

REVIEW

A Review of Factors Affecting the Susceptibility of Juvenile Salmonids to Avian Predation

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Abstract

We reviewed studies of piscivorous colonial waterbird predation on juvenile salmonids to synthesize current knowledge of factors affecting fish susceptibility to avian predators. Specifically, we examined peer-reviewed publications and reports from academic, governmental, and nongovernmental agencies to identify commonalities and differences in susceptibility of salmonids to avian predation, with a focus on mark–recovery studies in the Columbia River basin. Factors hypothesized to influence salmonid susceptibility to avian predation were grouped into four general categories: (1) salmonid species and populations, (2) environmental factors, (3) prey density, predator density, and migration timing, and (4) prey characteristics. Our review focused on predation by Caspian terns *Hydroprogne caspia*, double-crested cormorants *Nannopterum auritum*, and gull species *Larus* spp. as these are the most well-studied avian predators of salmonids. Results indicated that predator–prey interactions varied across salmonid species and populations and species of avian predator. Inferences across studies supported multiple hypotheses regarding predator–prey dynamics, including environmental factors that influence prey exposure to predators (e.g., river flows, turbidity, alternative prey), variation in predator and prey abundances, predator characteristics (e.g., foraging behavior, colony location), and prey characteristics (e.g., fish length, condition). Mark–recovery studies of avian predation on fish populations have greatly improved our understanding of the factors affecting fish susceptibility to avian predation, the relative contributions of abiotic and biotic factors to predation susceptibility, and the extent to which avian predation affects fish survival and the viability of prey populations. Future studies that jointly model predation and survival and the factors affecting those processes will further broaden our understanding of predator–prey dynamics and directly evaluate the effects of predation on prey population dynamics.

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Questions of whether fish survival and population viability are affected by avian predation has been the subject of research for decades (e.g., Steinmetz et al. 2003; Cowx 2008). Mark–recovery studies are increasingly used to investigate avian predation on a variety of fish species (e.g., Pacific salmon *Oncorhynchus* spp., Atlantic Salmon *Salmo salar* and Brown Trout *Salmo trutta*, suckers [family Catostomidae], Roach *Rutilus rutilus*, Common Bream *Abramis brama*, Yellow Perch *Perca flavescens*, and others) in coastal and inland ecosystems across North America and Europe (Dieperink et al. 2001; Jepsen et al. 2010; Evans et al. 2012, 2016b; Osterback et al. 2013; Scopettone et al. 2014; Skov et al. 2014; Weitkamp et al. 2014). Application of fish mark–recovery studies to investigate avian predation is expanding rapidly due to recognition of avian predation as a substantial source of fish mortality in some systems (Dieperink et al. 2001; Steinmetz et al. 2003; Teuscher et al. 2015; Evans et al. 2019b; Payton et al. 2019) and the generality of these approaches across common fish tag types and survey methods (e.g., passive integrated transponder tags [Ryan et al. 2001], coded wire tags [Evans et al. 2011], radio telemetry tags [Schreck et al. 2006], acoustic tags [Evans et al. 2016c], and Carlin tags [Feltham and MacLean 1996]). Although diverse in application, mark–recovery studies share multiple commonalities in their ability to identify individual- and cohort-level factors affecting predator–prey interactions, predation mortality, and the relative susceptibility of prey species, populations, and individuals. Although mark–recovery studies have been widely used for more than 20 years to investigate the relative susceptibility of fish populations to avian predation across North America and Europe, no comprehensive synthesis summarizing the knowledge gained from these studies is currently available.

Herein, we synthesize mark–recovery studies of avian predation on fish species and populations to inform our current knowledge on the factors affecting fish susceptibility to avian predation. Our review provides crucial information on how predation risk varies among individuals within a prey population and elucidates possible mechanisms responsible for variation in risk among populations. Our synthesis includes results from mark–recovery studies investigating avian predation on anadromous Pacific salmon and Atlantic Salmon and Brown Trout populations across North America and Europe. However, the >20-year history of research on avian predation of salmonids in the Columbia River basin provides a substantial component of this synthesis. Our review concentrates on publications and publicly available reports of original studies investigating avian predation on salmonid populations. We identify common trends across studies, highlight important differences, and note inconsistencies when observed. Our review focused on predation by Caspian terns *Hydroprogne caspia* (hereafter “terns”), double-crested cormorants *Nannopterum auritum*

(hereafter “cormorants”), and a variety of gull species *Larus* spp. (hereafter “gulls”) as these are the most well-studied avian predators of salmonid populations. Where data were available, relationships with American white pelicans *Pelecanus erythrorhynchos*, herons (family Ardeidae), or other avian predators were also described. Our conclusions are generalizations based on our interpretation and understanding of these studies.

METHODS

Our review focused on studies of avian predation on anadromous salmonids (e.g., Sockeye Salmon *O. nerka*, Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, steelhead *O. mykiss*, Atlantic Salmon, and sea-run Brown Trout when available) that applied some form of mark–recovery methods to estimate predation rates or to investigate fish susceptibility to avian predation. We emphasized mark–recovery studies due to their ability to investigate population-specific (e.g., evolutionarily significant unit [ESU] or distinct population segment, hereafter simply “ESU”), cohort-specific (e.g., migration timing, age-class), and individual-specific (e.g., fish length and rear type) factors affecting susceptibility to predation. We conducted a search on Google Scholar using the keywords “avian predation,” “salmon,” and “tag,” which identified ~700 entries. We then refined the search by only including studies that analyzed a mark–recovery data set quantifying some aspect of avian predation on the above-mentioned fish species. We also expanded our search when new citations were identified in those selected papers. Although our primary review was limited to the above metrics, we also included information from relevant observational or diet analysis studies investigating biomass or number of salmonids consumed when findings are especially supportive or contradictory of those from mark–recovery studies. We do not quantify specific relationships in this review (i.e., meta-analysis) but instead compare, contrast, and summarize patterns observed across studies. Inclusion of findings from unpublished reports may reduce publication bias; however, publication bias, along with the possibility for spurious results from any single study, remain possible. Studies describing opportunistic tag recoveries associated with avian predation or studies that did not directly analyze tag recovery data were generally excluded from our review (e.g., Montevecchi et al. 1988; Aarestrup et al. 2000; Karppinen et al. 2014; Schwinn et al. 2017). Full citations are provided in References.

Our review is separated into four general sections or categories of factors that influence fish susceptibility to avian predation: (1) salmonid species and populations, (2) environmental factors, (3) prey density, predator density, and migration timing, and (4) prey characteristics. We selected these categories based on common hypotheses and to remain relatively consistent with the foundational

TABLE 1. Examples of common hypotheses used to explain variation in susceptibility of juvenile salmonids to avian predation.

Hypotheses	Explanation
Environmental factors	
Exposure	Environmental factors that increase prey exposure to predation (e.g., travel time, river discharge rate, turbidity) increase predation susceptibility.
Alternate prey	Environmental factors that enhance availability of alternative prey (e.g., marine forage fish) decrease predation susceptibility.
Spatial heterogeneity	Spatial factors that influence predation susceptibility (e.g., increased predation risk near dams and at other bottlenecks to out-migration).
Prey density, predator density, and migration timing	
Predator swamping	Increased numbers of prey decrease an individual's susceptibility to predation.
Prey switching	Increased numbers of prey increase susceptibility to predation due to predator functional response (increased per capita consumption of salmonids) and/or numerical response (increased number of individual predators).
Proportional predation	Avian predation on prey populations is proportional to relative prey availability.
Predator density	Predation susceptibility increases as the number of predators increases (e.g., number of individuals attending a colony).
Prey characteristics	
Bigger is better	Larger prey are less susceptible to predation.
Size selectivity	Smaller and larger prey are relatively less susceptible to predation (e.g., difficult to capture [small], exceed predator gape width [large]).
Individual quality	Prey in degraded condition (e.g., injured, diseased, stressed, poor osmoregulation) are more susceptible to predation.
Rearing	Rearing in hatchery environments promotes behavioral characteristics that increase predation susceptibility.

work of Leopold (1933), which broadly classified these and other factors affecting predation (Table 1). Given the differences observed among avian predator species, each subsection discusses predator-specific relationships for terns, cormorants, gulls, and other predator species when data were available.

RESULTS

Salmonid Species and Populations

Most mark–recovery studies evaluating salmonid population-specific susceptibility to avian predation found that predation susceptibility varied considerably among salmonid species and avian predator species (Table 2). In many Northern Hemisphere systems, the breeding season for colonial waterbirds (March–August) coincides with the peak out-migration period of anadromous juvenile salmonids (April–August) resulting in considerable, yet dynamic, spatial and temporal overlap among avian predator species and prey populations (Evans et al. 2012, 2016a; Adkins et al. 2014). Given the lack of generality across bird species (terns, cormorants, gulls), relative susceptibility to predation is summarized by bird species.

For terns, studies consistently found higher predation susceptibility for steelhead relative to salmon species (e.g., Chinook Salmon, Coho Salmon, Sockeye Salmon) in

TABLE 2. Relative susceptibility of salmonid species or populations to predation by Caspian terns (Tern), double-crested cormorants (Cormorant), and mixed gull species (Gull). See Supplement A available in the online version of this article for further details.

Predator	Relative susceptibility
Tern ^a	Steelhead > Sockeye Salmon ≈ Coho Salmon ≈ yearling Chinook Salmon > subyearling Chinook Salmon
Cormorant ^b	Steelhead ≈ Sockeye Salmon ≈ Coho Salmon ≈ yearling Chinook Salmon ≈ subyearling Chinook Salmon
Gull ^c	Steelhead > Sockeye Salmon ≈ yearling Chinook Salmon ≈ subyearling Chinook Salmon

^aCollis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012, 2016a, 2016c, 2019c; Zamon et al. 2013; Roby et al. 2015, 2017a, 2017b.

^bCollis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2016b, 2016c, 2019c; Frechette et al. 2012; Zamon et al. 2013; Roby et al. 2015.

^cEvans et al. 2012, 2016c; Roby et al. 2015.

freshwater and estuary systems (Table 2; Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Good et al. 2007; Evans et al. 2012, 2016a, 2016c; Zamon et al. 2013; Roby et al. 2015, 2017a, 2017b). For instance, predation rates were often two to three times higher on steelhead than on salmon species when comparing estimates from the same colony, in the same year (Collis et al. 2001; Antolos et al. 2005; Evans et al. 2012, 2016c). Within salmonid populations, susceptibility to tern predation was generally lowest for subyearling Chinook Salmon, followed by similar levels of risk for Sockeye Salmon, Coho Salmon, and yearling Chinook Salmon (Table 2 and citations therein). Lower Columbia River Chinook and Coho Salmon populations may experience higher susceptibility to predation from terns nesting in the Columbia River estuary relative to Chinook and Coho Salmon populations originating farther upriver, providing exceptions to these generalities (Sebring et al. 2013; Zamon et al. 2013). In San Francisco Bay, California, fall-run subyearling Chinook Salmon were more susceptible to tern predation than spring-run yearling Chinook Salmon, which may have been driven by differences in migration or run timing, releases of hatchery fish in close proximity to colony sites, and subsequent exposure to tern predation between these ESUs (Evans et al. 2011).

For cormorants, most studies found little to no support for differences in predation susceptibility between steelhead and salmon species or between salmon ESUs in freshwater and estuary systems (Table 2; Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2016a, 2016c, 2019c; Zamon et al. 2013; Roby et al. 2015). Lower Columbia River Chinook and Coho Salmon populations experienced higher predation susceptibility to cormorants nesting in the Columbia River estuary, differences that may be due to the greater abundance and late run timing of these populations relative to other populations of juvenile salmonids in the Columbia River basin (Sebring et al. 2013; Zamon et al. 2013). In two other estuaries in Oregon, cormorants disproportionately depredated Coho Salmon relative to steelhead, which may be attributable to increased estuary residency time for Coho Salmon smolts in those systems (Clements et al. 2012).

For gulls, information was generally less available. Studies found some evidence of higher predation susceptibility for steelhead relative to salmon species and minor variation among salmon ESUs in susceptibility (Table 2; Frechette et al. 2012; Evans et al. 2012, 2016c; Roby et al. 2015). Studies evaluating population-specific susceptibility to gull predation were generally restricted to freshwater systems in the Columbia River basin (Evans et al. 2012, 2016c; Roby et al. 2015); however, studies in nearshore and estuary systems have occurred in coastal California (Frechette et al. 2012; Osterback et al. 2014).

Salmonid species-specific susceptibility to avian predation was also observed across Atlantic Salmon and sea-run

Brown Trout. For example, in the River Skjern estuary (Denmark), Atlantic Salmon were more susceptible to great cormorant *Phalacrocorax carbo sinensis* predation than sea-run Brown Trout (Supplement A; Dieperink et al. 2002; Koed et al. 2006). However, Atlantic Salmon and sea-run Brown Trout displayed similar susceptibility when recoveries were combined across grebes (family Podicipedidae) and herons in the River Gudenå, Denmark (Supplement A; Jepsen et al. 1998).

Environmental Factors

Multiple studies identified associations between environmental factors and smolt susceptibility to avian predation (Table 3). Per capita (i.e., per bird) predation rates on salmonids were higher at breeding colonies located in freshwater systems relative to colonies in estuaries, a result supported by mark–recovery (Evans et al. 2012; Hostetter et al. 2022) and diet composition studies (Collis et al. 2002; Roby et al. 2002; Lyons 2010). Similarly, susceptibility of salmonid smolts to both tern and cormorant predation in the Columbia River estuary were related to large-scale climatic indices (North Pacific Gyre Oscillation and spring upwelling), likely due to associations with availability of marine forage fish (alternative prey) in the estuary (Table 3; Lyons et al. 2014; Evans et al. 2016a).

Terns, cormorants, and gulls are central-place foragers (i.e., animals where foraging bouts leave from and return to a central location [e.g., a nest or colony]; Orians and Pearson 1979), and the susceptibility of an individual fish to predation generally decreased with increasing distance from breeding colonies (Table 3; Schreck et al. 2006; Frechette et al. 2012, 2015; Meyer et al. 2016; Evans et al. 2016c, 2019c; Roby et al. 2017b; Hostetter et al. 2018; Chiamonte et al. 2019). It is important to note, however, that multiple studies have documented long-distance foraging trips of piscivorous colonial waterbirds from breeding colonies (e.g., >20 km; Frechette et al. 2012; Evans et al. 2016c; Meyer et al. 2016; Roby et al. 2017a, 2017b; Chiamonte et al. 2019), with Caspian terns regularly commuting >30 km and occasionally >90 km from inland nesting colonies to forage in the Columbia River basin (Table 3; Evans et al. 2016c; Roby et al. 2017a, 2017b). American white pelicans have also been documented to forage >100 km from their nesting colony (Scoppettone et al. 2014).

Additional factors associated with increased fish susceptibility to tern predation included longer out-migration travel times (Hostetter et al. 2012; Evans et al. 2013) and increased turbidity (Hostetter et al. 2012). Predation rates by terns were often higher in the open waters of a reservoir relative to near dams (Table 3; Evans et al. 2016c). Hypotheses for these increases in susceptibility included increased exposure to predation due to longer out-migration travel times (Hostetter et al. 2012; Evans et al. 2013), decreased prey reaction times in more turbid waters (Hostetter et al. 2012 and

TABLE 3. Environmental factors associated with the relative susceptibility of juvenile (smolt) salmonids to predation by Caspian terns (Tern), double-crested cormorants (Cormorant), mixed gull species (Gull), and other predator species (Other). See Supplement B.

Factor	Tern	Cormorant	Gull	Other
Transit time/river discharge	Faster transit times reduced susceptibility ^a			
Freshwater versus marine or brackish areas	Higher per capita predation in freshwater areas ^b	Higher per capita predation in freshwater areas ^c	Highly variable within and across river reaches ^d	Susceptibility sometimes highest near ocean entry ^e
Near dam versus open waters or reservoirs	Predation increased in open waters of reservoirs ^f	No differences observed ^g	Predation concentrated near dams ^h	Variable but can be concentrated at dams or shallow areas ⁱ
Distance to colony	Decreased susceptibility with distance from colony but documented >90 km ^j	Decreased susceptibility with distance from colony ^k	Decreased susceptibility with distance from colony ^l	Generally decreased susceptibility with distance from colony but long distances documented ^m
Ocean conditions	Related to susceptibility in estuary ⁿ	Related to susceptibility in estuary ^o		

^aHostetter et al. 2012; Evans et al. 2013.

^bEvans et al. 2012; Hostetter et al. 2022.

^cEvans et al. 2012; Hostetter et al. 2022.

^dEvans et al. 2016c; Roby et al. 2017b.

^eDieperink et al. 2001, 2002; Koed et al. 2006.

^fEvans et al. 2016c.

^gEvans et al. 2016c.

^hEvans et al. 2016c; Roby et al. 2017b.

ⁱKoed et al. 2002; Miyamoto et al. 2018.

^jSchreck et al. 2006; Evans et al. 2012, 2016c, 2019b, 2019c; Roby et al. 2017a, 2017b; Hostetter et al. 2018; Payton et al. 2019.

^kSchreck et al. 2006; Evans et al. 2016c, 2019c; Meyer et al. 2016; Chiaramonte et al. 2019.

^lFrechette et al. 2012; Frechette et al. 2015.

^mEvans et al. 2016b, 2016c; Meyer et al. 2016; Chiaramonte et al. 2019.

ⁿEvans et al. 2016a.

^oLyons et al. 2014; Evans et al. 2016a.

citation therein), and broadly searching for prey across a variety of habitats within foraging range of the breeding colony (Cuthbert and Wires 1999).

Additional factors associated with increased fish susceptibility to cormorant predation included decreased turbidity, possibly due to increased prey encounter rates (Hostetter et al. 2012 and citations therein), and relatively consistent predation susceptibility across habitats, including the open waters of reservoirs and near dams (Table 3; Evans et al. 2016c). The volume of water spilled at dams was positively associated with smolt susceptibility to cormorant predation in the Columbia River estuary (Evans et al. 2016a).

For gulls, predation was often concentrated near dams relative to the open waters of reservoirs (Evans et al. 2016c; Roby et al. 2017b). Increased susceptibility of salmonid smolts to gull predation near dams was potentially linked to the close proximity (<20 km) of many gull colonies to dams in the Columbia River basin (Ruggerone 1986; Evans et al.

2016c). Information directly linking environmental factors to susceptibility of salmonid smolts to gull predation, however, were generally lacking (Table 3).

For American white pelicans, there was no evidence of concentrated foraging in open reservoirs versus dams on the Columbia River (Evans et al. 2016c). Similar to terns, pelicans were capable of commuting long distances (>100 km) to forage on salmonids (Evans et al. 2016c) and other fish (Scopettone et al. 2014; Evans et al. 2016b).

Atlantic Salmon and sea-run Brown Trout susceptibility to predation by great cormorants and gray herons *Ardea cinerea* was highest in estuaries and near regions of ocean entry (Table 3; Dieperink et al. 2001, 2002; Koed et al. 2006). Overall, results across Pacific and Atlantic salmonids indicate predation risk is highly variable across estuaries and driven by multiple factors (Table 3). For example, susceptibility to avian predation in estuaries may increase due to salinity gradients (Dieperink et al. 2001, 2002; Koed et al. 2006;

Kennedy et al. 2007) or decrease due to increased availability of alternative prey (Lyons et al. 2014; Evans et al. 2016a).

Prey Density, Predator Density, and Migration Timing

Multiple studies identified relationships between juvenile salmonid predation susceptibility and prey density, predator density, or migration timing (Table 4). Susceptibility to tern and cormorant predation increased as colony size increased (Table 4; Evans et al. 2016a; Hostetter et al. 2022). For example, colony-specific tern predation rates increased as the number of terns counted increased within (weekly) and across (annual) breeding seasons. Tern and cormorant colony size, however, was not the sole factor influencing predation rates. Predation can remain fairly constant across varying colony sizes, or conversely, predation may vary substantially even though colony size remained similar, with both situations often attributed to variation in other environmental factors (Table 4; Good et al. 2007; Hostetter et al. 2012; Evans et al. 2013, 2019c; Lyons et al. 2014; see also “Environmental Factors” above). Information on the relationship between juvenile salmonid susceptibility and gull colony size, however, was lacking in the literature (Table 4).

Predator-specific functional responses may best explain the relationships between prey abundance and smolt susceptibility to avian predation (Table 4; Evans et al. 2016a; Roby et al. 2017b; Hostetter et al. 2022). Tern predation on steelhead smolts followed a type II functional response, whereby individual smolt susceptibility to tern predation declined as smolt abundance increased (Hostetter et al. 2012, 2022; Roby et al.

2015, 2017a, 2017b; Evans et al. 2016c). Conversely, cormorants displayed type II and type III functional responses depending on colony location (Hostetter et al. 2022), implying that the response of cormorants to changes in salmonid abundance may vary in freshwater versus estuarine environments. Whether this is driven by predator attraction, prey switching, predator swamping, or other seasonal factors remains unknown (Table 4; Hostetter et al. 2012, 2022; Roby et al. 2015, 2017a, 2017b; Evans et al. 2016c). In our review, only two studies presented relationships between prey abundance and juvenile salmonid susceptibility to gull predation (Roby et al. 2017b; Hostetter et al. 2022). Here, steelhead susceptibility to gull predation remained similar across a wide range of smolt abundances, most reflective of a type I functional response or the increasing period of a type III functional response (Table 4).

Prey Characteristics

Fish length was the most common individual fish characteristic recorded and regularly associated with variation in susceptibility to tern and gull predation (Table 5 and citations therein). A quadratic function of length best described susceptibility to tern and gull predation, where susceptibility was lower for shorter (<175 mm) and longer (>225 mm) individuals (Hostetter et al. 2012; Osterback et al. 2014; Evans et al. 2019a). Conversely, most studies found no support for an effect of smolt length on susceptibility to cormorant predation across a variety of fish lengths (125–375 mm; Table 5; Hostetter et al. 2012; Chiaramonte et al. 2019). Kennedy et al. (2007) found no

TABLE 4. Influence of prey density, predator density, and run-timing factors on relative susceptibility of juvenile (smolt) salmonids to predation by Caspian terns (Tern), double-crested cormorants (Cormorant), mixed gull species (Gull), and other predator species (Other). See Supplement C for further details.

Factor	Tern	Cormorant	Gull	Other
Prey density	Susceptibility decreased as prey density increased (i.e., predator swamping) ^a	Relationships varied by colony location ^b	Similar susceptibility across variable prey densities ^c	Susceptibility increased as prey density increased ^d
Predator density	Increased susceptibility as predator density increased ^e	Variable within and across seasons ^f		
Run timing	Increased susceptibility for late season out-migrants ^g	Increased susceptibility in May–June ^h		Increased susceptibility for early season migrants or following hatchery releases ⁱ

^aHostetter et al. 2012; Roby et al. 2015, 2017a, 2017b.

^bHostetter et al. 2012; Roby et al. 2015, 2017b; Evans et al. 2016a.

^cRoby et al. 2017b.

^dMiyamoto et al. 2018.

^eGood et al. 2007; Hostetter et al. 2012; Evans et al. 2013, 2019c.

^fZamon et al. 2013; Sebring et al. 2013; Roby et al. 2015; Evans et al. 2016a.

^gRoby et al. 2015; Evans et al. 2016c.

^hEvans et al. 2016a.

ⁱFeltham and MacLean 1996; Källo et al. 2020.

TABLE 5. Individual prey characteristics (e.g., fish length, rearing type, condition) associated with the relative susceptibility of juvenile (smolt) salmonids to predation by Caspian terns (Tern), double-crested cormorants (Cormorant), mixed gull species (Gull), and other predator species (Other). See Supplement D for further details.

Factor	Tern	Cormorant	Gull	Other
Fish length	Susceptibility was highest for fish 175–225 mm and lower for shorter and longer individuals ^a	No relationship (~125–300 mm) ^b	Susceptibility was highest for fish 175–225 mm and lower for shorter and longer individuals ^c	Variation by predator species ^d
Rearing type	No consistent differences ^e	No consistent differences ^f	Hatchery-reared susceptibility > naturally reared susceptibility ^g	Differences, when observed, partially attributed to length, condition, or run timing ^h
Fish condition	Degraded condition increased susceptibility ⁱ	Degraded condition increased susceptibility ^j	No relationship detected but known to scavenge ^k	Maybe related to osmoregulation ^l

^aHostetter et al. 2012; Evans et al. 2019a.

^bHostetter et al. 2012; Evans et al. 2019a.

^cOsterback et al. 2014; Roby et al. 2017b.

^dFeltham and MacLean 1996; Dieperink et al. 2001, 2002; Kennedy et al. 2007; Sebring et al. 2013; Teuscher et al. 2015; Miyamoto et al. 2018; Chiamonte et al. 2019; Källo et al. 2020.

^eCollis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2016a, 2019c; Hostetter et al. 2012; Roby et al. 2015.

^fCollis et al. 2001; Ryan et al. 2003; Hostetter et al. 2012; Evans et al. 2012, 2016a, 2019c; Roby et al. 2015.

^gEvans et al. 2019a.

^hKennedy et al. 2007; Sebring et al. 2013; Osterback et al. 2014; Payton et al. 2020.

ⁱSchreck et al. 2006; Hostetter et al. 2012; Roby et al. 2015; Evans et al. 2019a.

^jHostetter et al. 2012; Roby et al. 2015.

^kEvans et al. 2016c, 2019a; Pollet et al. 2020.

^lKennedy et al. 2007.

consistent relationship between steelhead length (mean = 154 mm) and avian predation susceptibility in the Columbia River estuary; however, Kennedy et al. (2007) combined recoveries across predator species (terns and cormorants), which may have masked predator-specific relationships observed in other studies.

Smolts in degraded condition (e.g., descaling, body injuries, disease presence) were more susceptible to tern and cormorant predation. Differences in relatively susceptibility, however, were often small and inconsistent, with degraded fish only slightly more susceptible than nondegraded fish to tern and cormorant predation (Table 5; Schreck et al. 2006; Hostetter et al. 2012; Roby et al. 2015; Evans et al. 2019a). There was no support for condition-dependent susceptibility to gull predation where results were reported (Evans et al. 2019a). Gulls are, however, known to scavenge dead fish or kleptoparasitize (steal) fish from other predators, like terns (Evans et al. 2016c; Pollet et al. 2020). Lower gill Na⁺/K⁺-ATPase activity (osmoregulatory ability) in fish was consistently linked to increased predation susceptibility in estuaries (Table 5; Schreck et al. 2006; Kennedy et al. 2007).

Smolt rearing type (hatchery, wild) often showed no appreciable or consistent differences in predation

susceptibility for terns, cormorants, or gulls (Table 5; Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2016a; Hostetter et al. 2012). For instance, Evans et al. (2016a) found no consistent trend in the relative susceptibility of Chinook Salmon or steelhead by rear type to cormorant predation by salmonid ESU, by week, and across all weeks during a 10-year period. Increased predation of hatchery-reared individuals was occasionally observed in terns and gulls, but concurrent differences in smolt length or run timing may also explain these results (Ryan et al. 2003; Kennedy et al. 2007; Hostetter et al. 2012; Roby et al. 2015; Evans et al. 2016a, 2019c). Increased susceptibility of naturally reared or wild smolts were observed in two studies, with wild steelhead more susceptible than hatchery steelhead to gull predation in coastal California (Osterback et al. 2014) and wild subyearling Chinook Salmon more susceptible than hatchery subyearling Chinook Salmon to American white pelican predation in the Columbia River (Payton et al. 2020).

DISCUSSION

Our review supported the hypothesis that variation in juvenile salmonid susceptibility to avian predation is

associated with a dynamic suite of environmental variables, predator characteristics, and prey characteristics. Our review included multiple predator species, prey species, and river systems, systems with unique attributes that influenced predator–prey interactions in complex ways. We demonstrated how synthesizing results across numerous studies revealed commonalities across prey and predator species, while also identifying important differences across space (e.g., marine versus freshwater systems) and time (e.g., within versus across years). Across salmonids, the juvenile life stage is important to population viability and is often subject to high mortality (Kareiva et al. 2000; McClure et al. 2003; Good et al. 2007; Quinn 2018), with bird predation increasingly recognized as a substantial source of total juvenile mortality in multiple systems (Dieperink et al. 2001; Schreck et al. 2006; Clements et al. 2012; Evans et al. 2019a; Payton et al. 2019). A detailed understanding of the mechanisms influencing fish susceptibility to avian predation, however, is only recently coming to light.

Synthesizing and consolidating >20 years of studies investigating salmonid susceptibility to avian predation provides important information for managers and researchers interested in (1) assessing if avian predation may be an important aspect of a managed fisheries system (e.g., distance to bird colonies, size of colonies, diversity of predator and prey communities), (2) what populations and life stages (e.g., fish sizes) may be most affected, (3) expected relationships given the predator and prey communities, and (4) approaches used to investigate these topics. An increasing wealth of information is now available as a baseline to evaluate bird–fish predator–prey dynamics; however, numerous important aspects of these relationships remain unresolved.

Salmonid Species and Populations

Identifying the relative susceptibility of prey populations is often a first step in understanding the possible mechanisms underlying predator–prey interactions. For example, higher susceptibility of juvenile steelhead to tern predation is often attributed to differences in species-specific length (e.g., steelhead > salmon species), migration timing, and behavioral characteristics (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012). Studies expanding on these hypotheses provided strong support for length-selective tern predation (Hostetter et al. 2012; Evans et al. 2019c) and variability due to migration timing (Hostetter et al. 2012; Roby et al. 2015, 2017a). Conversely, susceptibility to cormorant predation was relatively consistent across salmonid populations. Cormorant predation also showed little to no length selectivity (Hostetter et al. 2012; Chiramonte et al. 2019). Species- and ESU-level variation in susceptibility to tern and cormorant predation may therefore be largely driven by

variation in individual fish characteristics (e.g., length), migration or run timing, and the subsequent biotic (e.g., predator and prey densities) and abiotic (e.g., river flow, temperature) factors associated with migration timing.

Environmental Factors

Avian predation of juvenile salmonids occurs in spatially and temporally complex systems. Local- and large-scale environmental factors influence juvenile salmonid survival and susceptibility to avian predation. Relationships with large-scale climate indices in the Columbia River estuary and lower per capita predation rates in estuarine relative to freshwater systems were common across predator species and likely arise from complex factors influencing the availability and abundance of forage fishes in estuary systems (Collis et al. 2002; Roby et al. 2002; Lyons et al. 2014; Evans et al. 2019c).

Estuaries may act as survival bottlenecks for migrating juvenile salmonids. Local conditions, however, greatly influence the suite of predators (e.g., birds, mammals, fish), environmental factors (e.g., salinity, flow), and individual fish characteristics (e.g., osmoregulatory ability) influencing predation susceptibility in these areas (Dieperink et al. 2001; Schreck et al. 2006; McMichael et al. 2010; Clements et al. 2012). Smolts less physiologically prepared to enter marine water were disproportionately consumed by birds in the Columbia River estuary, an area of high predation risk (Schreck et al. 2006; Kennedy et al. 2007). Outside of the Columbia River basin, avian predation of sea-run Brown Trout also concentrated on the first days that Brown Trout were exposed to brackish waters, possibly due to osmoregulatory stress experienced during this transition (Dieperink et al. 2001). In two other estuaries in Oregon, cormorants disproportionately depredated Coho Salmon relative to steelhead, which may be attributable to increased juvenile Coho Salmon estuary residency times (Clements et al. 2012).

Studies have attempted to identify the influence of environmental factors on salmonid survival for decades (Kareiva et al. 2000; McClure et al. 2003). Identifying these relationships is notoriously difficult due to the complexity of salmonid life histories, whereby different life stages use various habitats and experiences in one life stage may affect mortality in subsequent life stages (Budy et al. 2002; Ferguson et al. 2006; Muir et al. 2006; Schreck et al. 2006). Similar to relationships with salmonid survival, identifying the effects of environmental factors on within- and among-year variation in predation susceptibility remains challenging and is only partially understood.

Prey Density, Predator Density, and Migration Timing

Multiple studies indicated that earlier migrating individuals experienced higher survival compared with later migrating individuals of the same ESU (Scheuerell et al.

2009; Hostetter et al. 2011; Haeseker et al. 2012; Evans et al. 2014, 2016c). Avian predation was also a primary mortality source during juvenile out-migration for some populations (Evans et al. 2016b, 2019a; Payton et al. 2019). Although no single study has fully linked the dynamics of migration timing, survival, and avian predation, our synthesis provides several unique perspectives on these shared processes. First, predator swamping is now documented in multiple predator–prey studies, including studies of juvenile salmonid survival and predation (Hostetter et al. 2012, 2022; Roby et al. 2015, 2017a, 2017b; Furey et al. 2016). Predator swamping often occurs quickly under a type II functional response, where rates of consumption (i.e., prey consumed per predator per unit time) level off at an upper limit due to predator satiation or handling time, resulting in predation rates that decrease as prey abundance increases (Denno and Lewis 2009; Hostetter et al. 2022). Functional responses, however, vary among bird species due to diet specialization and differences in foraging strategies. For example, the diets of cormorants are generally more diverse and lower in percent salmonids relative to terns nesting at nearby colonies (Collis et al. 2002). As such, bird species may respond differently to increases in juvenile salmonid abundance, including reduced susceptibility due to predator swamping or sometimes increased susceptibility due to prey switching or local numerical responses through spatial redistribution (e.g., gulls forage on smolts when they are available; Hostetter et al. 2012, 2022; Roby et al. 2015, 2017a; Evans et al. 2016c). Differences in functional responses, however, do not imply that one predator species is consuming more or less salmonids than another but instead describe how each of these predator species respond to changes in prey abundance (Solomon 1949; Holling 1959).

Understanding functional responses, predator swamping, prey switching, migration timing, and prey survival in multipredator systems requires information on predator abundance, prey abundance, and per capita consumption or predation rates. Although most current analyses of per capita predation rates focus on annual colony size and annual predation rates (Evans et al. 2012, 2019c), there are also important insights to be gained from within season variation in these processes (e.g., Evans et al. 2013; Roby et al. 2017b). Accomplishing these objectives requires simultaneous studies to monitor colony attendance (i.e., number of breeding birds attending the colony throughout the breeding season), population-specific predation rates (mark–recovery studies), and prey availability (i.e., number of prey by species available as forage to avian predators). Some of these topics may be preliminarily explored using new analytical procedures and existing data (e.g., comparisons of predation rates, consumption rates, colony sizes, and how they relate to survival), while others will require empirical studies (e.g.,

concurrent monitoring of colonies, diets, and mark–recovery efforts).

Prey Characteristics

Length-selective susceptibility to tern and gull predation occurred within the size range of most juvenile salmonids (60–300 mm). Length-selective predation by terns was most frequently documented in steelhead populations, with predation susceptibility highest for smolts ranging from 175–225 mm in length and lower for shorter and longer individuals (Hostetter et al. 2012; Evans et al. 2019a). Most juvenile salmonids (e.g., Chinook Salmon, Sockeye Salmon) are <175 mm and studies of predation on salmonids generally display a linear, positive relationship between length and predation susceptibility (Hostetter et al. 2015; Roby et al. 2017a). Linear length-selective tern predation, whereby longer fish suffer disproportional predation pressure, directly contrasts with multiple studies supporting a “bigger is better” hypotheses for salmonid survival where juvenile survival increases for longer individuals (Zabel et al. 2005; Hostetter et al. 2011, 2015; Evans et al. 2014; Faulkner et al. 2019). While both length-selective predation and length-selective survival are now well described, the direct link between these processes and effects on prey populations remain largely unexplored.

Hatchery-rearing systems may select for individuals that are more surface oriented, less able to endure sustained swimming, more aggressive, and less experienced with predators relative to their naturally reared counterparts (reviewed by Maynard et al. 1995; Sundström et al. 2004). Additionally, hatchery-reared fish are often longer than their naturally reared equivalents, making it difficult to disentangle competing hypotheses describing the influences of inherent behavioral tendencies and length selectivity on survival and predation of hatchery versus naturally reared smolts (Miyamoto et al. 2018). Hypotheses for behavioral tendencies increasing avian predation susceptibility are logical but thus far are unconvincingly supported. For example, multiple studies observed little support for differences in the predation susceptibility of hatchery versus naturally reared individuals of the same ESU, and when observed, differences were often small and inconsistent (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012, 2016a, 2019c). Instead, factors such as length, migration timing, and predator characteristics appeared to better explain differences in smolt susceptibility to avian predation relative to inherent differences between hatchery and naturally reared salmonids.

Comparing studies across multiple regions within a watershed (e.g., inland and estuary colonies in the Columbia River basin) and across watersheds (e.g., coastal Oregon, California, Idaho, Denmark, Scotland) improves our understanding of commonalities versus system-specific

findings related to salmonid susceptibility to avian predation. For example, relative susceptibility among salmonid populations sometimes varied by watershed, likely due to unique predator and prey communities and environmental conditions. Mechanistic relationships (e.g., fish length, distance to colony, functional responses), however, often displayed commonalities across regions. For instance, predation susceptibility declined with distance to colony for terns, cormorants, and gulls both within the Columbia River basin and across other studied regions (Table 3; Supplement B). Similarly, more than 10 studies investigated relationships between fish length and tern and gull predation susceptibility in multiple watersheds and together suggested that shorter fish were too small to be energetically valuable (or too difficult to capture) or that longer fish were too large to be consumed (Dieperink et al. 2001, 2002; Hostetter et al. 2012; Sebring et al. 2013; Osterback et al. 2014; Evans et al. 2019a; Källo et al. 2020; Table 5; Supplement D). Linking mechanistic selection pressures to variation in population-level susceptibility across watersheds remains an area of needed research with the capacity to elucidate commonalities across systems and identify important system-specific considerations.

CONCLUSIONS

Predation is often a key source of mortality in natural systems, although the influence of predators on prey population dynamics can be highly variable. Salmonid–bird predator–prey dynamics are complex multipredator, multiprey systems that are influenced by a variety of individual-, population-, and landscape-level processes. In particular, the spatial and temporal overlap of avian predators and fish populations create a host of unique dynamics regarding the predator–prey interactions that lead to unique influences across systems. The importance of predation as a key factor in population fluctuations may range from nearly negligible to substantial and with direct influences on population growth rates. Fish mark–recovery studies focused on avian predation of juvenile salmonids provide tremendous opportunities to jointly investigate survival, predation, and the ecological processes determining prey–population dynamics (Rosenbaum and Rall 2018; Evans et al. 2019b; Payton et al. 2019). Further, integrating predator–prey analyses into larger survival studies will provide increased understanding of mortality threats, cumulative risks, individual- and population-levels drivers of predation risk, and the spatial and temporal resolution to prioritize conservation efforts when needed.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.