation on prey populations and evaluating the efficacy of predator management actions. In the Columbia River basin, USA, predation by Caspian Terns (*Hydroprogne caspia*) on U.S. Endangered Species Act (ESA)-listed juvenile salmonids (smolts; *Oncorhynchus* spp.) has led to predator management actions to reduce predation; however, the assumption that reduced predation translates into greater salmonid survival, either within the life stage where predation occurs or across their lifetime, has remained untested. To address this critical uncertainty, we analyzed a long-term (2008–2018) mark–recapture–recovery data set of ESA-listed steelhead trout (*O. mykiss*) that were tagged (*n* = 78,409) and subsequently exposed to predation during smolt out-migration through multiple river reaches (spatial scales), jointly estimating weekly probabilities of steelhead survival, mortality due to bird predation, and mortality due to other causes. This concurrent estimation across time-stratified cohorts allowed for the direct measurement of the strength, magnitude, and direction of relationships between survival and Caspian Tern predation. Estimates of Tern predation on steelhead were substantial in most years, with cumulative annual estimates ranging from 0.075 (95% creditable interval = 0.058–0.099) to 0.375 (0.290–0.461). Increases in Tern predation probabilities were associated with statistically significant decreases in steelhead survival probabilities in all evaluated years and salmonid life stages (smolt out-migration and smolt-to-adult returns). Results provide novel evidence that predation by Caspian Terns may have been a super-additive source of mortality during the smolt life stage and a partially additive source of mortality to the adult life stage. Annual estimates of the difference between observed survival and baseline survival (i.e., in the absence of Tern predation) ranged from 0.052 (0.017–0.103) to 0.314 (0.172–0.459) during the steelhead smolt life stage and from 0.011 (0.001–0.029) to 0.049 (0.025–0.078) to the adult life stage. The estimated levels of compensation have important implications for predator management actions aimed at increasing the survival of endangered salmonids, and the modeling approach developed herein provides a framework to directly quantify the impacts of source-specific mortality factors on prey populations.

Key words: capture–recapture–recovery; compensatory mortality; hierarchical Bayesian model; population dynamics; predator–prey dynamics; state-space models.

Introduction

Predator–prey dynamics are fundamental to evolutionary and ecological processes (Holling 1959), yet the full impact of predation on prey populations has been a topic of continuing debate (Serrouya et al. 2015). Assessing the effects of predation on prey populations generally requires information about (1) the number or proportion of available prey consumed, (2) which individuals or life stages are targeted by which predators, and (3) the levels at which other mortality sources or vital rates may compensate for predation (Caswell 2001, Mills 2012). Most predator–prey studies focus on kill rates and predation probabilities (Vucetich et al. 2011). Relatively large kill and predation probabilities, however, do not necessarily imply that predators are limiting prey populations. Metrics measuring how a prey population responds demographically may be more pertinent (Serrouya et al. 2015). For example, largely compensatory predation has little effect on prey survival probabilities

at any level of kill or predation probability, but rather is associated with decreases in mortality from other sources (Sandercock et al. 2011). Conversely, when predation is a substantial source of mortality and largely additive, it may depress prey survival and population growth (Taylor 1984). Although the role of compensation is vital to assess the effects of predation on prey populations, it often remains unmeasured, or imprecisely described, even in well studied predator–prey systems.

Understanding the effects of predators on prey populations requires quantifying survival probabilities, predation probabilities, and the relationship between these two processes. The relevance of these relationships may be scale dependent, with different mechanisms of compensation acting with varying significance, contingent on scope. Large-scale, density-dependent additive mortality can be quantified based on changes in population growth rates (which incorporate survival, movement, and reproduction), whereas in field studies, inference is more typically drawn from shorter time scales, such as evaluating what proportion of losses were part of the "doomed surplus" vs. losses that could have been avoided (Errington and Hamerstrom 1935). Thus, the scale at which the relationship between predation and survival is evaluated can have important implications for inferences with respect to the impact of predation on prey populations and prospective conservation intervention on behalf of the prey.

As computational capabilities have increased, so too has the sophistication of methods that employ multistate, mark–recapture–recovery data to jointly estimate probabilities of survival and multiple causes of mortality (Schaub and Pradel 2004, Gimenez et al. 2007). The integration of data from multiple mortality sources is of distinct value to investigations of compensatory mortality, which involves the interplay of baseline survival and all relevant, measurable mortality sources (Lebreton and Pradel 2002, Schaub and Lebreton 2004, Wolfe et al. 2015). Furthermore, associations among source-specific mortality and demographic rates may also be scale dependent, whereby decreasing mortality in certain life stages may do little to reverse overall population declines across broader time scales (Crouse et al. 1987). As a result, the efficacy of predator management strategies to enhance prey survival and persistence may be dependent on spatial or temporal scale, whereby short-term improvements in survival may address management needs at a local scale but diminish across broader extents important to species persistence. Long-term, multifacetted data sets are therefore of principal importance in answering these large-scale uncertainties.

Anadromous salmonids (*Oncorhynchus* spp.) in the Pacific Northwest region of North America are the subject of great conservation concern and, therefore, have been the focus of countless long-term research and management programs (see Quinn [2005] for additional details). Each year in the Columbia River basin, USA, thousands of U.S. Endangered Species Act (ESA)-listed salmonids are tagged during the smolt (juvenile) life stage

with Passive Integrated Transponder (PIT) tags to gather information on their behavior and survival following release. During out-migration, salmonid smolts are exposed to predation by multiple species (fish, birds, and mammals), mortality associated with passage through hydroelectric dams, disease, and a host of other mortality factors (Nelson et al. 1991). Predator–prey interactions involving piscivorous colonial waterbirds and ESA-listed salmonid populations are of particular interest (NOAA 2014). For example, previous research has identified predation by Caspian Terns (*Hydroprogne caspia*) as a substantial source of mortality for anadromous ESA-listed steelhead trout (*O. mykiss*) during their smolt life stage, with several studies documenting annual predation probabilities in excess of 20% of available fish (Collis et al. 2001, Evans et al. 2012, Evans et al. 2016, Payton et al. 2019; Evans et al. , *in press*). Concerns relating to the impact of Terns on steelhead smolt survival have prompted the implementation of management actions aimed at reducing predation by reducing the number of Terns that nest and forage on fish in the region (USFWS 2005, USACE 2014). However, the assumption that reduced predation translates into greater survival at the smolt or smolt-to-adult life stages has, to this point, been largely untested. Furthermore, linking mortality in one life stage to cumulative survival across multiple life stages is especially important for populations of anadromous salmonids, where life stage specific mortality rates can be high, the specific cause(s) and locations of mortality are often unknown, and the rate at which smolts survive to adulthood is a principal factor influencing population growth and persistence (Kareiva et al. 2000).

Herein we develop a multi-state, multinomial model to investigate whether reductions in Caspian Tern predation have been associated with increases in steelhead survival during the smolt and smolt-to-adult (i.e., adult recruitment) life stages. We used a long-term mark–recapture–recovery data set involving ESA-listed Upper Columbia River steelhead trout that were exposed to predation from multiple piscivorous waterbird species and colonies to measure the degree to which predation by Caspian Terns was an additive vs. compensatory source of mortality. Our modeling framework simultaneously estimated prey survival, probabilities of predation, and the relationships between these two processes. Levels of additive mortality were evaluated over two imbricate spatial scales encompassing two different steelhead life stages and management units: (1) smolt out-migration and (2) smolt-to-adult returns.

Methods

Additivity, compensation, and a conceptual model

To provide context for understanding data collection, model development, and empirical results, we first describe the theoretical relationships between survival and predation across the spectrum of additivity/

compensation. We then develop a conceptual description of the modeling framework and key parameters employed for the evaluation of predation as an additive or compensatory source of mortality.

For any given system absent predation, it is assumed some proportion of prey will survive with the compliment proportion succumbing to some "baseline" mortality source. Additive mortality (a) refers to the proportionate reduction in prey survival associated with increases in predation. Conversely, compensation ($1 - a$) refers to proportionate decreases in prey mortality due to other mortality sources in response to increases in predation. For example, under the complete compensation hypothesis ($a = 0$), increases in predation do not decrease survival, but instead proportionately decrease mortality from other sources ($1 - a$; Fig. 1). Five classifications are commonly used to describe the spectrum of possible compensatory and additive mortality relationships: (1) over-compensation ($a < 0$); (2) complete compensation ($a = 0$); (3) partial compensation ($a \in (0, 1)$); (4) complete additivity ($a = 1$); and (5) super-additivity ($a > 1$; Fig. 1; Burnham and Anderson 1984, Schaub and Lebreton 2004, Sandercock et al. 2011, Wolfe et al. 2015).

Mark–recapture–recovery data allow for the unbiased estimation of survival (φ) and source-specific probabilities of mortality (e.g., predation; θ), given supplemental data sufficient to identify unique probabilities of recovery for each mortality source (Schaub and Pradel 2004, Gimenez et al. 2007, Payton et al. 2019). Simultaneous estimation of these parameters from an all-inclusive data set further allows for the measurement of functional relationships between these processes (e.g., $\varphi = f(\theta)$). The functional expression of the classic compensatory mortality model was described by Anderson and Burnham (1976)

$$\phi = \phi^0 - a\theta \tag{1}$$

where θ denotes the predation probability (replacing anthropogenic harvest, K, used by Anderson and Burnham [1976]), ϕ^0 denotes baseline survival probability (the

expected probability of survival in the absence of predation), and a (equal to the factor of baseline survival, bS^0, used by Anderson and Burnham [1976]) measures the additive portion of predation whereby increases in predation probability directly result in linear decreases in survival probability, φ. It follows that the direct impact of predation on survival can be represented and measured by $\phi^\Delta = \phi^0 - \phi$, the difference between baseline survival probabilities and observed probabilities of survival.

Because survival, predation, and mortality from other causes (e.g., "natural" mortality in discussions of anthropogenic harvest) depict all possible outcomes available for individuals of the prey population, the associated probabilities of these outcomes collectively partition the unit interval (i.e., the respective probabilities sum to 1; Fig. 1). Consequently, for any given level of compensation, there exists a level of predation that saturates the system (θ^{sat}) and the compensatory or additive capacity of a system is overwhelmed by predation. This point, commonly illustrated in the relevant literature as an inflection point in plots of survival vs. predation, indicates where mortality from other causes is exhausted ($1 = \phi + \theta^{\mathrm{sat}}$), and, as a result, declines in survival are directly inverse to greater levels of predation (i.e., predation is necessarily completely additive; see Schaub and Lebreton 2004, Lebreton 2005, Sandercock et al. 2011; Fig. 1). Analogously, given a sufficient level of additivity, there exists a predation saturation point at which no individuals can survive, with declines in other mortality directly inverse to greater levels of predation (Fig. 1). This inflection point can be expressly enumerated as a function of baseline survival and level of additivity

$$\theta^{\mathrm{sat}} = \begin{cases} \frac{1 - \phi^0}{1 - a}, & \text{when } a < \phi^0 \\ \frac{\phi^0}{a}, & \text{when } a \geq \phi^0 \end{cases} \tag{2}$$

where the first subfunction represents the point at which "natural" mortality is zero and thus predation
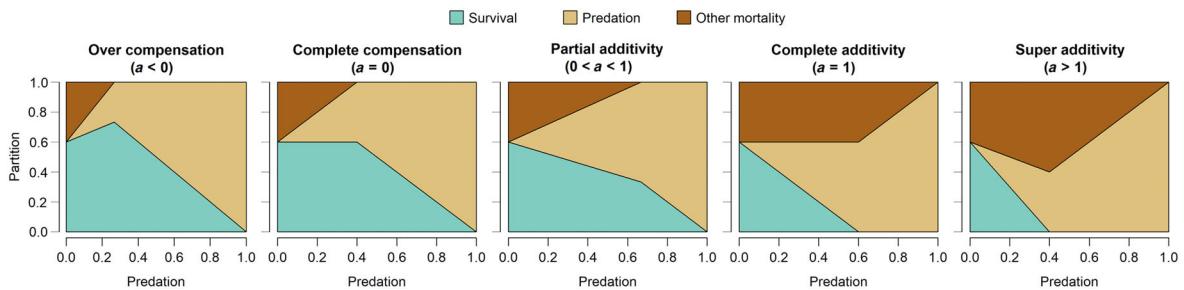

Fig. 1. Visual representations of the partitioning of survival, predation, and other mortality given baseline survival of 0.6 and various levels of additivity ($a = -0.5, 0, 0.6, 1, 1.5$). Under assumptions of complete or over-compensation (panels a–b), increases in the proportion of individuals succumbing to predation (x-axis) reduces the proportion of animals succumbing to "other mortality" (i.e., other mortality = 0). Conversely, under assumptions of additive predation, greater proportions of individuals succumbing to predation are associated with decreased proportions of surviving individuals (panels c–e). With too great a level of predation, the proportion of individuals surviving is 0 (panels d and e).

equals the complement of survival. The second subfunction represents the point at which survival is zero; thus, all non-depredated individuals die due to other (natural) sources of mortality (Fig. 1). In this study, we implemented a multinomial modeling approach that explicitly recognized the inherent constraints of the parameter space to simultaneously estimate survival, multiple sources of natural and predation mortality, and additivity (a), and, accordingly, measure the direct effect of predation on prey survival (i.e., the difference between baseline survival probabilities and observed probabilities of survival; ϕ^Δ).

Data collection

We used an 11-yr data set (2008–2018) of uniquely marked (tagged) juvenile steelhead in the Columbia River basin, USA, and their subsequent recaptures (detections of live fish) and recoveries (detections of dead fish) to evaluate survival, predation, and the relationship between these processes (Table 1, Fig. 2). Each spring (April–June), migrating steelhead smolts were captured at Rock Island Dam (RIS) on the middle Columbia River (river kilometer [Rkm] 729, as defined by distance to the Pacific Ocean), marked with PIT tags, and released into the tailrace of the dam to resume their outmigration to the Pacific Ocean (Fig. 2). Fish were randomly selected and tagged in numbers proportionate to the run-at-large volitionally passing RIS each week. Following release, tagged steelhead could be recaptured (passively detected alive) as smolts at Bonneville Dam (BON, Rkm 234) and at a vessel-towed pair-trawl net detection system in the Columbia River estuary (EST, Rkm 75), and recaptured as returning adults at BON following 1–3 yr of ocean residency. Each year following the breeding season of piscivorous colonial waterbirds

(August–September), tags from depredated steelhead smolts were recovered from up to eight different breeding colonies of Caspian Terns and from up to seven other breeding colonies of piscivorous waterbirds, including California Gulls (*Larus californicus*), Ring-billed Gulls (*L. delawarensis*), and Double-crested Cormorants (*Phalacrocorax auritus*; referred to as "other colonies"; Fig. 2).

Model development

State-space models are effective tools for modeling multiple categories of mortality and evaluating the temporal variation among the associated probability estimates (Gimenez et al. 2007, Servanty et al. 2010). The incorporation of supplementary year- and source-specific recovery data allows for the unbiased estimation of mortality probabilities (Schaub and Pradel 2004, Payton et al. 2019). We employed a multi-state mark–recapture–recovery model to develop year (y)- and week (w)-specific vectors of estimates of segment survival probabilities ($\phi_{y,w}$, where $\phi_{y,w,j}$ indicates the probability of an individual, released in week w of year y and alive entering segment j, surviving and exiting segment j), and matrices of predation probabilities for up to 15 cause-specific mortality sources within each segment ($\Theta_{y,w}$, where $\Theta_{y,w,j,h}$ indicates the probability of an individual, released in week w of year y and alive entering segment j, dying due to the hth hazard, or source of mortality, in segment j). Temporal correlation among weekly probabilities of predation, other mortality, and recapture was addressed through logistic random-walk models (see Payton et al. 2019).

The modeling framework described herein provides for an evaluation of the additive effect of aggregate predation on survival within a single segment. For each year,

TABLE 1. Numbers of steelhead smolts PIT tagged and released at Rock Island Dam that were subsequently recaptured alive at downstream PIT-tag detection arrays, recovered dead on Caspian Tern breeding colonies, or recovered dead on breeding colonies of other piscivorous waterbird species.

Year	Released	Sampling weeks	Rock Island Dam to Bonneville Dam			Bonneville Dam to Pacific Ocean			Adult returns Live
			Live	Dead (Terns)	Dead (Other)	Live	Dead (Terns)	Dead (Other)	Live
2008	7,271	11	390	477	70	81	425	64	220
2009	7,114	11	427	571	97	110	377	54	77
2010	7,365	11	977	474	99	104	318	79	88
2011	7,756	11	153	462	62	72	164	106	46
2012	6,712	10	348	332	62	96	106	72	67
2013	5,893	10	396	433	83	118	138	27	61
2014	7,663	10	528	298	139	137	211	127	65
2015	7,069	10	701	367	262	103	130	60	5
2016	6,764	9	711	265	185	87	87	20	–
2017	7,436	10	406	201	185	77	159	9	–
2018	7,366	10	584	68	138	82	123	25	–
Total	78,409	113	5,621	3,948	1,382	1,067	2,238	643	629

Note: The numbers of tagged smolts that returned as adults to Bonneville Dam are also provided; dashes indicate that complete adult returns for those cohorts were not available.
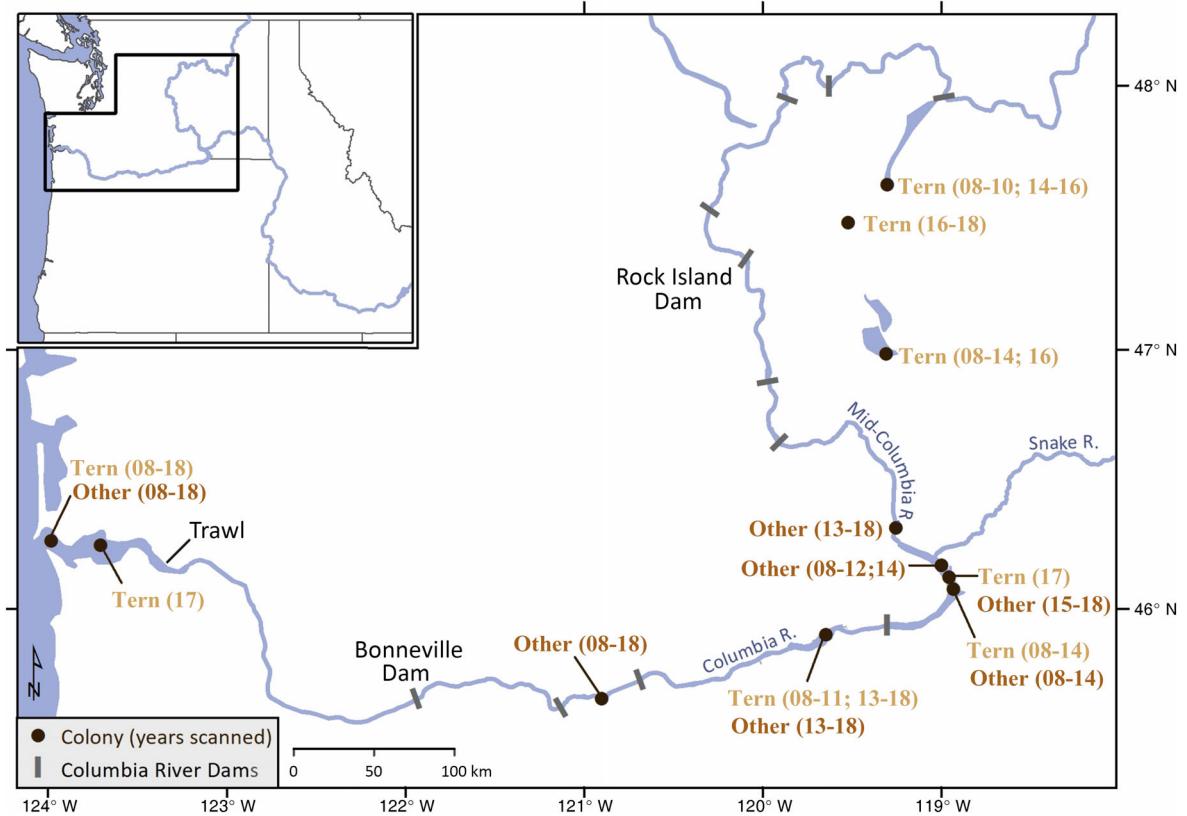
Fig. 2. Map depicting the reach of the Columbia River associated with the study. Steelhead were tagged and released from Rock Island Dam, recaptured (passively detected alive) at Bonneville Dam (as smolts), at the Trawl (as smolts), or returning to Bonneville Dam (as adults) following 1–3 yr in the Pacific Ocean. Tags were recovered from eight Caspian Tern breeding colonies and seven breeding colonies of other piscivorous waterbird species located throughout the region in the years provided in parentheses.

aggregate predation probabilities were estimated in the first segment ($j = 1$) for up to eight breeding colonies of Caspian Terns ({TERNS}; $\Theta_{y,w,1,\{\text{TERNS}\}} = \sum_{h \in \{\text{TERNS}\}} \Theta_{y,w,1,h}$) and up to seven of other piscivorous waterbird species ({OTHER}, $\Theta_{y,w,1,\{\text{OTHER}\}} = \sum_{h \in \{\text{OTHER}\}} \Theta_{y,w,1,h}$). A third and final category, referred to as "unexplained mortality," comprised the unaccounted for remainder of the unit interval ($\Theta_{y,w,1,\text{unexplained}} = 1 - \phi_{y,w,1} - \sum_{h \notin \{\{\text{TERNS}\} \cup \{\text{OTHER}\}\}} \Theta_{y,w,1,h}$). Two independent analyses were undertaken, measuring additivity within two imbricate spatial scales representing two anadromous salmonid life stages: (1) smolt out-migration from RIS to arrival at BON and (2) smolt-to-adult migration from RIS (as smolts) to return at BON (as adults; see Fig. 2). For the smolt out-migration life stage, all tag recaptures and recoveries (including those downstream of the first segment) were used to inform recapture and survival probabilities at Bonneville Dam. For the smolt-to-adult (SAR) life stage, the full system was considered a single segment with all recoveries used to inform predation probabilities and recaptures of returning adults at Bonneville Dam used to estimate survival. Recapture probabilities of the returning adults were assumed to be

1.0, which follows previous precedents in this study system (Keefer et al. 2008, Evans et al. 2014).

To describe the relationships among these probabilities, we employed the general compensatory/additive statistical framework summarized by Lebreton (2005). The numerous, prominent sources of mortality and limited survival to adulthood considered in the present study necessitated that careful, explicit attention be paid to the compact parameter space geometry during the construction of estimates and uncertainty intervals. Although it is unlikely that avian predators account for all steelhead mortality during out-migration, a consequence of the large amounts of uncertainty inherent to the recovery of tags from bird colonies was that non-trivial portions of the associated posterior distributions amassed near the parameter space boundary for the smolt-specific analysis (i.e., where avian predation is the complement of survival; Payton et al. 2019; see Fig. 3). Likewise, for the smolt-to-adult life-stage analysis, the dearth of steelhead adult returns was associated with the marginal posterior distributions of survival probabilities amassing near the adjacent parameter space boundary. Such considerations were incongruous with the use of correlation measures

(e.g., between survival and predation) to derive inference about levels of compensation/additivity as has been employed by previous researchers. We instead explicitly described survival in the first river segment ($\phi_{y,w,1}$) as a function of baseline survival ($\overline{\phi}^0$, where $\overline{\phi}^0_y$ refers to the average baseline survival rate across the relevant segment in year y), Tern predation ($\Theta_{y,w,1,\{TERNS\}}$), the additive effects of Tern predation (**a**, where a_y refers the level additivity across the relevant segment in year y) and predation by other bird species ($\Theta_{y,w,1,\{OTHER\}}$). This further allowed for the direct estimation of a measure of foremost importance to managers: the difference in survival associated with Tern predation ($\phi^\Delta_{y,w} = \phi^0_{y,w} - \phi_{y,w,1}$); where $\phi^0_{y,w}$ represents the baseline survival rate in week w of year y after the incorporation a weekly random effect about the annual baseline survival rate assuming $\text{logit}\left(\phi^0_{y,w}\right) = \text{logit}\left(\overline{\phi}^0_y\right) + \varepsilon_{y,w}$, and $\varepsilon_{y,w} \sim \text{normal}(0, \sigma^2_\phi)$.

The compensatory model defining weekly survival can be expressed as a piecewise function

$$
\phi_{y,w,1} = \begin{cases} \phi^0_{y,w} - a_y\Theta_{y,w,1,\{TERNS\}}, & \text{when } \Theta_{y,w,1,\{TERNS\}} \leq \theta^{sat}_{y,w} \\ 1 - \Theta_{y,w,1,\{OTHER\}} - \Theta_{y,w,1,\{TERNS\}}, & \text{when } \Theta_{y,w,1,\{TERNS\}} > \theta^{sat}_{y,w} \text{ and } a < \phi^0_{y,w} \\ 0, & \text{when } \Theta_{y,w,1,\{TERNS\}} > \theta^{sat}_{y,w} \text{ and } a \geq \phi^0_{y,w} \end{cases} \quad (3)
$$

Here, the first subfunction is the reparameterized compensatory mortality model described by Schaub and Lebreton (2004), while the second and third subfunctions describe the enforced boundary constraints whereby survival, Tern predation, and the measured subset of other (natural) mortality must sum to 1. This enumeration is helpful in demonstrating that, while the relationship between survival and predation is effectively completely additive or completely compensatory when $\Theta_{y,w,1,\{TERNS\}} > \theta^{sat}_{y,w}$, predation probabilities greater than the saturation point provide only binary, indirect information about levels of baseline survival and additivity, e.g.

$\Theta_{y,w,1,\{TERNS\}} > \frac{1-\phi^0_{y,w}}{1-a_y}$.

Additional details and a simulation study evaluating the bias, precision, and coverage of estimates provided by this parameterization framework are presented in Appendix S1.

The constraints imposed by this additive/compensatory mortality framework were integrated into the joint mortality and survival modeling framework of Payton et al. (2019). This mark–recapture–recovery model estimates probabilities of survival, informed directly from downstream detections (recaptures and recoveries), and probabilities of predation, informed indirectly through the recovery of PIT tags from depredated fish on piscivorous waterbird colonies. Recoveries are the result of two stochastic processes (Hostetter et al. 2015). First, a PIT tag consumed by a bird must be deposited on the bird's breeding colony. Second, the deposited tag must be recovered by researchers on the breeding colony

following the breeding season. Independent annual probabilities of tag deposition for each colony included in this study were informed by previous research (Hostetter et al. 2015), incorporated here through informative Beta priors, and assumed constant within each year. Probabilities of tag recovery varied within each year, with tags deposited earlier in a breeding season less likely to be retrieved than those deposited later. For each bird colony in each year, parameters defining unique logistic retrieval probability functions were estimated based on the intentional sowing of tags on each colony prior to, during (when possible), and after the breeding season (Hostetter et al. 2015, Payton et al. 2019). Full details of the mathematical construction model and posterior distribution are described in Appendix S2.

Model implementation

Prior distributions for all probabilities were defined to be either uniform for univariate parameters (i.e., baseline survival, recapture) or Dirichlet(**1**) for multivariate parameters (i.e., survival and mortality). Average annual probabilities of baseline survival were assumed to be mutually independent. Annual values of additivity were assumed to be unique but similar among years (i.e., $a_y \sim \text{normal}\left[\mu_a, \sigma^2_a\right]$). We assigned $\mu_a \sim \text{normal}([1/2], 3)$ as the enumeration of a vague a priori assumption that predation by Caspian Terns was likely equal parts additive and compensatory mortality, with less prior credibility given to hypotheses of over-compensatory or super-additive mortality mechanisms. As with the $\overline{\phi}^0_y$ random errors in the joint mortality and survival model, we assumed a weakly informative prior of half-normal(0, 5) for both σ^2_ϕ and σ^2_a.

The models were analyzed using the software STAN (Stan Development Team 2015), accessed through R version 3.1.2 (R Development Core Team 2014), and using the rstan package (version 2.8.0; Stan Development Team 2015). To simulate random draws from the joint posterior distribution, we ran four Hamiltonian Monte Carlo (HMC) Markov Chain processes. Each chain contained 4,000 warm-up iterations followed by 4,000 posterior iterations thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013); only chains with zero reported divergent transitions were accepted. Posterior predictive checks compared simulated and observed annual aggregate raw recapture and recovery counts to ensure model estimates reflected the data observed. Reported estimates represent simulated

posterior medians along with 95% highest (posterior) density intervals (95% credible interval [CRI]) calculated using the HDInterval package (version 0.1.3; Meredith and Kruschke 2016).

RESULTS

Survival and predation

A total of 78,409 steelhead smolts were captured, tagged, and released at RIS during 2008–2018. Annual sample sizes of tagged steelhead smolts ranged from 5,893 to 7,756 over the course of 9–11 sampling weeks each year (Table 1). The median weekly sample size of tagged steelhead was 421 smolts, but sample size varied considerably (5–2,780 smolts). Across all 11 study years, a total of 5,621 smolt tags were recaptured (detected) at BON and 1,067 smolt tags were recaptured at the pair-trawl net detector in the Columbia River estuary (Table 1). A total of 629 tagged returning adult steelhead were recaptured at BON over the first eight years of the study (steelhead spend 1–3 yr at sea before returning as adults to spawn, so adult returns were not evaluated in all 11 study years). A total of 3,948 smolt tags were recovered from Caspian Tern colonies upstream of BON compared to 1,382 smolt tags recovered from other bird colonies (almost entirely gull colonies) upstream of BON. A total of 2,238 smolt tags were recovered from Caspian Tern colonies located near the mouth of Columbia River downstream of BON compared to 643 smolt tags recovered from other bird colonies (entirely cormorant colonies) downstream of BON (Table 1).

Annual estimates of cumulative steelhead smolt survival probabilities from RIS to BON averaged 0.452 (95% CRI = 0.426–0.474). Annual smolt survival probabilities ranged considerably, from a low of 0.272 (95% CRI = 0.233–0.311) in 2015 to a high of 0.554 (95% CRI = 0.400–0.652) in 2011 (Table 2). During 2008–2015 (years with complete adult returns), estimated annual SAR probabilities from RIS (as a smolt) to BON (as an adult) averaged 0.011 (95% CRI = 0.010–0.012), ranging from a low of 0.001 (95% CRI = 0–0.001) for smolts that out-migrated in 2015 to a high of 0.030 (95% CRI = 0.026–0.034) for smolts that out-migrated in 2008 (Table 2).

Annual estimates of predation probabilities by Caspian Terns from all colonies that foraged on steelhead smolts upstream of BON ranged from a low of 0.039 (95% CRI = 0.027–0.057) in 2018 to a high of 0.288 (95% CRI = 0.205–0.366) in 2009. Comparisons of smolt mortality from Caspian Tern predation to other bird predation upstream of BON indicated that, in 7 of the 11 years, predation by Caspian Terns was responsible for the majority of all colonial waterbird predation and possibly the plurality of all smolt mortality during the smolt life stage (Table 2). With the inclusion of predation by Caspian Terns nesting near the mouth of the Columbia River downstream of Bonneville Dam, estimates of cumulative Tern predation probabilities ranged annually from 0.075 (95% CRI = 0.058-0.099) to 0.375 (95% CRI = 0.290–0.461) during smolt out-migration from RIS to the Pacific Ocean (Table 2).

Estimated annual cumulative predation probabilities from all species of piscivorous colonial waterbirds (i.e., terns, gulls, and cormorants) and their colonies combined were substantial, ranging from 0.310 (95% CRI = 0.262–0.374) to 0.532 (95% CRI = 0.427–0.642). Cumulative colonial waterbird predation explained an estimated 41.7% (95% CRI = 29.6–55.9) to 70.0% (95% CRI = 53.1–86.7) of total steelhead smolt mortality during out-migration from RIS to BON.

Compensatory/additive analysis

There was strong evidence that Caspian Tern predation was an additive source of mortality for all spatial scales, years, and life stages (smolt, SAR) evaluated. Estimates of a, yearly measures of the magnitude of the negative linear relationship between aggregate Tern predation and survival, were significantly greater than zero in all years and spatial scales, with annual estimates of smolt survival and SAR probabilities consistently lower than the respective baseline estimates (Figs. 3 and 4, Table 2).

For smolt survival, estimates of a averaged 1.406 (95% CRI = 1.012–1.814), suggesting that Caspian Tern predation upstream of BON was a super-additive source of mortality during the smolt life-stage ($a > 1$). Estimates of a were similar among years, ranging from 1.264 (95% CRI = 0.531–1.855) to 1.507 (95% CRI = 0.980–2.152; Table 2), and were not significantly correlated with annual estimates of baseline survival (ϕ^0) or with estimates of annual predation probabilities by Caspian Terns ($\hat{r}^2 = 0.032$, 95% CRI = -0.547–0.593; $\hat{r}^2 = -0.104$, 95% CRI = -0.705–0.493; respectively). Estimates of ϕ^Δ (the difference between baseline and observed survival) for steelhead smolts were consistently greater than zero in all years, ranging nominally from 0.052 (95% CRI = 0.017–0.103) to 0.027 (95% CRI = 0.012–0.045; Table 2). Consequently, observed annual smolt survival probabilities to BON were estimated to be 29.0% less on average (95% CRI = 22.7–34.3; Fig. 3) than baseline survival probabilities (in the absence of Tern predation).

Estimates of a for the analysis of SAR probabilities were also significantly greater than zero in all years with complete adult returns (2008–2015; Fig. 4, Table 2). Results provide strong evidence that higher Caspian Tern predation probabilities were associated with lower SAR probabilities in all years. The weighted average annual estimate of a was 0.052 (95% CRI = 0.017–0.103), with the negative linear relationship between estimates of Caspian Tern predation probabilities and estimates of SAR probabilities evident in all years, even those of markedly low adult returns (Fig. 4). Nominal
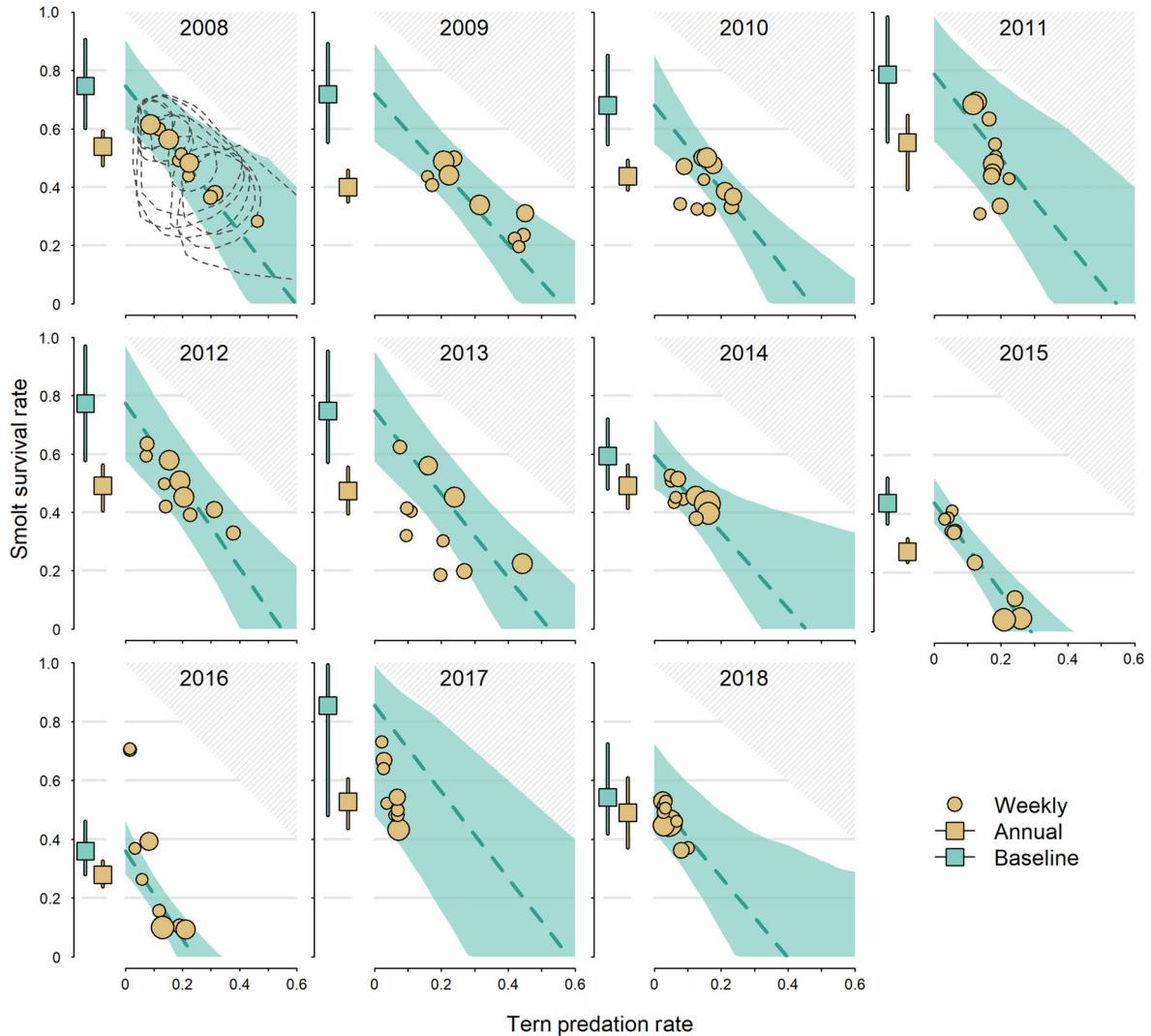
FIG. 3. Weekly probability estimates of steelhead smolt survival and Caspian Tern predation along with the estimated annual relationships between survival and predation during out-migration from Rock Island Dam to Bonneville Dam. The plotted joint estimates of survival and predation were derived from a mark–recapture–recovery model without an assumed functional relationship between them. The size of light brown circles depicts relative numbers of steelhead smolts tagged and released each week at Rock Island Dam. Approximate 95% credible regions are depicted for joint survival and predation estimates in 2008 to demonstrate uncertainty but omitted from other years for intelligibility. Dashed lines represent the best fit estimate of the linear relationship and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of smolt survival with Tern predation (light brown box) and baseline smolt survival in the absence of Tern predation (light blue box) are also provided (error bars denote 95% CRI).

estimates of ϕ^Δ ranged from 0.012 (95% CRI = 0.005–0.024) to 0.049 (95% CRI = 0.025–0.078; Table 2, Fig. 4). Years of lower estimated steelhead SAR probabilities, or lower estimated Caspian Tern predation probabilities, were associated with relatively smaller estimates of ϕ^Δ. For example, smolts released in 2015, a year in which mortality from sources other than Tern predation was among the highest estimated (Table 2), had estimated weekly SAR probabilities considerably lower than average. The estimate of ϕ^Δ_{2015}, however, was still measurable and almost certainly larger than zero ($\widehat{\phi}^\Delta_{2015}$ = 0.011

[95% CRI = 0.001–0.029]; $\widehat{\text{prob}}\left[\phi^\Delta_{2015} \le 0\right] < 0.001$). After accounting for predation by Caspian Terns from all eight colonies in the Columbia River basin, including the large colony in the Columbia River estuary, observed steelhead SARs were, on average, 71.1% less than the respective estimated baseline probabilities (95% CRI = 65.3–76.8; Fig. 4). Collectively, results provide evidence that weekly cohorts of tagged steelhead smolts returned to the Columbia River as adults in smaller proportions after experiencing higher rates of Caspian Tern predation as smolts (Table 2, Fig. 4). As with smolt out-

TABLE 2. Estimated cumulative predation probabilities (95% credible intervals) by Caspian Terns and other piscivorous colonial waterbirds, and survival of PIT-tagged steelhead smolts released at Rock Island Dam during 2008–2018, with estimates of the magnitude of the association between Caspian Tern predation probabilities on steelhead survival (a, additivity), and the difference in steelhead survival probabilities from estimated baseline survival probabilities (Φ^{Δ}).

Source	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Rock Island Dam to Bonneville Dam as Smolts											
Term predation	0.164	0.288	0.173	0.156	0.204	0.197	0.086	0.110	0.083	0.048	0.039
Mortality	(0.124–0.226)	(0.205–0.366)	(0.128–0.244)	(0.117–0.207)	(0.138–0.305)	(0.143–0.276)	(0.064–0.113)	(0.080–0.160)	(0.062–0.109)	(0.036–0.063)	(0.027–0.057)
Other bird predation	0.076	0.127	0.114	0.071	0.081	0.114	0.151	0.303	0.236	0.218	0.170
Mortality	(0.053–0.102)	(0.088–0.174)	(0.083–0.149)	(0.049–0.097)	(0.056–0.111)	(0.082–0.154)	(0.118–0.191)	(0.242–0.375)	(0.183–0.298)	(0.170–0.272)	(0.127–0.215)
Out-migration	0.540	0.401	0.438	0.554	0.491	0.473	0.492	0.272	0.279	0.528	0.490
Survival	(0.479–0.595)	(0.350–0.455)	(0.390–0.488)	(0.400–0.652)	(0.409–0.566)	(0.393–0.552)	(0.416–0.563)	(0.233–0.311)	(0.248–0.324)	(0.443–0.609)	(0.367–0.601)
Estimates of a	1.264	1.292	1.455	1.412	1.427	1.435	1.338	1.507	1.490	1.411	1.394
	(0.531–1.855)	(0.677–1.821)	(0.811–2.272)	(0.606–2.295)	(0.761–2.118)	(0.837–2.133)	(0.498–2.08`)	(0.980–2.152)	(0.879–2.207)	(0.620–2.345)	(0.520–2.315)
Estimates of $\phi\Delta$	0.192	0.314	0.244	0.221	0.276	0.260	0.129	0.168	0.108	0.149	0.066
	(0.083–0.291)	(0.172–0.459)	(0.108–0.404)	(0.107–0.391)	(0.135–0.421)	(0.142–0.396)	(0.036–0.233)	(0.098–0.235)	(0.028–0.192)	(0.038–0.295)	(0.011–0.128)
Rock Island Dam to adult return at Bonneville											
Term predation	0.258	0.375	0.254	0.198	0.237	0.262	0.153	0.143	0.110	0.110	0.075
Mortality	(0.207–0.323)	(0.290–0.461)	(0.201–0.328)	(0.156–0.250)	(0.172–0.342)	(0.124–0.188)	(0.202–0.344)	(0.124–0.188)	(0.109–0.193)	(0.087–0.138)	(0.090–0.133)
Other bird predation	0.104	0.153	0.147	0.111	0.116	0.129	0.200	0.330	0.246	0.223	0.179
Mortality	(0.078–0.134)	(0.111–0.202)	(0.112–0.186)	(0.082–0.144)	(0.084–0.148)	(0.094–0.168)	(0.161–0.244)	(0.266–0.403)	(0.193–0.308)	(0.173–0.276)	(0.135–0.224)
Return Survival to adult	0.030	0.011	0.012	0.006	0.010	0.010	0.008	0.001	NA	NA	NA
	(0.026–0.034)	(0.009–0.013)	(0.010–0.015)	(0.004–0.008)	(0.008–0.012)	(0.008–0.013)	(0.006–0.010)	(0–0.001)	NA	NA	NA
Estimates of a	0.190	0.102	0.114	0.120	0.106	0.052	0.122	0.113	NA	NA	NA
	(0.097–0.305)	(0.048–0.171)	(0.056–0.189)	(0.040–0.232)	(0.040–0.232)	(0.017–0.103)	(0.056–0.216)	(0.008–0.316)	NA	NA	NA
Estimates of $\phi\Delta$	0.049	0.022	0.027	0.022	0.025	0.012	0.019	0.011	NA	NA	NA
	(0.025–0.078)	(0.015–0.055)	(0.012–0.045)	(0.006–0.044)	(0.009–0.050)	(0.005–0.024)	(0.008–0.039)	(0.001–0.029)	NA	NA	NA

Notes: Values are reported as medians with 95% credible intervals. NA denotes cohorts where complete adult returns were not available.
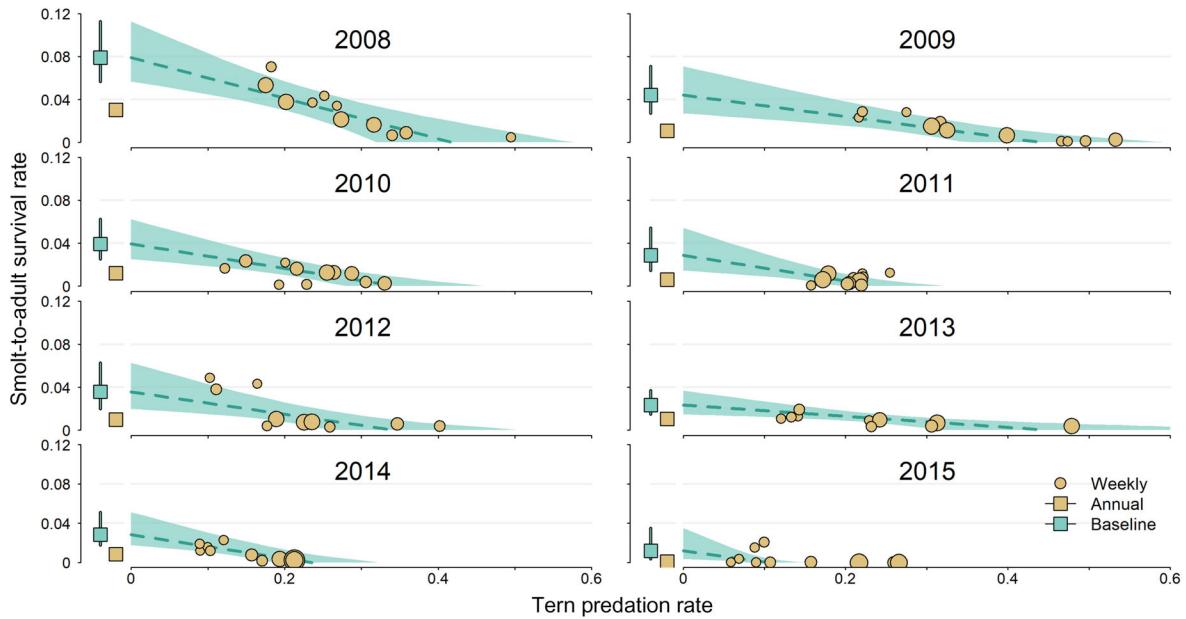
FIG. 4. Estimated annual relationships between PIT-tagged steelhead smolt-to-adult survival probabilities and Caspian Tern predation probabilities during smolt out-migration from Rock Island Dam to the Pacific Ocean. The plotted joint estimates of survival and predation were derived from a mark-recapture-recovery model without an assumed functional relationship between them. The size of the light brown circles depicts the relative numbers of steelhead smolts tagged and released each week at Rock Island Dam. Dashed lines represent the estimate of the best linear fit to the data and shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of survival with Tern predation (light brown box) and baseline survival in the absence of Tern predation (dark blue box) are also provided (error bars denote 95% CRI).

migration, estimates of a and ϕ^0 were not significantly correlated among years or with estimates of annual predation probabilities by Caspian Terns ($\hat{r} = 0.080$, 95% CRI = -0.670–0.812, and $\hat{r} = 0.061$, 95% CRI = -0.733–0.751, respectively).

DISCUSSION

In our study, the estimated additive effects of Caspian Tern predation on steelhead trout were statistically significant within and across overlapping salmonid life stages, despite Tern predation occurring only during the smolt life stage. Independent of baseline survival conditions and the magnitude of Caspian Tern predation each year, a persistent pattern was evident: for each additional 10 steelhead smolts consumed by Caspian Terns, ~14 fewer smolts from that cohort survived out-migration to Bonneville Dam. These results have important implications for management actions focused on increasing steelhead survival in the Columbia River. Further, Tern predation during the steelhead smolt life stage was estimated to be a partially additive source of mortality at the scale of SARs, with estimated observed survival probabilities significantly lower than estimates of baseline survival (survival in the absence of Tern predation) in all study years. Again, regardless of baseline survival conditions and the level of Caspian Tern predation, a persistent pattern was observed whereby, on average, for

every 10 steelhead smolts consumed by Terns, one less individual from that cohort returned to the Columbia River as an adult to Bonneville Dam. Over a scale as large as SARs, representing the vast majority of an anadromous salmonid's potential lifespan, any source of mortality encountered early on will be mostly compensatory. Considering the limited rate in which juvenile salmonids survive to adulthood (Quinn 2005), it is important to consider how specific mortality sources during different life stages affect the overall viability of endangered salmonid species (NOAA 2014).

Mechanisms of super-additivity over large scales are generally driven by density-dependent processes relating to population regulation (e.g., fecundity; Kokko and Johnstone 2001, Liermann and Hilborn 2001). In contrast, there are fewer predation-related super-additive mechanisms within a single lifespan (i.e., prior to reproduction), whereby predation reduces the average survival probability of individuals not consumed by the predator in question (Sandercock et al. 2011). An additive effect of predation can result from predators selecting larger, fitter individuals (i.e., those less likely to die otherwise). Limited information indicates that Terns disproportionately depredate fish in degraded condition and that predation selectivity is a concave function of fork length where smaller and larger individuals are less susceptible (Hostetter et al. 2012), however, survival is often a linear function of fork length (i.e., bigger is better; Zabel et al.

2005, Hostetter et al. 2015*b*). Thus, predation selectivity may play a role in the additive effects estimated here but such mechanisms cannot fully explain the super-additivity of the relationships observed in the juvenile life stage.

The foraging behavior of Caspian Terns may also be a possible mechanism of super-additivity. Caspian Terns plunge dive to capture prey (Smith and Mudd 1978, Cuthbert and Wires 1999), where unsuccessful foraging attempts can result in some proportion of lethally or sub-lethally injured prey (i.e., latent mortality). Latent smolt mortality associated with Caspian Tern foraging activity was likely correlated with fluctuations in Caspian Tern predation probabilities in the present study, but was unobserved, unmeasured, and unaccounted for (Reimchen 1988). This latent mortality is analogous to "crippling losses" seen in harvest management (game injured or killed but not retrieved; Williams et al. 2002, Schaub and Lebreton 2004, Servanty et al. 2010). With harvest management, crippling loss may be estimated via reward tags and minimized through hunter training (Norton and Thomas 1994, Williams et al. 2002); however, data sufficient for estimation of crippling loss from predation due to Caspian Terns were not available with respect to this study.

An additional mechanism of super-additivity in the present study was the theft of prey captured by Caspian Terns by other species of fish-eating birds (i.e., kleptoparasitism). For example, an unknown, but possibly substantial, proportion of smolts captured by Caspian Terns and brought back to the breeding colony to feed mates or young was kleptoparasitized by communally-nesting gulls *Larus* spp. (Garcia et al. 2010, Patterson 2012, Adkins et al. 2014). These smolt losses, however, were not incorporated into Tern predation probabilities, but rather enumerated as consumed by gulls. The theft of killed prey is common in predator–prey systems and, as another mechanism of super-additivity, can increase predation probabilities and potentially increase the impact of predation on prey populations (Krofel et al. 2012, Tallian et al. 2017). Steelhead smolts in particular, due to their large size and high energy content, are targeted by kleptoparasitic gulls at Caspian Tern colonies (D. D. Roby, *personal observation*).

Several factors proved invaluable for reaching conclusions about the additive effects of Caspian Tern predation on steelhead survival. Direct quantification of rates of additivity relies on explicit unbiased estimates of predation probabilities rather than raw counts of recoveries. The estimation of predation probabilities requires auxiliary information to identify recovery probabilities unique to each measured mortality source (Gauthier and Lebreton 2008, Gimenez et al. 2012, Tavecchia et al. 2012, Hostetter et al. 2015). Only by directly estimating both the probability that a tag from a depredated fish was deposited on a bird's breeding colony, and the probability that a tag was recovered given it was deposited, were we able to further explore and measure relationships between survival and predation. Furthermore, the

prolonged out-migration season of steelhead trout allowed us to delineate temporal cohorts that could be treated as pseudo-replicates within each year. Thus, we did not have to assume an invariable baseline survival rate, either among or within years, and could also allow the relationship between survival and predation to vary among years. This provided a more accurate reflection of the biological systems under consideration.

Identifying a negative relationship between survival probabilities and predation probabilities does not by itself indicate that predation is an additive source of mortality that affects prey populations (Sandercock et al. 2011, Serrouya et al. 2015). Negative relationships may also be consistent with some other ecological process driving both declines in survival and increases in predation. In other words, observational studies, without appropriate experimental controls and prescribed manipulation of treatment parameters, do not allow for definitive statements about causation. The introduction of management actions to reduce predation by reducing the number of Caspian Terns nesting in the Columbia River basin (USFWS 2005, USACE 2014), however, did result in a greater experimentally driven range of estimates of Tern predation probabilities. This wider range of observed probabilities facilitated the development of broader inferences and may mitigate some concerns of extrapolation inherent to the interpretation of baseline survival probabilities. Furthermore, the similarity in the annual relationships across 11 yr of out-migration data and eight years of smolt-to-adult returns, suggests that Caspian Tern predation on juvenile steelhead has had appreciable, consistent impacts on smolt survival probabilities during out-migration, as well as smolt-to-adult return probabilities. Given the magnitude of Caspian Tern predation probabilities on ESA-listed Upper Columbia River steelhead smolts and the observed relationship between Tern predation probabilities and steelhead survival probabilities, the evidence suggests that Tern predation may have an appreciable effect on on-going and future recovery plans for this ESA-listed salmonid population.

Conclusions

Our results provide new information about the impacts of predation on survival of prey using a multinomial state-space model and mark–recapture–recovery data set involving multiple predators, spatial scales, years, and animal life stages. Evidence from this model indicates that mortality from predation was primarily additive and, therefore, had a credible, significant impact on prey survival. Predator–prey models should account for, or at least assess, additive effects of predation across life stages in order to avoid exaggerating the potential benefits from management actions aimed at reducing predator populations to enhance prey populations. As such, it is important to design studies that concurrently estimate survival and predation to evaluate these

relationships and inform the efficacy of management strategies aimed at the reduction of predation impacts on prey populations of conservation concern.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2193/full

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k98sf7m3r