

## ARTICLE

# Predation probabilities and functional responses: How piscivorous waterbirds respond to pulses in fish abundance

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**Abstract**

How predators respond to changes in prey abundance (i.e., functional responses) is foundational to consumer–resource interactions, predator–prey dynamics, and the stability of predator–prey systems. Predation by piscivorous waterbirds on out-migrating juvenile steelhead trout (*Oncorhynchus mykiss*) is considered a factor affecting the recovery of multiple Endangered Species Act-listed steelhead populations in the Columbia River basin. Waterbird functional responses, however, may vary by predator species and location, with important implications to predator management strategies. We used a 13-year dataset on waterbird abundance across seven breeding colonies (three Caspian tern [*Hydroprogne caspia*], two double-crested cormorant [*Nannopterum auritum*], and two California and ring-billed gull [*Larus californicus* and *Larus delawarensis*] colonies) and steelhead tag-recovery data (>645,000 tagged and >32,000 recovered steelhead) to quantify weekly predation probabilities and functional responses across waterbird species, colonies, and years. Weekly predation probabilities were highly variable, ranging from 0.01 to 0.30 at tern colonies, 0.01 to 0.20 at cormorant colonies, and 0.03 to 0.13 at gull colonies. Per capita predation probabilities were an order of magnitude higher at inland tern and cormorant colonies relative to estuary colonies of the same species. Terns displayed Type II functional responses across colonies and years, where predation probabilities peaked at low steelhead abundances and declined as steelhead abundance increased (i.e., predator swamping). Cormorants nesting at the large estuary colony (several thousand birds) displayed a Type III functional response, but cormorants nesting at the smaller inland colony (several hundred birds) displayed a Type II response. Consumption probabilities of steelhead by gulls remained consistent across a large range of steelhead availability, suggesting a Type I or a Type III functional response, but a lack of colony abundance data prevented quantifying functional responses. The level of tern predation combined with Type II functional responses indicate possible

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population-level impacts that could destabilize small or declining prey populations. Conversely, the apparent Type III functional responses of gulls and estuary nesting cormorants are indicative of prey switching behaviors targeted at periods of high steelhead abundance. Our results illustrate the complexity of predator–prey interactions and the importance of quantifying predator- and location-specific functional responses when predicting the efficacy of management strategies to enhance prey populations.

#### KEYWORDS

functional response, mark-recovery, predation, predator swamping, predator–prey dynamics, salmonid, waterbird

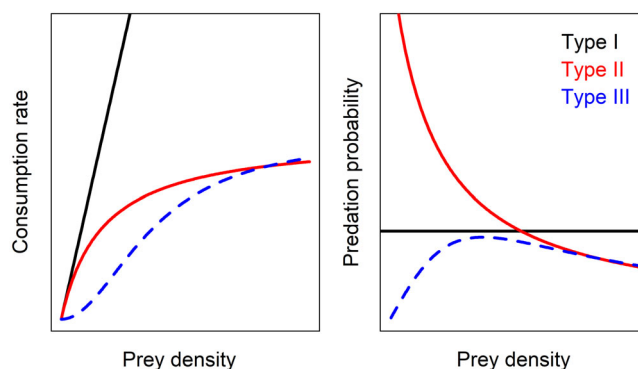
## INTRODUCTION

Pulses in resource availability can produce abundant yet ephemeral foraging opportunities for consumers (Yang et al., 2008). In predator–prey systems, prey synchrony can overwhelm the ability of consumers to exploit temporary prey abundances (i.e., predator swamping) or lead to increased predation through predator attraction or behavioral mechanisms (e.g., behavioral aggregation, prey switching; Armstrong et al., 2016; Ims, 1990; Yang et al., 2008). Predator-specific foraging strategies generally mediate the ability of predators to respond to pulses in prey availability (Armstrong et al., 2016). For example, it is commonly hypothesized that generalist and mobile consumers exploit temporary food resources through behavioral responses (i.e., movement, prey switching; Andersson & Erlinge, 1977). Conversely, restrictions on handling or consumption time (i.e., time required to pursue, kill, and eat prey) may constrain specialist and spatially restricted predators, especially when pulses in prey abundance are spatially or temporally limited (Armstrong et al., 2016; Holling, 1959a; Ims, 1990; O'Donoghue, Boutin, Krebs, Zuleta, et al., 1998). Understanding how predators respond to changes in prey abundance is crucial to predicting the effects of shifting predator or prey characteristics and the stability of predator–prey systems (Armstrong et al., 2016; Chan et al., 2017; Ellis et al., 2020; O'Donoghue, Boutin, Krebs, Murray, & Hofer, 1998; O'Donoghue, Boutin, Krebs, Zuleta, et al., 1998).

Functional responses describe how the rate of prey consumption by individual predators is related to changes in prey abundance (Holling, 1959a, 1959b; Solomon, 1949). Predator functional responses are foundational to behavioral and population ecology (Abrams, 1990), foraging theory (Stephens & Krebs, 1986), resource limitation (Hassell, 1978), and the stability of predator–prey systems (Oaten & Murdoch, 1975). Functional responses are commonly categorized into three types (Figure 1; Solomon, 1949; Holling, 1959a):

- Type I: The number of prey killed per predator per unit time is directly proportional to prey density.
- Type II: The number of prey killed per predator per unit time increases with increasing prey density, but levels off at an upper threshold due to limitations imposed by handling time.
- Type III: The number of prey killed per predator per unit time increases slowly with increases in prey density when prey are scarce, increases rapidly with increases in prey density when prey densities are moderate, and levels off at high prey densities.

While functional responses were originally formulated in terms of number of prey consumed per predator per unit time (Holling, 1959a; Solomon, 1949), many studies now examine functional responses using predation rates or probabilities (i.e., changes in per capita predation probability as a function of prey abundance; Figure 1; Juliano, 2001).



**FIGURE 1** Type I, Type II, and Type III functional responses expressed as per capita consumption rates (i.e., number of prey consumed per predator per unit time; left) and per capita predation probabilities (i.e., proportion of prey consumed per predator per unit time; right).

Evaluating functional responses using predation probabilities is particularly advantageous for mark-recapture studies, which are widely used to quantify cause-specific mortality probabilities across a diversity of ecosystems and taxa (e.g., Lebreton et al., 1992; Schaub & Pradel, 2004).

In the Columbia River basin, United States, avian predation on out-migrating juvenile salmonids (*Oncorhynchus* spp.) is considered a factor affecting the recovery of some salmonid populations listed under the U.S. Endangered Species Act (ESA; NOAA, 2008). Combined across multiple breeding colonies of piscivorous waterbirds, avian predation on out-migrating juvenile steelhead (*O. mykiss*) can exceed 30% but varies greatly across salmonid species (Evans et al., 2012, 2016, 2019; Payton et al., 2019). Predation or consumption (hereafter simply “predation”) rates by three taxa of avian predators are particularly notable: Caspian terns (*Hydroprogne caspia*; hereafter tern), double-crested cormorants (*Nannopterum auritum*; hereafter cormorant), and mixed colonies of California and ring-billed gulls (*Larus californicus* and *L. delawarensis*; hereafter gulls; Evans et al., 2016; Hostetter et al., 2015; Payton et al., 2019). Foraging ecology across these three avian taxa is highly variable. Gulls are generalists that forage on a variety of aquatic and terrestrial food resources and are known to scavenge dead and moribund fish (Winkler, 2020). Cormorants are pursuit-divers of aquatic prey, but their diets include a variety of fish species and sizes across a diversity of habitats (Dorr et al., 2020). Terns, conversely, have a relatively restricted range of prey types and sizes, and forage for fish by plunge-diving in the top meter of the water column (Cuthbert & Wires, 2020). Disparities in foraging ecology among these waterbird species are also evident from previous diet studies, where juvenile salmonids can comprise 30%–80% of tern diets (by mass) compared to 15%–45% of cormorant diets and 0%–15% of California and ring-billed gull diets in the Columbia River basin (Collis et al., 2002; Roby et al., 2002). How these different predator-species respond to pulses in out-migrating juvenile salmonid abundance and if these relationships are consistent across space (e.g., inland vs. estuary) and time, however, remains poorly understood.

Herein, we investigate species-specific predation probabilities and functional responses using mark-recovery data collected across three avian predator taxa nesting on five different islands over a 13-year study in the Columbia River basin. Our study evaluates the form and support for different functional responses among multiple predator species in a natural system. We also explore how functional responses vary by colony location. Here, we predicted increased evidence of predator swamping at

colonies located in freshwater regions relative to estuary locations due to lower prey diversity and faster transit times for steelhead smolts in freshwater portions of the basin. Overall, this study provides several novel insights into predator–prey dynamics and interactions across trophic levels by exploring how multiple predators respond to rapid changes in prey abundance and comparing functional responses across a spectrum of specialist to generalist predators replicated across multiple locations and years.

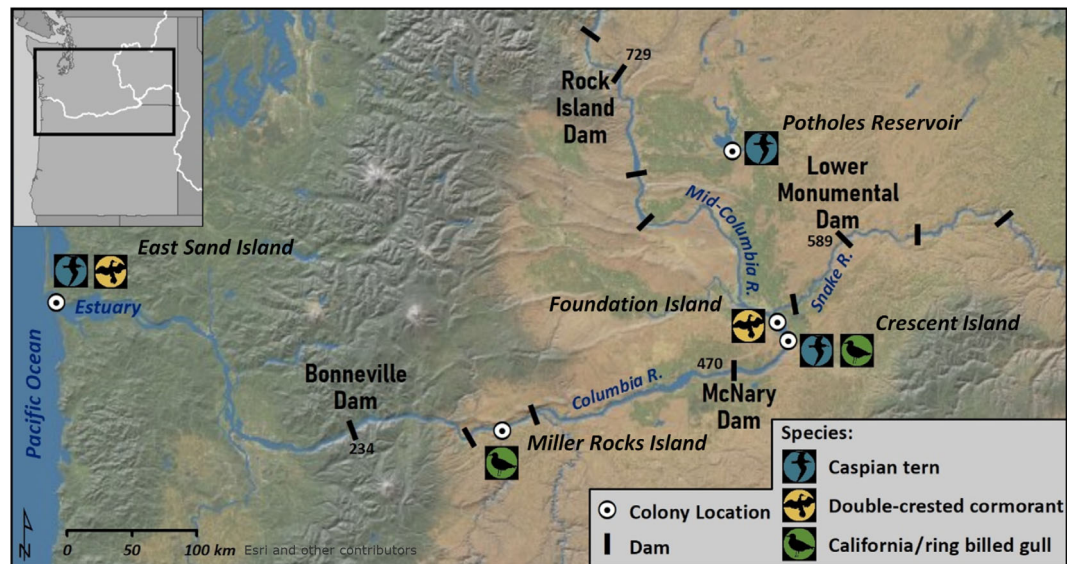
## METHODS

### Study area

This study was conducted at three Caspian tern colonies, two double-crested cormorant colonies, and two mixed colonies of California and ring-billed gulls in the Columbia River basin (Figure 2). Colonies were located in the inland portion of the basin (i.e., Columbia Plateau region; Adkins et al., 2014) and in the Columbia River estuary (Figure 2). Predation probabilities were quantified using detection and recovery data from passive integrated transponder (PIT) tags, where tagged out-migrating juvenile steelhead were detected upstream of avian colonies while passing Rock Island Dam (river kilometer [rkm] 730 on the mid-Columbia River), Lower Monumental Dam (rkm 589 on the Snake River), McNary Dam (rkm 470 on the mid-Columbia River), and Bonneville Dam (rkm 225 on the lower-Columbia River; Figure 2) and recovered from the aforementioned seven bird colonies (Figure 2; Evans et al., 2012). While our study period included 2007–2019, we restricted colony-specific analyses to years in which both counts of birds and recovery of PIT tags occurred at a given colony (Table 1).

### Colony monitoring

Boat, aerial, and observation blind-based surveys were used to count the number of birds nesting at each colony. Counts were generally conducted weekly at tern colonies on East Sand Island (ESI), Crescent Island (CSI) and in Potholes Reservoir islands (PTI), and the cormorant colony on Foundation Island (FDI; Figures 2 and 3). Counts of cormorants nesting on ESI in the Columbia River estuary were collected via aerial photography once per week or every other week and recorded as the number of active nests. For consistency of comparisons, the number of adult cormorants nesting on ESI was calculated as  $2 \times$  the number of active nests. In



**FIGURE 2** Locations of piscivorous waterbird nesting colonies and hydroelectric dams within the Columbia River basin, USA, where colony monitoring and mark-recovery data were collected. Bird colony locations included East Sand Island, Miller Rocks Island, Crescent Island, Foundation Island, and Potholes Reservoir islands.

**TABLE 1** Data used to investigate predation/consumption probabilities and functional responses.

Predator	Island	Years	No. weeks/year	No. birds	Steelhead	
					Available	Recovered
Tern	PTI	6 (2008–2013)	6 (6–7)	416 (169–589)	6751 (5653–7904)	333 (281–419)
Tern	CSI	8 (2007–2014)	7 (5–9)	496 (115–729)	24,866 (6925–50,511)	454 (97–1042)
Tern	ESI	12 (2007–2018)	7 (5–8)	9358 (2373–18,922)	19,995 (8698–56,380)	1289 (292–4336)
Cormorant	FDI	6 (2007–2012)	7 (5–9)	363 (72–683)	31,857 (6925–50,511)	353 (76–653)
Cormorant	ESI	8 (2007–2015)	5 (3–6)	24,600 (16,020–32,568)	20,425 (6899–56,380)	733 (111–1545)
Gull	CSI	8 (2007–2014)	7 (5–9) <sup>a</sup>	7157 (5601–7187) <sup>a</sup>	24,866 (6925–50,511)	117 (41–249)
Gull	MRI	13 (2007–2019)	7 (5–10) <sup>a</sup>	4446 (3223–6016) <sup>a</sup>	14,949 (5453–31,817)	136 (31–341)

Note: Columns denote predator species, nesting island, years, annual number of weeks with adequate predator and prey data, weekly bird counts, and annual numbers of tagged steelhead available and recovered on a bird colony (mean and range for all columns). Avian predators included Caspian terns (Tern), double-crested cormorants (Cormorant), and California and ring-billed gulls (Gull) nesting on islands in the Columbia River basin (Crescent Island [CSI], Foundation Island [FDI], East Sand Island [ESI], Potholes Reservoir Islands [PTI], Miller Rocks [MRI]). See Figure 2 for locations of breeding colonies and hydroelectric dams.

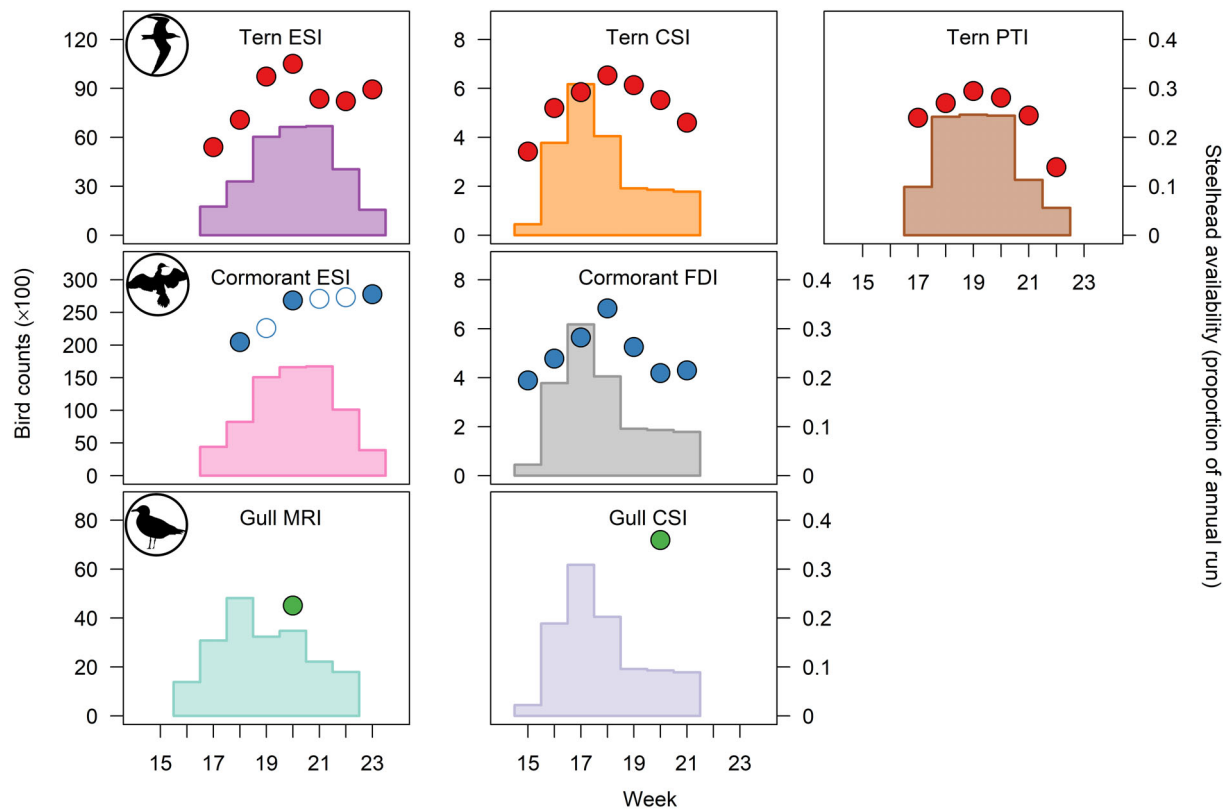
<sup>a</sup>Counts of gull colonies occurred once per year during the peak of the nesting season in late-May.

weeks without nest count data from the ESI cormorant colony, we interpolated abundance as the average of the previous and subsequent weeks (Figure 3). Data on gull abundances were more limited for gull colonies on Miller Rocks (MRI) and on CSI, which were only counted on one occasion per breeding season, when the number of active nests was near its maximum. We therefore estimate weekly predation probabilities associated with gull colonies but do not explicitly quantify per capita predation probabilities and functional responses. Additional colony monitoring details are found in Collis et al. (2002) and Adkins et al. (2014).

## Fish tagging and recovery

Each year, tens of thousands of juvenile steelhead are PIT-tagged and released throughout the Columbia River basin (PSMFC, 2020). A portion of PIT-tagged juveniles are subsequently detected passing downstream hydroelectric dams during out-migration to the Pacific Ocean (Figure 2). Following Evans et al. (2012), we considered PIT-tagged steelhead detected at the nearest dam upstream of a bird colony with adequate PIT tag detection capabilities as available to avian predators at the subsequent downstream colony (Figure 2). Restricting





**FIGURE 3** Weekly predator abundance (circles) and prey availability (histograms) by colony and bird species in 2012. Avian predators include Caspian terns (top row), double-crested cormorants (middle row), and California and ring-billed gulls (bottom row) nesting on islands in the Columbia River basin (Crescent Island [CSI], Foundation Island [FDI], East Sand Island [ESI], Potholes Reservoir islands [PTI], Miller Rocks [MRI]). Y-axes vary by panel as noted. For ESI cormorants, filled and open circles denote observed and interpolated counts, respectively. See Appendix S1 for complete set of colony  $\times$  year data.

analyses to detected steelhead ignores the unknown number of tagged steelhead alive and undetected at dams, but greatly simplifies the modeling process and still allows for an unbiased estimation of predation probabilities (i.e., probability of predation given an individual was alive at a dam; Evans et al., 2012). We restricted analyses to the middle 95% of the annual steelhead out-migration period to prevent issues associated with excessively small weekly sample sizes of available fish that could occur during the leading and trailing weeks of each run. Steelhead availability corresponded to approximately 5–10 weeks (April–June) at inland locations and 5–8 weeks (April–June) at estuary locations (Table 1). Detection data were retrieved from the PIT Tag Information System, a regional salmonid tag database maintained by the Pacific States Marine Fisheries Commission, during January 2020 (PSMFC, 2020).

Recovery of PIT tags on bird colonies followed the methods of Ryan et al. (2001) and Evans et al. (2012), where colonies were scanned for PIT tags each year after nesting birds dispersed at the end of the breeding season

(August–November) using flat-plate or pole-mounted PIT tag antennas.

## Predation probabilities

The probability of recovering an available PIT-tagged steelhead on a bird colony is the product of three probabilities: (1) the probability a tagged steelhead was consumed (predation probability  $\theta$ ), (2) the probability a tag from a consumed steelhead was deposited on a breeding colony (deposition probability  $\psi$ ), and (3) the probability a tag deposited on-colony was detected by researchers during scanning efforts (detection probability  $p$ ; Hostetter et al., 2015). For simplicity, parameters are indexed by week ( $j$ ) and year ( $k$ ), while subscripts for predator species and colony are dropped but note that analyses were conducted independently for each colony and species. We assumed the number of PIT-tagged steelhead recovered in week  $j$  of year  $k$  ( $n_{jk}$ ) is a binomial random variable. Specifically,

$$n_{jk} \sim \text{binomial}(N_{jk}, \theta_{jk} \psi p_{jk}), \quad (1)$$

where  $N_{jk}$  is the number of PIT-tagged steelhead available in week  $j$  of year  $k$ ,  $\theta_{jk}$  is the predation probability in week  $j$  of year  $k$ ,  $\psi$  is the predator-specific deposition probability, and  $p_{jk}$  is the probability of detecting a tag deposited in week  $j$  of year  $k$ . To account for imperfect detection processes ( $p_{jk}$ ), PIT tags with known codes were distributed across each bird colony on multiple occasions during the breeding season and logistic regression was used to predict weekly detection probabilities (Evans et al., 2012, 2019; Hostetter et al., 2015). Previous studies also quantified bird species-specific tag deposition probabilities at tern, cormorant, and gull colonies in the Columbia River basin (Hostetter et al., 2015). To account for detection and deposition probabilities herein, we used informative priors derived from these previous studies (Hostetter et al., 2015; Payton et al., 2020) to inform detection probabilities ( $p_{jk}$ ) and predator-specific deposition probabilities ( $\psi$ ; see Appendices S1–S3).

Predation probabilities ( $\theta_{jk}$ ) were modeled as a weekly random walk on the logit-scale reflecting the tendency of predation probabilities to vary in a correlated pattern across weeks within a year (Payton et al., 2020). Specifically,

$$\theta_{1k} \sim \text{beta}(1, 1) \quad \text{for Week 1,} \quad (2)$$

$$\text{logit}(\theta_{jk}) \sim \text{Normal}(\text{logit}(\theta_{(j-1)k}), \sigma_k^\theta) \quad \text{for Week 2, 3, ..., } J, \quad (3)$$

where  $\sigma_k^\theta$  describes the year-specific standard deviation (SD) of the random walk.

## Functional responses

Functional responses describe how per capita (i.e., per bird) predation probabilities are related to prey abundance (Juliano, 2001; Figure 1). Only slight modifications to the previously described predation probability submodel (Equations (1)–(3)) are required to model weekly per capita predation probabilities. Specifically, for functional response analyses we define predation probability in week  $j$  of year  $k$  ( $\theta_{jk}$ ) as a function of per capita predation probability ( $\gamma_{jk}$ ) and predator abundance ( $C_{jk}$ ),

$$\theta_{jk} = \gamma_{jk} C_{jk}, \quad (4)$$

which is equivalent to deriving per capita predation probabilities as the predation probability divided by the number of predators ( $\gamma_{jk} = \theta_{jk} / C_{jk}$ ).

We fit three models for per capita predation probabilities to investigate Type I, II, and III functional responses (Juliano, 2001),

$$\text{logit}(\gamma_{jk}) = \beta_{0k}^\gamma \quad \text{Intercept only,} \quad (5)$$

$$\text{logit}(\gamma_{jk}) = \beta_{0k}^\gamma + \beta_{1k}^\gamma N_{jk} \quad \text{Linear,} \quad (6)$$

$$\text{logit}(\gamma_{jk}) = \beta_{0k}^\gamma + \beta_{1k}^\gamma N_{jk} + \beta_{2k}^\gamma N_{jk}^2 \quad \text{Quadratic.} \quad (7)$$

Equation (5) assumes that per capita predation probabilities ( $\gamma_{jk}$ ) are not related to prey abundance ( $N_{jk}$ ; Type I; Figure 1). This lack of a relationship in the per capita *predation probabilities* translates into a linear relationship in per capita *consumption rates*, where a constant proportion of prey are consumed regardless of prey abundance (Type I; Figure 1). Equation (6) allows a linear relationship between per capita predation probabilities and prey abundance (Type II if  $\beta_{1k}^\gamma < 0$ ), where decreasing per capita predation probabilities reflect a leveling off of per capita consumption rates as prey abundance increases (Figure 1). Finally, Equation (7) allows a quadratic relationship between per capita predation probabilities and prey abundance. Here, Type III functional responses are supported when per capita predation probabilities initially increase then decrease as a function of increasing prey abundance ( $\beta_{1k}^\gamma > 0$  and  $\beta_{2k}^\gamma < 0$ ; Ellis et al., 2020; Juliano, 2001; Figure 1). The quadratic model (Equation (7)) does not enforce a Type III response though. For example, when both  $\beta_{1k}^\gamma$  and  $\beta_{2k}^\gamma$  are  $< 0$ , per capita predation probabilities are highest at minimal prey abundances and continually decline as prey abundance increases, indicating a Type II response (Juliano, 2001).

For analysis purposes we used the number of PIT-tagged steelhead ( $N_{jk}$ ) as an index for the total number of steelhead available (tagged + untagged steelhead). During our study, tens of thousands of steelhead were annually tagged upriver of our study sites and volitionally released into the river and tributaries to continue out-migration. Thus, we expected the general trend in run-timing for tagged steelhead to be similar to the total population (Marsh et al., 1999; Table 1). Changes in the numbers of PIT-tagged steelhead available across years, however, may reflect changes in tagging studies more than changes in total steelhead abundance (Table 1). We therefore standardized prey abundance as weekly proportions of the total annual run ( $\delta_{jk}$ ) where  $\delta_{jk} = N_{jk} / \sum_{j=1}^J N_{jk}$ . As such, weekly proportions sum to 1.0 within a year and functional responses describe relationships between per capita predation probabilities and *proportional* changes in prey abundance.

## Model fitting

We modeled functional responses independently for each colony, but shared information across years through a hyperparameter. For each colony we assumed,

$$\beta_{0k}^y \sim \text{Normal}(\mu_0, \sigma_0), \quad (8)$$

$$\beta_{1k}^y \sim \text{Normal}(\mu_1, \sigma_1), \quad (9)$$

$$\log(\beta_{2k}^y) \sim \text{Normal}(\mu_2, \sigma_2), \quad (10)$$

where  $\mu$  and  $\sigma$  describe colony-specific means and SDs, respectively. We used a log-normal distribution for  $\beta_{2k}^y$  to enforce  $\beta_{2k}^y > 0$ , then simply subtracted rather than added  $\beta_{2k}^y$  in Equation (7). We found this greatly improved convergence while preventing ecologically implausible concave relationships where per capita predation probabilities indefinitely increased as prey abundance increased (Juliano, 2001).

Equations (5)–(7) were fit to each colony-specific dataset, with support for each functional response evaluated by summarizing the direction and significance of  $\mu$  and  $\beta^y$  parameters (Ellis et al., 2020; Juliano, 2001). We quantified the  $\Pr(\mu_1 < 0)$  to evaluate support for Type II responses across years and estimated each  $\beta_{1k}^y$  and  $\beta_{2k}^y$  to investigate the shape of annual responses. Similarly, support for a Type III response across years was quantified as the  $\Pr(\mu_1 > 0)$ , where  $\beta_{1k}^y$  and  $\beta_{2k}^y$  describe the shape of annual responses in the quadratic model. Type I functional responses are supported when parameters do not differ from zero (i.e., no evidence that per capita predation probabilities are related to prey abundance). Type I functional responses imply per capita consumption increases indefinitely; Type I responses are improbable in most vertebrate predator–prey systems (Jeschke et al., 2004). Instead, evidence for constant or increasing per capita predation probabilities as prey abundance increases likely capture the lower end of a Type III functional response, suggesting that the range of prey abundances was insufficient to cover the inflection point where per capita predation probabilities decline (Figure 1).

## Implementation

We implemented all models in a Bayesian framework using the software package stan (Stan Development Team, 2018) accessed through R version 3.6.2 (R Development Core Team, 2018) using the package rstan version 2.19.3

(Stan Development Team, 2020). We ran four parallel Hamiltonian Monte Carlo simulations containing 2000 adaptation iterations, followed by 2000 posterior iterations. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al., 2013). Chains were not considered valid and accepted unless Gelman–Rubin statistics for all parameters were  $< 1.01$  and zero divergent transitions were reported. Posterior predictive checks were used to evaluate model fit with respect to colony-specific weekly recovery counts (Gelman et al., 2013) and found no evidence for a lack of fit. We present estimated results as posterior medians along with 95% highest posterior density intervals (95% credible intervals [CrI]). For brevity, in-text figures display results from 2012, a year with data available at all colonies, while annual results from all years are provided as appendices.

Unless previously noted, vague priors were used for all parameters. Specifically, we used  $\text{Normal}(0, 5)$  for the regression slope hyperparameters ( $\mu_1$  and  $\mu_2$ ), and Half – normal(0, 5) for SDs. We used a weakly informative prior of  $\text{inv.logit}(\mu_0) \sim \text{Beta}(1, 13)$  for the per capita predation probability intercept hyperparameter (i.e., the proportion of out-migrating juvenile steelhead consumed by a single bird). This weakly informative prior had little influence on posterior distributions but prevented unrealistic values in the MCMC estimation process where a single colony could consume all out-migrating steelhead during a given week (i.e.,  $\theta_{jk} \geq 1.0$ ; Equation (4)), causing the model to crash. We used informative priors to describe predator-specific deposition probabilities where  $\psi^{\text{Tern}} \sim \text{Beta}(16.20, 6.55)$ ,  $\psi^{\text{Cormorant}} \sim \text{Beta}(15.98, 15.29)$ , and  $\psi^{\text{Gull}} \sim \text{Beta}(33.71, 183.61)$ , which reflects prior knowledge of the expected mean and variance of deposition probabilities ( $E[\psi] = 0.71, 0.51$ , and  $0.16$  for terns, cormorants, and gulls, respectively; Hostetter et al., 2015).

## RESULTS

### Colony monitoring

Analyses included up to 13 years of colony-specific bird count and smolt tag recovery data (Table 1). During the steelhead out-migration period, bird abundance varied dramatically across colonies, weeks, and years (Table 1, Figure 3). Weekly counts of terns at the ESI colony ranged from 2373 to 18,922, with a multi-year mean of 9358 individuals (Table 1), while weekly counts of terns nesting on CSI in the Columbia Plateau region ranged from 115 to 729, with a multi-year mean of 496 individuals (Table 1). Weekly counts of cormorants at the ESI

colony ranged from 16,020 to 32,568, with a multi-year mean of 24,600 individuals, while weekly counts of cormorants at the FDI colony in the Columbia Plateau region ranged from 72 to 683, with a multi-year mean of 363 individuals (Table 1). At gull colonies, count data consisted of one survey per year during peak colony attendance, with a multi-year mean of 4446 and 7157 individuals for gulls nesting at the MRI and CSI colonies, respectively (Table 1).

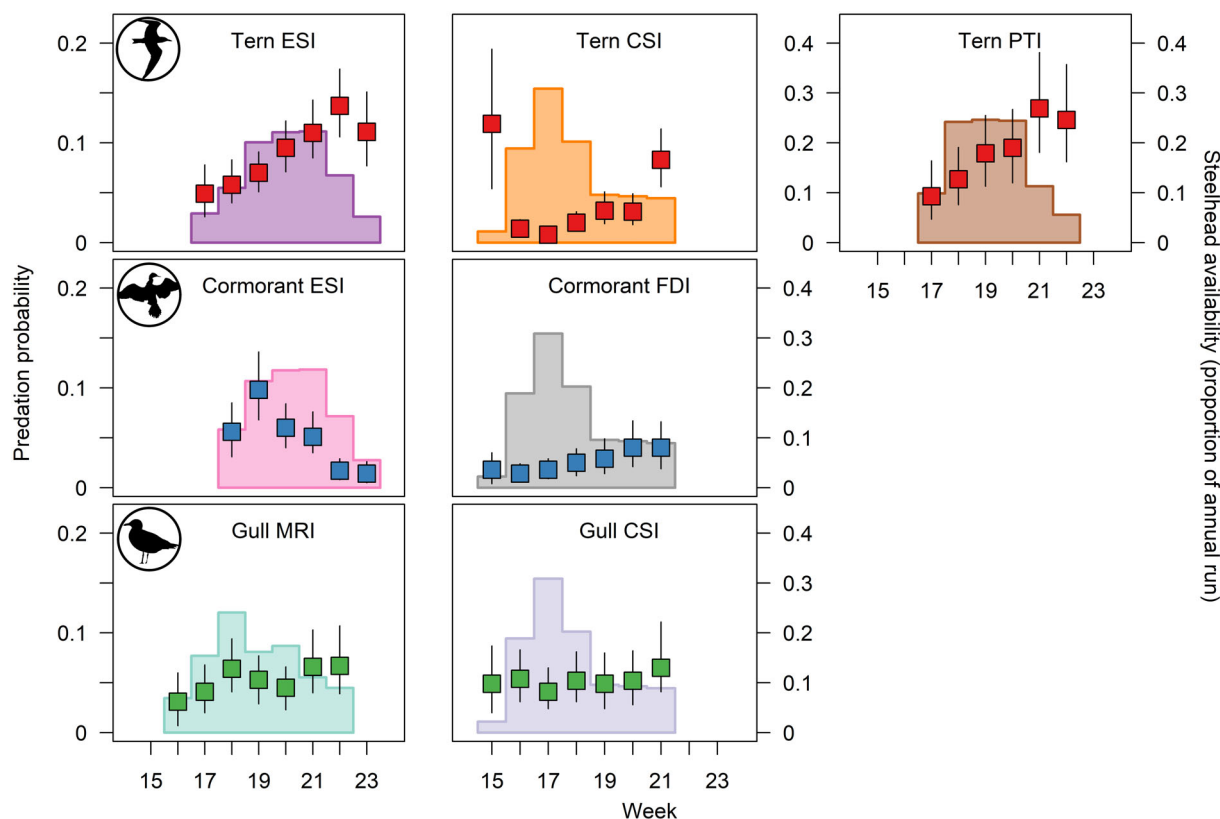
## Steelhead availability and recovery

During 2007–2019, >645,000 detections of PIT-tagged steelhead smolts at dams were used to measure prey availability and >32,000 of these tags were subsequently recovered on the seven waterbird nesting colonies (Table 1). Numbers of available PIT-tagged steelhead varied from <200 to >18,000 individuals per week, providing a large range of prey abundances over which to evaluate functional responses (Table 1, Figure 3; Appendix S1).

The numbers of tags annually recovered on a given bird colony ranged from 31 (MRI gulls in 2018) to 4336 (ESI terns in 2010), with the highest numbers of tags recovered on the large tern and cormorant colonies in the Columbia River estuary (Table 1).

## Predation probabilities

Weekly predation probabilities varied by predator species, location, year, and week (Figure 4; Appendix S2). Weekly predation probabilities at tern colonies were generally highest and most variable, ranging from 0.01 to 0.30 of available steelhead (Figure 4; Appendix S2). For cormorants, weekly predation probabilities differed markedly between colony locations, with predation probabilities generally higher (0.01–0.20) at the large cormorant colony in the estuary (thousands of breeding birds) and lower (0.01–0.06) at the much smaller colony in the Columbia Plateau region (several hundred breeding birds; Table 1, Figure 4; Appendix S2). At gull colonies, weekly predation



**FIGURE 4** Weekly predation probabilities (squares indicate medians, vertical bars indicate 95% credible intervals) and prey availability (histograms) by colony and bird species in 2012. Avian predators include Caspian terns (top row), double-crested cormorants (middle row), and California and ring-billed gulls (bottom row) nesting on islands in the Columbia River basin (Crescent Island [CSI], Foundation Island [FDI], East Sand Island [ESI], Potholes Reservoir islands [PTI], Miller Rocks [MRI]). Y-axes for predation probability are consistent across all panels except the tern PTI panel. See Appendix S2 for complete set of colony × year results.



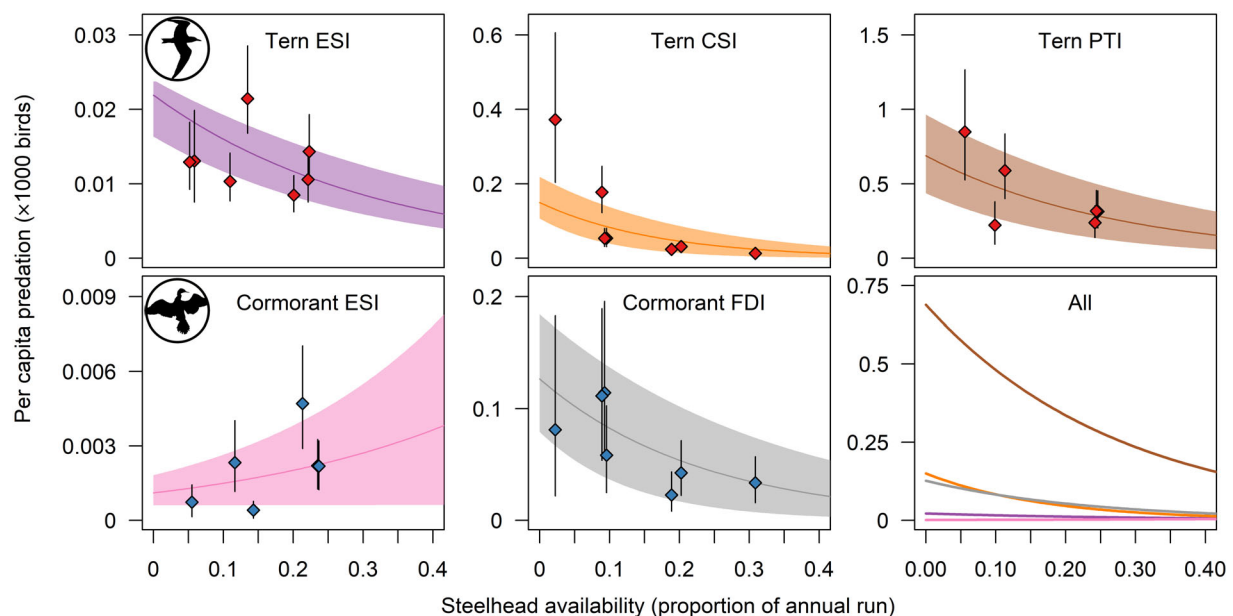
probabilities generally ranged from 0.03 to 0.13 (Figure 4), with less inter-week variation in predation probabilities relative to weekly tern and cormorant predation probabilities (Appendix S2).

Per capita predation probabilities were an order of magnitude higher at inland tern and cormorant colonies relative to estuary colonies (Figure 5). When standardized to 1000 birds (i.e., expected weekly predation probabilities for a colony of 1000 birds), predation probabilities for terns were generally between 0.01 and 0.02 in the estuary, but between 0.10 and 0.50 at inland colonies (Figure 5; Appendix S3). Similarly, per capita predation probabilities standardized to 1000 birds for cormorants were between 0.005 and 0.010 in the estuary, but between 0.10 and 0.20 at the inland colony (Figure 5; Appendix S3). Higher per capita predation probabilities at inland colonies relative to estuary colonies was consistent across all years (Appendix S3).

## Functional responses

We found overwhelming support for a Type II functional response across all three tern colonies (Figure 5, Table 2; Appendix S3). At all tern colonies, per capita predation probabilities declined as prey

availability increased, and there was no evidence for a decline in per capita predation probabilities at low prey availability (Figure 5, Table 2; Appendix S3). For terns nesting in the estuary (ESI), there was a 1.00 probability that  $\mu_1 < 0$  in the linear and quadratic models, indicating that per capita predation probabilities were highest at minimal prey availability and declined as prey availability increased (i.e. Type II response; Table 2). Median estimates of annual relationships were negative in all 12 years analyzed for ESI terns (i.e.,  $\beta_{1k}^{\lambda} < 0$  for all  $k$ ; Appendix S3: Figure S1). Conversely, there was no evidence of a decline in per capita predation probabilities at low prey availability required for a Type III functional response ( $\Pr(\mu_1 > 0) = 0.00$  in the quadratic model; Table 2). At the CSI (inland) tern colony, there was also a 1.00 probability that  $\mu_1 < 0$  in the linear and quadratic models, again indicating that per capita predation probabilities declined with increasing steelhead abundance (Table 2). We found no support for a Type III functional response at the CSI tern colony ( $\Pr(\mu_1 > 0) = 0.00$  in the quadratic model; Table 2). At the PTI tern colony, there was a 0.98 and 0.93 probability that  $\mu_1 < 0$  in the linear and quadratic model, respectively (Table 2). Support for a Type III functional response at the PTI tern colony was low, with a 0.07 probability that per capita predation probabilities declined at low prey availability (Table 2).



**FIGURE 5** Weekly per capita predation probabilities as a function of relative steelhead availability in 2012 and colony-specific functional response curves (median and 95% credible interval). Avian predators include Caspian terns (top row) and double-crested cormorants (bottom row) nesting on islands in the Columbia River basin (Crescent Island [CSI], Foundation Island [FDI], East Sand Island [ESI], Potholes Reservoir islands [PTI]). Y-axes vary by panel to emphasize the shape of functional responses, with functional responses for all bird species (medians) displayed on a single y-axis in the bottom right panel. See Appendix S3 for complete set of colony  $\times$  year results.

**TABLE 2** Support for Type II and Type III functional responses describing piscivorous waterbird predation on passive integrated transponder (PIT) tagged steelhead smolts out-migrating from the Columbia River basin.

Predator	Island	Linear		Quadratic	
		$\mu_1$	$\text{Pr}(\mu_1 < 0)$	$\mu_1$	$\text{Pr}(\mu_1 > 0)$
Tern	PTI	-3.32 (-6.52 to -0.47)	0.98	-3.02 (-6.35 to 1.05)	0.07
Tern	CSI	-5.32 (-8.40 to -2.25)	1.00	-5.11 (-8.39 to -1.92)	0.00
Tern	ESI	-2.97 (-3.50 to -2.47)	1.00	-3.16 (-3.97 to -2.15)	0.00
Cormorant	FDI	-3.03 (-6.10 to 0.53)	0.96	-2.82 (-6.22 to 0.71)	0.06
Cormorant	ESI	3.01 (0.20 to 5.83)	0.02	3.27 (0.26 to 6.26)	0.99

Note: Type II responses require a negative relationship between per capita predation probabilities and prey abundance ( $\mu_1 < 0$ ), while Type III responses necessitate a polynomial relationship where  $\mu_1 > 0$  (i.e., per capita predation probabilities increase at low prey availability). Values are posterior medians (95% credible intervals) of the hyperparameter ( $\mu_1$ ) from linear and quadratic models. Avian predators include Caspian terns (Tern) and double-crested cormorants (Cormorant) nesting on islands in the Columbia River basin (Crescent Island [CSI], Foundation Island [FDI], East Sand Island [ESI], Potholes Reservoir islands [PTI]).

Cormorant functional responses differed markedly by colony location (Table 2). For cormorants nesting in the estuary (ESI), there was strong support for a Type III functional response, where per capita predation probabilities increased with increasing prey availability at low prey abundances (Table 2, Figure 5; Appendix S3: Figure S4). The hyperparameter describing the initial increase ( $\mu_1$ ) was 3.27 (95% CrI = 0.26–6.26) with a 0.99 probability that  $\mu_1 > 0$  (Table 2). Both the linear and quadratic models indicated that per capita predation probabilities for ESI cormorants increased as prey availability increased (Table 2), but an inflection point where per capita predation probabilities begin to decline in the Type III response (e.g., due to handling or digestion time) was not observed (Figure 5; Appendix S3: Figure S4).

At the smaller inland cormorant colony (FDI), per capita predation probabilities generally declined as prey availability increased (Type II) with a 0.96 and 0.94 probability that  $\mu_1 < 0$  in the linear and quadratic models, respectively (Table 2, Figure 5; Appendix S3: Figure S5). Support for a Type III functional response was minimal, with only a 0.06 probability that per capita predation probabilities increased with increasing prey availability at low prey densities (Table 2). Type II functional responses were supported in all 5 years at the FDI cormorant colony; however, the 2008 relationship overlapped zero (Appendix S3: Figure S5).

We were unable to explicitly quantify annual functional responses for the CSI and MRI gull colonies due to a lack of weekly data on gull abundances at these two colonies (Table 1). Gull predation probabilities, however, remained largely constant across a large range of prey availabilities (Figure 4; Appendix S2). CSI and MRI gull colonies consisted of >3000 individuals when counted at the peak of the nesting season (Table 1), with gull nesting activities typically encompassing the

entire steelhead out-migration period of April–June (Thompson & Tabor, 1981). Relatively constant weekly predation probabilities across a wide range of prey availability and the presence of large numbers of gulls on-colony throughout the out-migration period for steelhead smolts (Figures 3 and 4; Appendix S2) are suggestive of Type I or III responses; however, these relationships could not be quantified due to a lack of weekly counts at gull colonies.

## DISCUSSION

Nesting terns, cormorants, and gulls consumed juvenile steelhead throughout the entire steelhead out-migration period. Per capita predation probabilities for terns reflected a Type II functional response, where predation probabilities were highest when steelhead availability was low and declined as prey availability increased. Cormorant functional responses varied by location, with strong support for a Type II response at a relatively small colony located in a freshwater ecosystem and a Type III response at a large cormorant colony located in an estuarine ecosystem. Functional responses for gulls could not be clearly identified, but weekly predation probabilities remained relatively constant across a wide range of prey availability, suggestive of a Type I functional response or a Type III response at prey abundances too low to reach an inflection point. Findings from this study provide novel insights into how predator foraging strategies affect the hypothesized drivers of avian predation probabilities on out-migrating juvenile steelhead, including the effects of run-timing on survival and predation probabilities (Evans et al., 2012, 2019; Hostetter et al., 2015; Payton et al., 2019) and predator swamping due to synchronous pulses of migratory prey (Furey et al., 2016; Hostetter et al., 2012).

The magnitude of tern predation combined with the consistent Type II functional responses of terns reveals several important considerations regarding the impacts of tern predation on steelhead populations. First, tern predation was frequently the source of substantial mortality for tagged juvenile steelhead, with weekly predation probabilities ranging from 0.01 to 0.30 across three tern colonies; which supports previous studies that identify tern predation as a substantial source of mortality for out-migrating juvenile steelhead (Evans et al., 2016, 2019; Payton et al., 2019). Second, per capita predation probabilities were an order of magnitude higher for terns nesting at inland colonies relative to terns nesting in the estuary, demonstrating how colony location plays a crucial role in per capita predation impacts (Roby et al., 2002). Tern abundance was much greater at the estuary colony (thousands of pairs) compared to inland colonies (hundreds of pairs); thus, weekly predation probabilities sometimes were similar in the two locations despite per capita predation rates that differed by an order of magnitude. Finally, the finding that tern predation probabilities increased as steelhead abundance declined without a reprieve at low steelhead abundance (Type II response), suggests that tern predation could be a destabilizing source of mortality for small or declining steelhead populations.

Predation probabilities for double-crested cormorants also varied by prey abundance; however, functional response types differed between by colony locations. Diets of cormorants in the estuary are more diverse than the diets of cormorants nesting at inland locations, reflecting a shifting mosaic of foraging opportunities in the Columbia River estuary (Anderson et al., 2004; Collis et al., 2002; Lyons et al., 2007; Peck-Richardson et al., 2018). Relative to the more specialized diets of terns, the diverse diet of cormorants in the estuary reflect prey switching in response to dynamic pulses in resources across a range of habitats (Collis et al., 2002; DeBruyne et al., 2013; Lawes et al., 2021) and prey species and sizes (Hostetter et al., 2012; Osterback et al., 2014). Alternatively, cormorants nesting at the inland colony access a less variable prey base punctuated by large pulses of out-migrating juvenile salmonids. Weekly predation probabilities demonstrate that inland-nesting cormorants utilize pulses in steelhead availability but are likely swamped by this brief yet superabundant resource (Type II response).

Predation probabilities on juvenile steelhead by gulls remained relatively consistent across a wide range of steelhead availabilities. This ability of gulls to respond to pulses in out-migrating juvenile steelhead may be a function of prey switching or behavioral aggregation, where gulls increase their consumption of steelhead during pulses in abundance, then forage elsewhere when steelhead abundance is low. Diets of inland-nesting gulls are

known to include a wide variety of terrestrial and aquatic food sources (Collis et al., 2002; Winkler, 2020). In the Columbia River basin, Collis et al. (2002) observed that juvenile salmonids accounted for just 3% of the diet of gulls nesting on Miller Rocks. By comparison, salmonids accounted for >30% and >70% of the diet of terns nesting on ESI and CSI, respectively (Antolos et al., 2005; Roby et al., 2002). Due to this lower reliance on salmonids as a primary prey source, per capita consumption of steelhead by gulls has the potential to increase substantially during pulses of high steelhead availability, resulting in relatively stable or even increasing predation probabilities across a large range of steelhead availabilities (i.e., Type I or lower end of a Type III response). Consumption rates that indefinitely increase with increasing prey abundance (Type I) are unlikely for most predators. Type I responses have been observed in field studies where a prey species comprises a small proportion of a predator's diet allowing the inflection point at which increasing per capita consumption decelerates to remain undetected (Chan et al., 2017; Ellis et al., 2020; Jeschke et al., 2004). Data on gull abundance across the steelhead out-migration period are required to quantify functional responses of gulls and evaluate the support for competing hypotheses describing how gulls respond to changes in fish abundance.

Changes in weekly steelhead availability are predominantly driven by factors other than predation, such as hatchery releases, river discharge, barging or transportation of juvenile salmonids, and water temperatures (Smith et al., 2002; Zabel, 2002). As such, our study addresses how multiple predator species respond to changes in seasonal prey availability and the consistency of these relationships across locations and years. Many fish species aggregate in high densities during critical life-history events (e.g., juvenile migration, adult spawning). Understanding whether prey aggregations attract or swamp predators (e.g., Gende et al., 2002; Middleton et al., 2013; Osterback et al., 2013; Quinn et al., 2003) and how this influences individual prey susceptibility to predation (Furey et al., 2016; Hostetter et al., 2012; Ims, 1990; Tucker et al., 2008) can be crucial for understanding the efficacy of predator management strategies to enhance prey population persistence. For example, predator attraction to prey aggregations may result in high levels of predation that reduce prey abundance, drive density-dependent Allee effects (Allee, 1931), and destabilize prey populations at low abundances (Type II functional response). In these situations, predation may affect the recovery of depleted prey populations even if it was not a cause of the original decline (Neuenhoff et al., 2018). Conversely, declines in predation at low prey abundances (Type III functional response) are stabilizing and, while they can regulate

prey populations, are less likely to drive prey populations toward extinction (Solomon, 1949).

Analysis of functional responses by predators often involves three interrelated objectives: (1) identify the shape of a functional response, (2) compare the support for a Type I, II, or III functional response, and (3) explore the mechanistic relationships affecting the functional response (e.g., Holling's disc equation; Holling, 1959b; Juliano, 2001). Our study addressed objectives 1 and 2, with empirical information comparing functional responses across multiple predators, locations, and years. Our use of proportional changes in prey availability allowed detailed insights into predator responses to changes in relative prey density (objectives 1 and 2); however, more detailed information on prey abundance is required to identify the prey density at which predation is limited by handling time or satiation and the mechanisms causing these relationships (Holling, 1959a, 1959b; Jeschke et al., 2002; Juliano, 2001; Tully et al., 2005). Technological and sampling advances may provide new opportunities to directly estimate spatio-temporal abundance of juvenile salmonids in the Columbia River basin that will greatly enhance future studies of functional responses and predator-prey dynamics. Similarly, integrating data on predator diets, abundance, seasonal variation in caloric demands, and changes in the prey base within and across seasons will be crucial for identifying the mechanistic processes leading to prey saturation for terns and the apparent lack thereof for cormorants nesting in the Columbia River estuary.

For ESA-listed salmonid populations, predator functional responses can play a critical role in evaluating the impact of predation and the efficacy of predator management strategies. Our study indicates that tern predation rates are highest for early- or late-season migrants due to predator swamping during periods of peak out-migration. Conversely, high concentrations of prey may attract cormorants and gulls that target periods of peak prey availability, thus leading to increased salmonid susceptibility at specific locations or times (e.g., en masse releases of hatchery reared steelhead smolts, at dams where smolts congregate, or during periods of highly synchronized out-migration). Understanding predator-specific responses can guide system-specific management actions focused on local (e.g., areas of prey concentrations) and landscape-level (e.g., inland vs. estuary) factors. Quantifying how predators respond to pulses in prey availability has direct implications for predator-prey dynamics and foraging ecology, while also providing critical information to identify predator- and location-specific predation impacts (Osterback et al., 2013; Payton et al., 2020; Roby et al., 2002), which can in turn guide targeted- and system-specific actions aimed at prey populations of conservation concern. Together, these results illustrate the complexity of predator-prey interactions in

natural systems and highlight the need to jointly investigate predator and prey abundance, predation probabilities, per capita predation probabilities, and predator foraging strategies to understand processes affecting complex communities of predators and their prey.

## AUTHOR CONTRIBUTIONS

Allen F. Evans, Nathan J. Hostetter, Quinn Payton conceived the study; Daniel D. Roby, Ken Collis, Allen F. Evans oversaw data collection; Quinn Payton, Nathan J. Hostetter, Allen F. Evans analyzed the data; Nathan J. Hostetter, Allen F. Evans, and Quinn Payton wrote the initial manuscript with substantial contributions from all authors.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data and R scripts (Hostetter et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.37pvmcvnm>.

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## SUPPORTING INFORMATION

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

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