

CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Relationships between Pacific salmon and aquatic and terrestrial ecosystems: implications for ecosystem-based management

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Abstract. Pacific salmon influence temperate terrestrial and freshwater ecosystems through the dispersal of marine-derived nutrients and ecosystem engineering of stream beds when spawning. They also support large fisheries, particularly along the west coast of North America. We provide a comprehensive synthesis of relationships between the densities of Pacific salmon and terrestrial and aquatic ecosystems, summarize the direction, shape, and magnitude of these relationships, and identify possible ecosystem-based management indicators and benchmarks. We found 31 studies that provided 172 relationships between salmon density (or salmon abundance) and species abundance, species diversity, food provisioning, individual growth, concentration of marine-derived isotopes, nutrient enhancement, phenology, and several other ecological responses. The most common published relationship was between salmon density and marine-derived isotopes (40%), whereas very few relationships quantified ecosystem-level responses (5%). Only 13% of all relationships tended to reach an asymptote (i.e., a saturating response) as salmon densities increased. The number of salmon killed by bears and the change in biomass of different stream invertebrate taxa between spawning and nonspawning seasons were relationships that usually reached saturation. Approximately 46% of all relationships were best described with linear or curved nonasymptotic models, indicating a lack of saturation. In contrast, 41% of data sets showed no relationship with salmon density or abundance, including many of the relationships with stream invertebrate and biofilm biomass density, marine-derived isotope concentrations, or vegetation density. Bears required the highest densities of salmon to reach their maximum observed food consumption (i.e., 9.2 kg/m² to reach the 90% threshold of the relationship's asymptote), followed by freshwater fish abundance (90% threshold = 7.3 kg/m² of salmon). Although the effects of salmon density on ecosystems are highly varied, it appears that several of these relationships, such as bear food consumption, could be used to develop indicators and benchmarks for ecosystem-based fisheries management.

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INTRODUCTION

Natural resource management, including fishing, hunting, and forestry, involves trade-offs between ecological, social, and economic interests. Balancing the management of these resources for human use while maintaining the other valued components of ecosystems requires both clear objectives and a good understanding of how exploitation will affect ecosystem structure and function (Pikitch et al. 2004). Six species of Pacific salmon (*Oncorhynchus* spp.) support valuable commercial, recreational, and Indigenous fisheries (Criddle and Shimizu 2014, Amberson et al. 2016), while also providing an important source of food and nutrients for many species in the marine, freshwater, and terrestrial realms (Helfield and Naiman 2001, Quinn et al. 2003, Williams et al. 2011, Field and Reynolds 2013).

Pacific salmon are widely distributed from Japan to Russia, and from Alaska to California. They influence the composition, structure, and functioning of streams, lakes, and riparian forests as they migrate upstream to their spawning grounds (Naiman et al. 2002). These impacts are thought to occur across many levels of these ecosystems, from changes in water chemistry and fitness of individual organisms to populations and communities. Because of their semelparous and anadromous life histories, Pacific salmon accumulate most of their biomass at sea, then migrate up streams and rivers to spawn. After spawning, their carcasses release nutrients such as nitrogen, carbon, and phosphorus, which enables a transfer of nutrients and energy across ecosystem boundaries, from the ocean to streams and adjacent forests (Cederholm et al. 1999). The influx of salmon can lead to direct or indirect effects via several mechanisms, including (1) nutrient subsidies to species that directly consume wild salmon or their carcasses, (2) fertilization through excretion or decomposition, with indirect ecological effects at higher trophic levels, and (3) disturbance or bioturbation of sediment during spawning (Gende et al. 2002, Janetski et al. 2009, Moore and Schindler 2010, Hocking and Reynolds 2011).

Recognition of the importance of salmon to aquatic and terrestrial ecosystems has resulted in repeated calls for incorporation of ecosystem-based management into fisheries management (Darimont et al. 2010, Wieckowski 2011, Levi et al. 2012). Despite being a key objective and strategy in Canada's Policy for the Conservation of Wild Pacific Salmon (Fisheries and Oceans Canada 2005) and being identified in some U.S. salmon fisheries plans (Alaska Department of Fish and Game 2001), progress towards ecosystem-based management has been slow (Mallick et al. 2016, Michael 2017). Beyond the spatial, temporal, political, and legal

challenges of implementing ecosystem-based management for Pacific salmon (Hoffman and Hildreth 2016, Mallick et al. 2016), there are also legitimate concerns about how to account for surrounding ecosystems in objectives, targets, and interventions (Nelitz et al. 2006, Williams et al. 2011). For example, which species or ecological processes should be included as indicators to monitor and assess the status of ecosystems? How do we establish benchmarks for each indicator to demonstrate ecosystem functioning? To answer these questions, we need to understand the shape, direction, and magnitude of the relationships between salmon abundance and ecosystem composition and processes across estuarine, freshwater, and associated terrestrial systems.

In this paper, we present a comprehensive review of published quantitative relationships between spawning Pacific salmon density or abundance and attributes and processes of terrestrial and freshwater ecosystems (described as "ecological responses" hereafter). Our work builds from previous reviews that described the effects of salmon by comparing streams with and without salmon (Naiman et al. 2002, Janetski et al. 2009). We expanded on these by identifying the functional shapes, magnitude, steepness, and direction of the relationships across a gradient of salmon density or abundance, which will answer the question posed over a decade ago: how many salmon are required to fulfill their ecological role (Gende et al. 2002, Naiman et al. 2002)? We identified whether these ecological responses increase indefinitely (within the ranges of data observed) or reach a plateau (i.e., an asymptote or maximum threshold) as salmon density increases. We also determined whether it was possible to identify ecosystem-based management indicators and benchmarks by quantifying the minimum salmon density required to obtain a level of saturation across multiple ecological responses. We also identified patterns and knowledge gaps across taxonomic groups and ecological processes in freshwater, terrestrial, and estuary ecosystems.

METHODS

We conducted a thorough literature review to collate studies that investigated relationships between Pacific salmon densities or abundance and ecological processes in freshwater, terrestrial, and estuary ecosystems. We identified studies, screened them for relevance and eligibility, and then extracted the necessary data (Fig. 1).

Literature search

We searched for peer-reviewed papers using specific search terms in the Web of Science (see Appendix S1:

Table S1) and found 3,693 articles published before December 2017, once duplicates were removed. We supplemented this search with an additional 35 peer-reviewed papers either provided by experts or based on our own knowledge of the literature, resulting in a total of 3,728 articles (Fig. 1).

During the screening process, we first assessed the relevance of each article by reading titles and abstracts. Papers were included at this stage if they mentioned the influence of Pacific salmon on an ecosystem near spawning and migration habitat (i.e., estuary, freshwater, or streamside terrestrial habitat). We excluded all other studies, including those that described how ecosystem factors influenced salmon densities or abundance (i.e., the opposite relationship to the one we are interested in). All articles were divided between two coauthors (JCW and JEP) to review at this title–abstract screening stage. We checked and revised an initial subset of each other's decisions and discussed any papers where differences occurred, to clarify and agree on a consistent protocol. If there was uncertainty around a study's relevance or eligibility based on the title and abstract we retained it

for assessment in the following stage of the screening process.

Study eligibility

The papers that were included at the title–abstract screening stage ($n = 146$) were then assessed for their eligibility by reading the full text and determining whether they met all the following inclusion criteria: (1) They studied the influence of one or more of six species of Pacific salmon (*Oncorhynchus keta* [chum salmon], *O. gorbuscha* [pink salmon], *O. kisutch* [coho salmon], *O. masou* [masu salmon], *O. nerka* [sockeye salmon], and *O. tshawytscha* [Chinook salmon]) in their native range on ecosystem components, either through nutrient subsidies, bioturbation, or other ecosystem processes; (2) they assessed habitats that were specifically influenced by Pacific salmon migration and spawning life cycle stages, including rivers, streams, estuaries, lakes, and riparian forests (but not marine habitats); (3) the sampling design measured a range of salmon densities or abundance across multiple streams, rivers, lakes, or

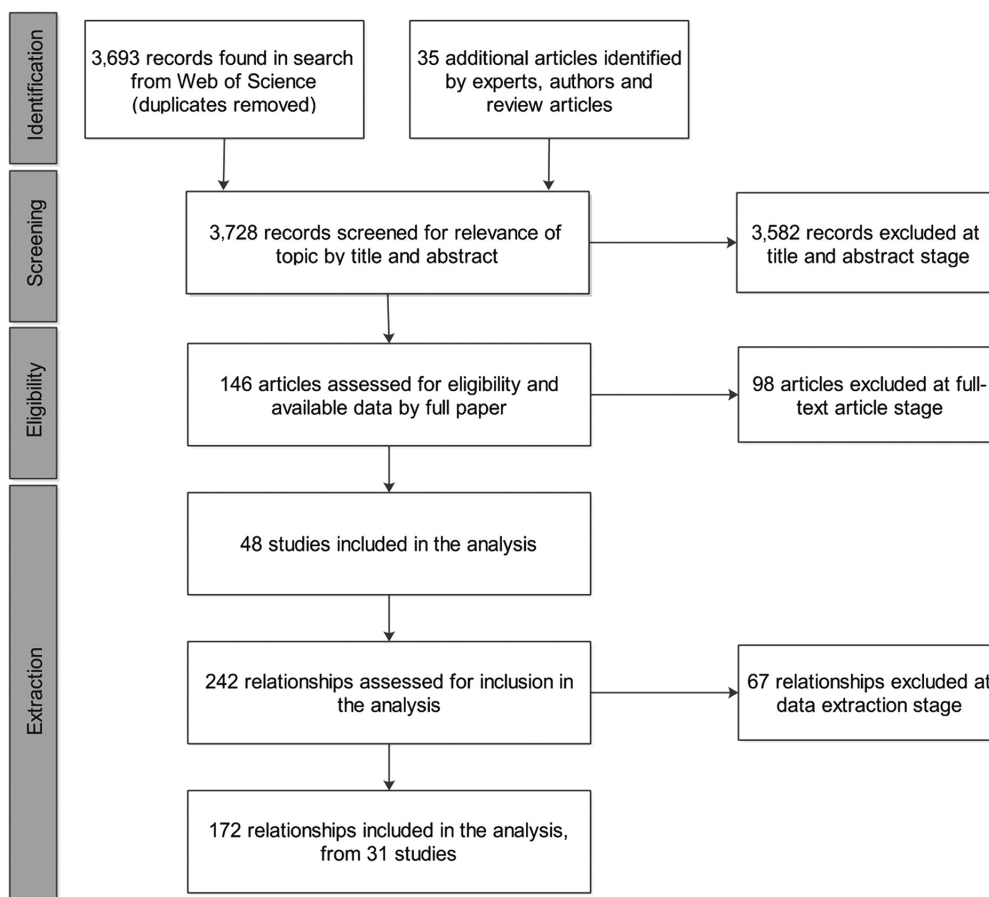


FIG. 1. Flow diagram of literature screening, eligibility, and data-extraction steps.

multiple years, and had data points for more than six total system–year combinations, including sites where no spawning salmon were present (to ensure a relationship could be estimated); and (4) they presented raw data on the relationship between salmon density or abundance and an ecosystem component (i.e., ecological response) in a graph or table.

We restricted the analysis to studies of live fish during their freshwater migration or spawning life-cycle stages, and excluded studies that involved carcass addition or salmon analogues because naturally spawning fish have different impacts on nutrient imports and habitat scouring compared to carcasses that have been artificially added to a system (Janetski et al. 2009). We also excluded studies of Pacific salmon in their nonnative range and studies that used artificial spawning channels, because results from these studies would not be readily applicable to natural systems. Based on these eligibility criteria, we included 48 of 146 relevant papers (Data S1). All of the studies were correlational, and the inferences we made of processes underlying the relationships were largely informed by the authors' interpretations within the original study.

Data extraction

Within the 48 eligible papers, we found 242 relationships across a gradient of salmon density or abundance, which included relationships between salmon and metrics of ecosystem structure and function (i.e., ecological responses) or isotopic concentrations found across these ecosystem components (i.e., isotopic responses). We extracted the data from eligible graphs using Plot Digitizer (Huwaldt and Steinhurst 2013). Most studies measured salmon abundance as either total biomass or number of salmon in a spawning stream or estuary (kg), or density as either average biomass or number of salmon per length of spawning reach (kg/m), or average biomass or number of salmon per area of a spawning reach (kg/m²). To allow for comparisons across studies that used different metrics, we standardized units of salmon density or abundance across all studies by converting numbers of salmon into salmon biomass using regional weight estimates of an average individual fish (i.e., number to kg, number/m² to kg/m², Appendix S1: Table S2; Gresh et al. 2000). Data presented with a log or other transformation were back-transformed before analysis.

We excluded 67 relationships based on the following rationales: they had incompatible units of salmon density ($n = 11$ relationships, e.g., kg/km² of bear range or kg per volume of water discharge, kg·m⁻³·s); they had small sample sizes ($n < 6$ system–year combinations, $n = 19$ relationships); the data points could not be digitized accurately because of tight clumping or overlap on the plot ($n = 13$ relationships); on closer inspection they did not fit our criteria ($n = 21$); or the response variable was an output of a model ($n = 3$ relationships). The

number of salmon–ecosystem relationships ranged from 1 to 23 per paper (5.5 relationships per paper, on average). If a paper presented relationships of multiple groups of species (e.g., taxa, guilds) and a graph combining these groupings together, we used the graph with combined data. For example, we included the relationship showing total aquatic insect abundance in Verspoor et al. (2011), but excluded the three plots showing the abundance of individual insect orders. If the authors presented multiple relationships of individual groupings but did not present a summary graph that combined these data sets into a total measure, we retained all individual relationships. After these steps, 172 relationships remained in the analysis (Data S2). We categorized each relationship into 1 of 15 broad response types; these response types included structural, functional, or composition attributes associated with abiotic nutrient pathways, individual organisms, populations, and ecological communities. These were further divided into 31 subcategories based on the response variable measured, for example: the concentration of isotope $\delta^{15}\text{N}$, the growth rate of individuals, population abundance or biomass, diversity of species, or a difference in vegetation density or forest structure (Table 1).

We were unable to combine data from multiple studies for a meta-analysis because of the diversity of response variables and experimental designs across studies. For example, the data points used across studies represented (1) different streams (or lakes) with salmon density averaged across multiple years/stream, (2) multiple years measured in one stream, (3) multiple stream–year combinations, or (4) multiple streams sampled below and above a salmon migration barrier. Because a meta-analysis was not feasible, we quantified and summarized the direction and shape of relationships between salmon and ecological or isotopic responses across these study designs.

Analysis

We fitted nonlinear ordinary least squares regression models to the 172 relevant data sets of salmon–ecological relationships using the “nls” R package. We compared the fit of nine functions: (1) a two-parameter Michaelis–Menten function, (2) a three-parameter Michaelis–Menten function, (3) a two-parameter exponential function, (4) a three-parameter exponential function, (5) a two-parameter power function, (6) a three-parameter power function, (7) a linear model, (8) a log-linear model, and (9) a null model showing the mean of the response variable (Appendix S1: Table S3).

These functions exhibit different response shapes. Michaelis–Menten and exponential models reach an asymptote. The log-linear and power functions are curved nonasymptotic relationships. Asymptotic and curved functions with two parameters assume that the curve passes through the origin, whereas those with three parameters estimate a y -intercept, suggesting that factors

TABLE 1. Specific ecological and isotopic response variables across ecological processes, and the number of relationships that demonstrated a positive, negative, or null relationship with the density of salmon.

Ecological process	Specific relationship metrics	Positive	Negative	Null	Total
Organism level					
Isotope	Isotope $\delta^{15}\text{N}$	30	0	15	45
	Isotope $\delta^{13}\text{C}$	7	0	8	15
	Isotope $\delta^{34}\text{S}$	0	0	3	3
	Difference in $\delta^{15}\text{N}$ (above/below stream barriers)	2	0	3	5
Nutrient enhancement	Change %N (above/below)	0	0	1	1
	Enhancement %MDN	1	0	0	1
	Enhancement %N	3	0	4	7
	Enhancement %P	1	0	2	3
	Fatty acid ratio	0	0	3	3
Food provision	Number killed	8	0	2	10
	Number killed per hour	1	0	0	1
	Proportion diet	3	0	0	3
	Proportion salmon killed†	1	3	3	7
	Relative weight eaten per body size	2	0	0	2
	Size difference (preference)	1	0	0	1
Growth	Growth rate	4	0	0	4
	Size	3	0	1	4
Phenology	Emergence date†	0	4	0	4
Mortality	Change in abundance	0	0	2	2
Population level					
Abundance	Abundance density	4	1	1	6
	Relative abundance per meter	1	3	0	4
	Total abundance	2	0	4	6
Biomass	Biomass density	1	2	13	16
	Prop change biomass (before/after spawning)	0	7	0	7
Population composition	Age composition of juveniles†	1	0	1	2
Phylogeny	Phylogenetic dispersion†	1	0	0	1
Ecosystem level					
Community structure	Community structure	1	0	0	1
Disturbance	Bed load accumulation	1	0	0	1
Diversity	Diversity of species	0	1	1	2
Productivity	Productivity C:N ratio†	0	1	0	1
Forest structure	Difference in vegetation density (above/below)	0	0	4	4
Grand total		79	22	71	172

†The ecological response variables that were excluded when summarizing the positive and negative relationships, as the direction of slope for these metrics could not be easily interpreted as a 'positive' or 'negative' ecological response. MDN = marine-derived nutrients.

other than salmon influence the presence of the ecological or isotopic response. A change in salmon density could have large or small effects on different ecological processes, depending on the shape of the response and the steepness of the curve at that density. For asymptotic relationships, the greatest increase in ecological response would be at low salmon densities, whereas for linear or nonasymptotic relationships, every extra spawning salmon would result in a constant incremental change.

The initial starting values, which are required to fit the nonlinear models, were estimated for each data set with rules of thumb to approximate intercepts, asymptotes, and slopes, described in Bolker et al. (2009). Several of these relationships were also fitted using self-start models where available if the models using manual starting parameters failed to converge. Self-starting models are a

feature within the "nls" R package, that automatically create initial values for parameter estimates. We checked the model assumptions of normality and homoscedasticity of residuals, the contour plots of confidence regions, and convergence diagnostics (Ritz and Streibig 2008). There are difficulties in automating diagnostic tests for nonlinear models, so we manually checked the diagnostic plots of models for each data set, using the "nlstools" R package (Baty et al. 2015). We excluded models that required more than 20 iterations to converge (Baty et al. 2015). We also excluded models that had standard errors of estimated parameters that were 1.5 times greater than parameter estimates, as we noticed that they often coincided with poor diagnostics and goodness of fit.

We compared models using Akaike information criterion corrected for small sample sizes (AIC_c ; Hurvich

and Tsai 1989). We identified the most parsimonious model (i.e., the “best” model) for each data set as the model with the lowest AIC_c value that had satisfactory diagnostic plots (Data S3). R^2 values are not an appropriate goodness-of-fit test for nonlinear models (Spiess and Neumeyer 2010). Instead, we included the null model (intercept only) to compare the fit of other models (Mac Nally et al. 2018). Using the “best” model for each data set, we compared the direction of relationships found across habitats, taxonomic groups, and types of responses (positive, negative, or null). For this comparison, we excluded 15 data sets for which a positive or negative the direction of the relationship could not be interpreted as a ‘positive’ or ‘negative’ ecological effect on a component of the ecosystem. Examples of these excluded responses include C:N ratio, shift in community structure, phylogenetic dispersion, and the proportion of total salmon killed by bears (Table 1).

Finally, we assessed the density or abundance of salmon that could provide a benchmark for each ecological or isotopic response. For relationships best described by asymptotic models (exponential and Michaelis–Menten, based on lowest AIC value), we found the asymptote at which the ecological or isotopic response would reach its maximum (y value) using the function’s parameter estimates (Appendix S1: Table S3). We used this estimate to backpredict the corresponding salmon density (x value) at 75% and 90% of the y value of the asymptote (Appendix S1: Table S3). These percentages of the asymptotes were chosen to demonstrate the steepness of the relationships and as possible thresholds for ecosystem-based management, and because it is not possible to identify the exact salmon density at which the asymptote is reached (when $x = \infty$). We also found the salmon densities at the 75% and 90% of the asymptote (i.e., the minimum value) for the negative relationships (see Fig. 3c for an example).

For relationships with nonasymptotic best models, we calculated the salmon densities that correspond to 75% and 90% of the maximum ecological or isotopic response (maximum y value measured in study). These results are presented separately from the asymptotic relationships because the linear or convex relationships may reach an asymptote at higher salmon densities. Our inferences here were limited by the ranges of salmon densities observed in the studies, and we acknowledge that the true variation and maximum range of salmon densities within each study area may be larger. When calculating thresholds, we excluded four relationships from Brahney et al. (2006) that measured salmon density in a lake fed by multiple salmon streams, which resulted in an accumulation of salmon at high densities and was not comparable with other study systems. Relationships from this paper were still included in the analyses summarizing the shape of the curves and types of relationships. We used the software R version 3.3.3 (R Development Core Team 2017) and RStudio version 1.1 (RStudio Team 2017) for statistical analysis, and R

packages “dplyr”, “ggplot2”, “muMin”, “rmarkdown”, and “investr” (Greenwell and Schubert Kabban 2014).

RESULTS

Available literature and knowledge gaps

The most common relationships studied were isotopic ratios across a diverse array of taxonomic groups ($n = 68$); food provision to bears, freshwater fish, and marine invertebrates ($n = 24$); and effects on population biomass ($n = 23$) or population abundance ($n = 16$) for biofilm, algae, periphyton, stream invertebrates, freshwater fish, plants and birds, which are described in the section ‘Ecological responses to salmon’ (Fig. 2). Overall, the effects of salmon density on ecosystem attributes and processes are extremely diverse and complex, though very few ecosystem-level processes have been studied (Table 1, with illustrative examples in Fig. 3).

The most commonly studied taxa were (1) stream invertebrates (Brahney et al. 2006, Moore and Schindler 2008, 2010, Campbell et al. 2011, Verspoor et al. 2011, Rinella et al. 2013, Harding and Reynolds 2014b), (2) freshwater fish (Moore et al. 2008, Bentley et al. 2012, Rinella et al. 2013, Nelson and Reynolds 2014, 2015, Swain et al. 2014, Swain and Reynolds 2015), (3) biofilm (combined with algae and periphyton, Brahney et al. 2006, Moore and Schindler 2008, Holtgrieve et al. 2010, Verspoor et al. 2010, Harding et al. 2014), (4) bears (Quinn et al. 2003, 2009, 2017, Holtgrieve et al. 2009, Cunningham et al. 2013, Peirce et al. 2013), and (5) plants (Bartz and Naiman 2005, Hocking and Reimchen 2009, Hocking and Reynolds 2011, Rinella et al. 2013, Hurteau et al. 2016; Fig. 2).

We found fewer than 10 relationships each for river sediment (Brahney et al. 2006, Macdonald et al. 2010), riparian soil (Bartz and Naiman 2005), water chemistry (Rinella et al. 2013), birds (Field and Reynolds 2011, 2013), marine invertebrates (Harding and Reynolds 2014a, Harding et al. 2015), and terrestrial invertebrates (Hocking and Reimchen 2009). Notably, we found no studies that quantified the relationship between salmon density and mammals (other than bears), reptiles, amphibians, or fungi.

Of the 172 relationships, 44% were from studies conducted on the central coast of British Columbia. A further 24% of the relationships were from Bristol Bay, Alaska, and the remainder were from studies conducted in other areas of British Columbia and Alaska. Relevant studies that were excluded due to our data eligibility criteria also came from Washington, Idaho, Japan, and Russia (Data S1).

Sockeye salmon accounted for 34% of relationships, and mixed populations of pink and chum salmon were studied in 33% of relationships (Data S2). We did not find any suitable studies that tested the effect of masu salmon. Almost two-thirds of relationships focused on the influence of salmon density or abundance on stream habitats (60%), and other relationships concerned

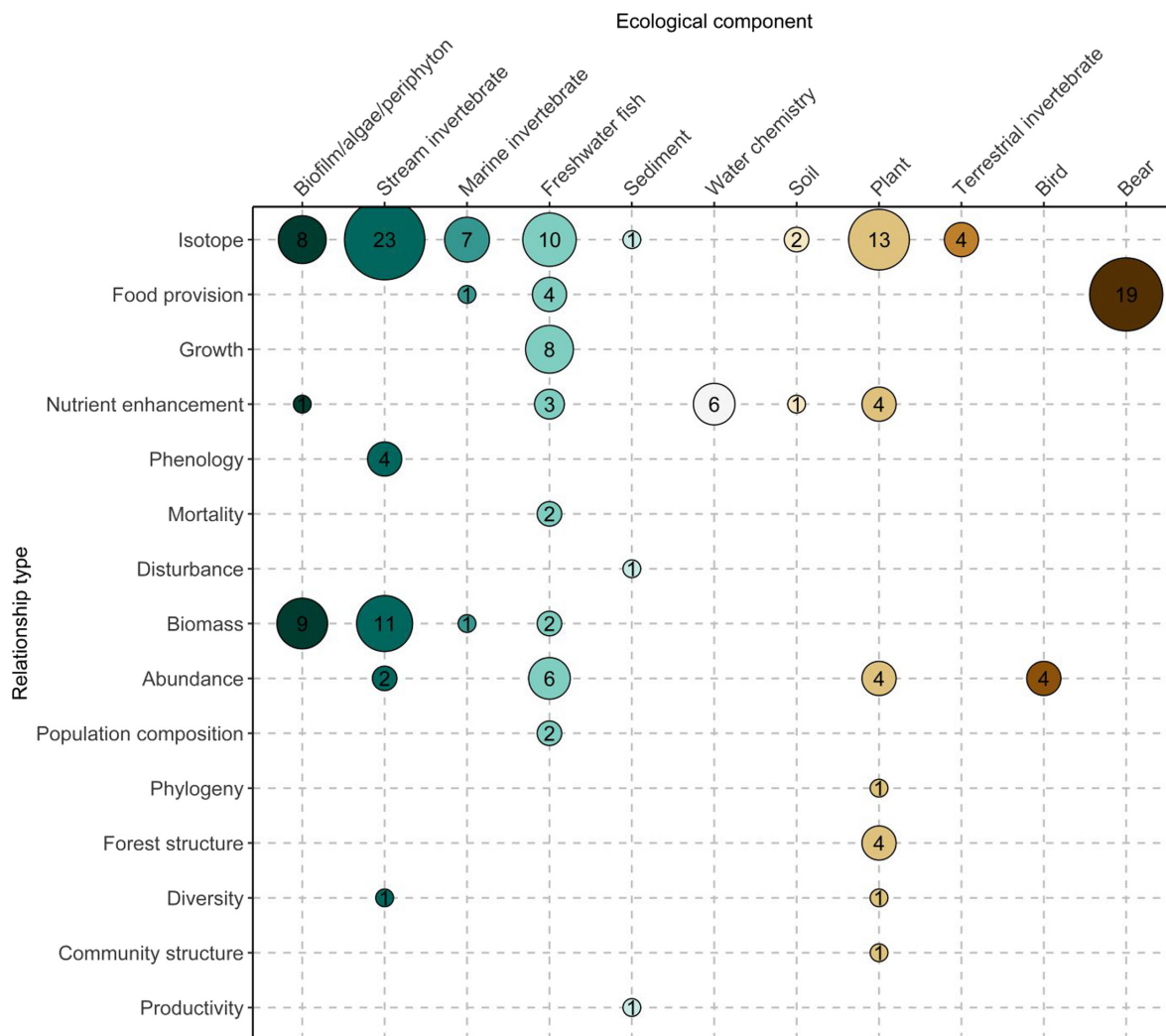


FIG. 2. Number of relationships describing the density or abundance of salmon and other ecosystem components included in the analysis, across ecosystem attributes or processes and taxonomic group ($n = 172$).

components of forests (30%), estuaries (6%), combined estuary and forest habitats (2%), and lakes (2%).

Ecological responses to salmon

Of the relationships between salmon density and the ecological attributes for which we assessed direction of slope ($n = 157$, i.e., 91% of all relationships), just under half showed positive correlations (48%). We found only a few negative relationships (9%), and the remaining data sets demonstrated no relationship between salmon density and the ecological or isotopic response (i.e., the null model). Relationships in terrestrial systems tended to be slightly more positive (64% positive, 8% negative, 28% null) than in aquatic habitats, where physical disturbance of the substrate occurs when the salmon are spawning, leading to reductions in biofilm and larval invertebrate biomass (41% positive, 9% negative, 50% null, Appendix S1: Table S4).

Marine-derived isotopes.—Marine-derived isotope concentrations were by far the most common response variable studied (40% of all relationships) and this was spread evenly across most taxonomic groups (Fig. 2). Isotopic analyses measure the uptake of marine-derived nutrients (e.g., $\delta^{15}\text{N}$) in plant and animal tissue and are often used as a tracer to indicate the uptake of salmon nutrients by freshwater and terrestrial biota. The majority of relationships with marine-derived stable isotope $\delta^{15}\text{N}$ were positive and curved or asymptotic (Fig. 4). For example, the stable isotope $\delta^{15}\text{N}$ increases in false azaleas (*Menziesia ferruginea*) as salmon density increases with a log-linear function (Fig. 3a). Fewer than a half of the $\delta^{13}\text{C}$ relationships were positive (Table 1). However, the links between stable isotopes and salmon nutrients are not always straightforward when trophic pathways are indirect (e.g., via soil and terrestrial plants), as microbial, hydrological, and geomorphic processes can amplify $\delta^{15}\text{N}$ beyond the

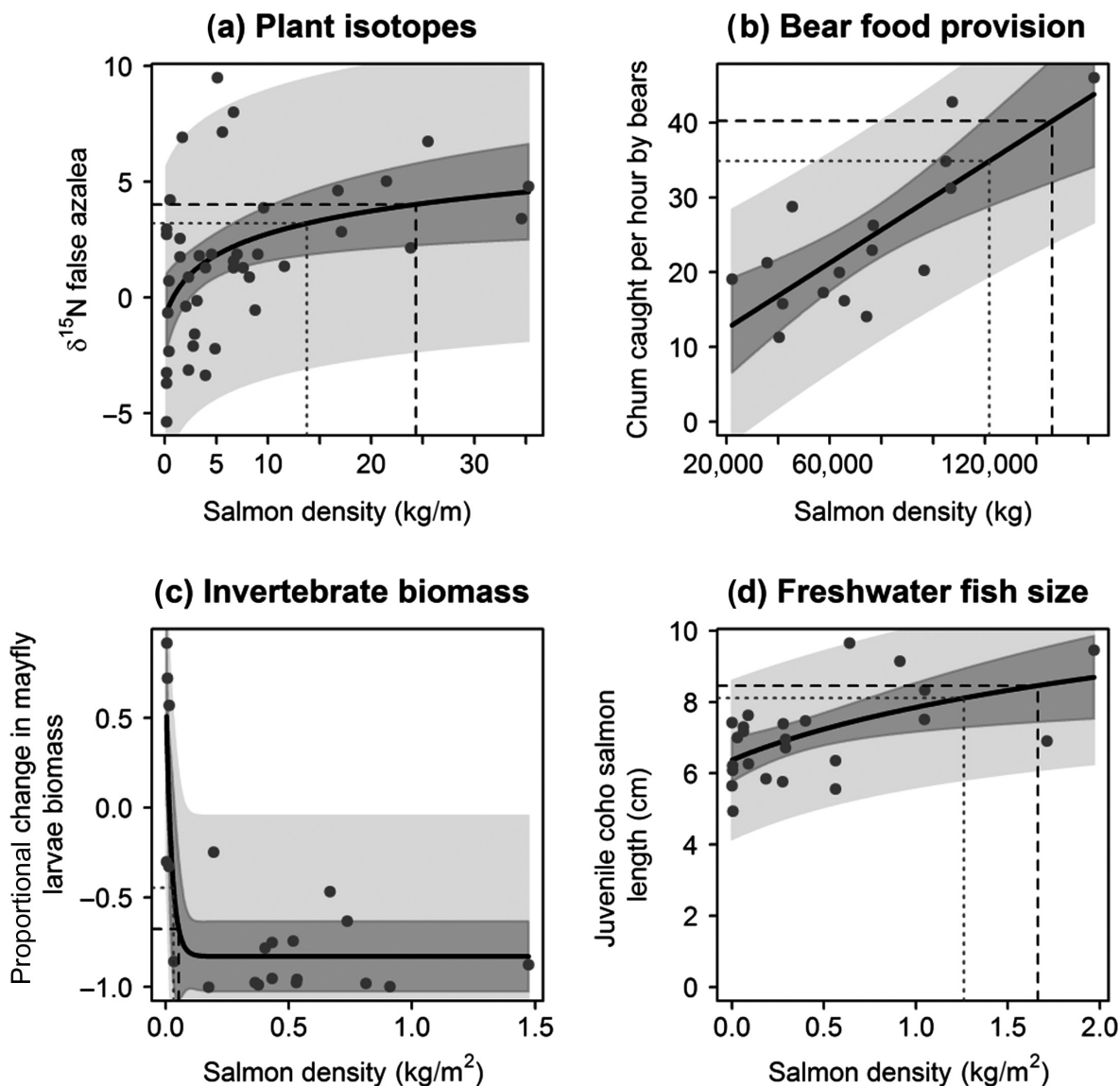


FIG. 3. Four illustrative examples of relationships between the density of salmon and different ecological attributes or processes (a) $\delta^{15}\text{N}$ of false azalea (Hocking and Reynolds 2011), (b) number of chum salmon caught per hour by bears (Peirce et al. 2013), (c) proportional change in mayfly larvae biomass (Ephemeroptera) (Moore and Schindler 2008), and (d) fork length size of juvenile age 0 coho salmon (Nelson and Reynolds 2015). Model fits are based on the best model, with confidence bands (dark shading) and prediction bands (light shading). The 90% (dashed black lines) and 75% thresholds (dotted gray lines) of the asymptote (or maximum response) of the best model for each relationship are shown. The best models for each plot were (a) log-linear, (b) linear, (c) three-parameter exponential function, and (d) log-linear.

contributions of salmon through fractionation, which occurs during denitrification (Schindler and Smits 2017). In addition, increases in or saturation of $\delta^{15}\text{N}$ are unlikely to provide information about how ecological components or processes of that system respond to changes in salmon density.

Food provision.—Food provision for individual organisms via direct consumption was studied frequently (14% of all relationships; Table 1), particularly for bears (Fig. 2). For example, in one study, as the total biomass

of salmon in a stream increased, the number of salmon caught—though not necessarily eaten—by bears per hour increased linearly (Fig. 3b). Most relationships associated with food provision were positive (Fig. 5).

Abundance and biomass.—Of the ecosystem components that measured a population-level response, the most commonly studied relationships quantified abundance or biomass (23% of all relationships; Fig. 2). Many studies assessed the biomass density or the change in biomass before and after salmon spawning (Table 1).

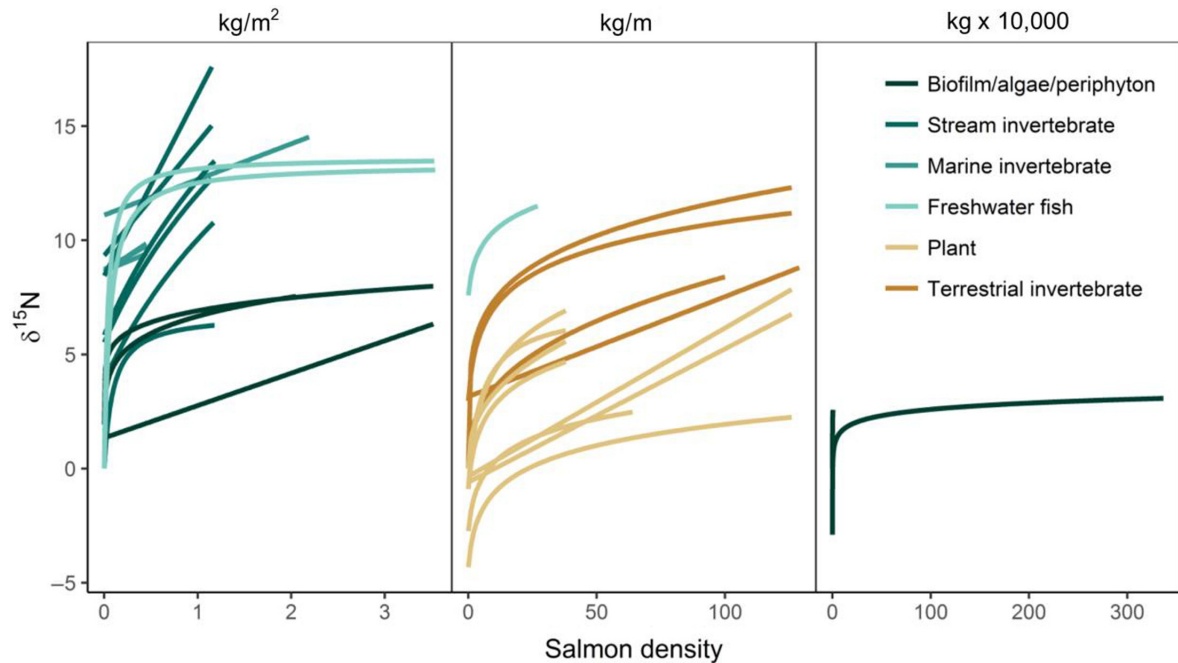


FIG. 4. Predicted relationships between relative $\delta^{15}\text{N}$ and salmon density across taxonomic groups and units of salmon density or abundance, based on “best” models for each data set. Null models were best models for nine stream invertebrate relationships, two plant relationships, two freshwater fish relationships, one algae/periphyton relationship, and one sediment relationship, and are not included here.

Salmon-derived nutrient subsidies elicited positive responses in abundance or density of birds in the forest and estuary (Field and Reynolds 2011, 2013). Some plant species, such as salmonberry, had increased abundance in streams with higher salmon densities, whereas blueberry and false azalea densities were lower (Fig. 6;

Hocking and Reynolds 2011). Correlations between salmon density and freshwater fish were variable, depending on the species measured (coho salmon or sculpin species) and season (spring prior to spawning or fall during spawning; Nelson and Reynolds 2014, Swain and Reynolds 2015).

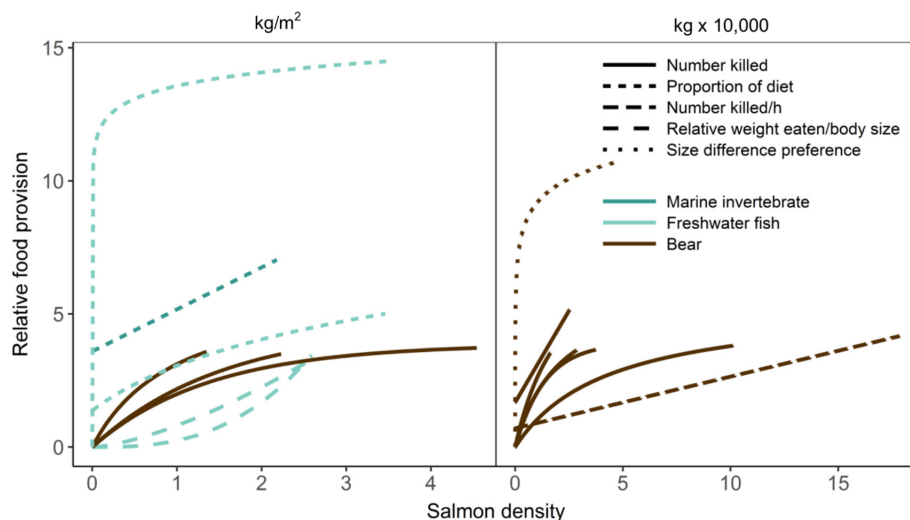


FIG. 5. Predicted relationships between relative food provision metrics and salmon across taxonomic groups and units of salmon density or abundance, based on “best” models for each data set. Seven relationships showing the proportion of salmon killed by bears and two null relationships for bears were not presented here. All relationships are scaled by the standard deviation of each data set, that is, true value/standard deviation.

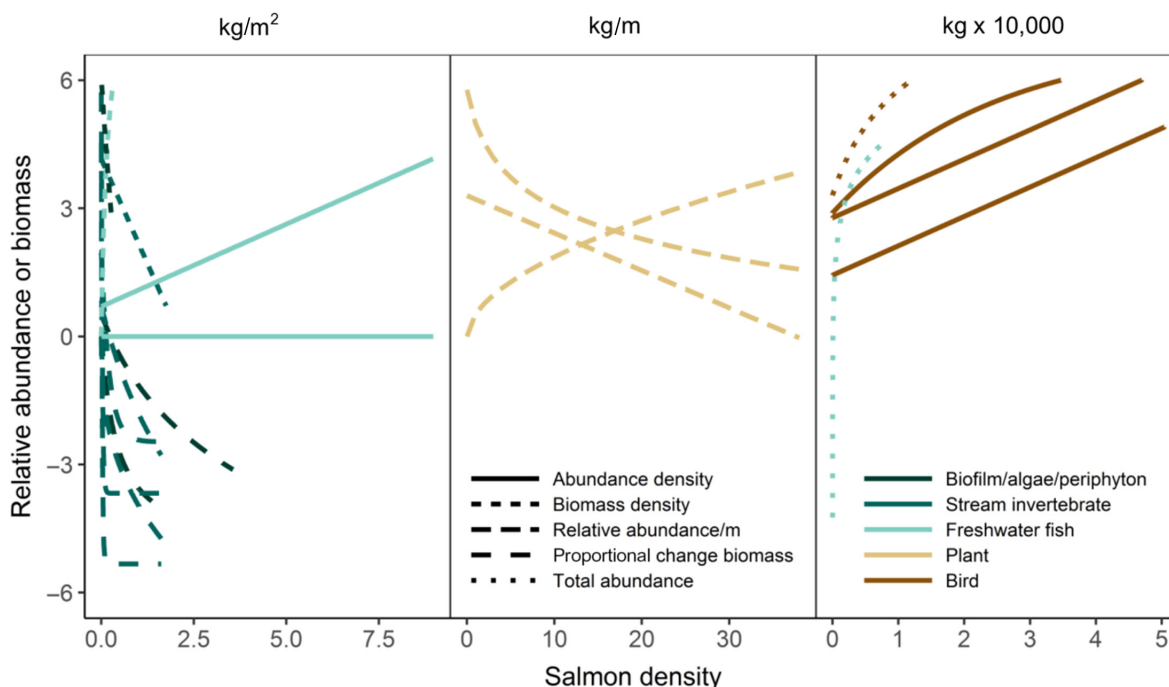


FIG. 6. Predicted relationships between abundance and biomass metrics and salmon, across taxonomic groups and units of salmon density or abundance, based on “best” models for each data set. Null models were the best models for the following relationships per taxa: six biofilm, seven stream invertebrates, four freshwater fish, and one marine invertebrate. All relationships are scaled by the standard deviation of each data set, that is, true value/standard deviation.

The reduction in biomass of aquatic invertebrates and algae from before and after spawning was often stronger in streams with high salmon densities (Moore and Schindler 2008), likely due to bioturbation and disturbance, with no evidence of a subsidy effect (Figs. 3c, 6). In contrast, studies that measured the relationships between salmon density and stream invertebrate or algal densities either during spawning or after spawning found variable results, i.e., positive (Harding et al. 2014; Verspoor et al. 2011), negative (Verspoor et al. 2010) or null models (Harding et al. 2014b; Holtgrieve et al. 2010). However, most of these relationships were best described as null models in our analysis, as we could not include covariates from the original models (Table 1; Data S2).

Other individual-, population-, and ecosystem-level responses.—Other ecological responses at the individual organism level included growth rate, size, nutrient enhancement, phenology, mortality, and disturbance due to salmon spawning (Fig. 2, Table 1). For example, juvenile coho salmon were larger in streams with more chum and pink salmon, even when accounting for stream width and pool depth (Fig. 3d, Nelson and Reynolds 2015). Other population-level relationships included population age composition of juvenile coho salmon and the phylogenetic dispersion of riparian plants, with both positive and null responses (Table 1). Overall, very few studies investigated the relationship between salmon density and ecosystem-level responses,

such as community or forest structure, species diversity, or productivity of an ecosystem (Bartz and Naiman 2005; Hocking and Reynolds 2011).

Functional shapes of salmon–ecological relationships

The shape (nonasymptotic, asymptotic, linear, or no effect) of the salmon–density relationships varied across and within response metrics. Almost a third of all relationships (31%) were best explained by curved nonasymptotic models (i.e., the model with lowest AIC_c value, $n = 172$). These included 37 log-linear functions and 17 power functions. Only 13% of relationships were best explained by a model with an asymptotic function (i.e., exponential or Michaelis–Menten function), while 15% of relationships were linear. A null (intercept only) model best described 41% of the relationships between salmon density and various ecological components. Of these 71 null relationships, the original studies also reported no relationship for 76% of the data sets, positive relationships for 17%, and negative relationships for 7%. There were no obvious patterns in the types of curves that best described salmon–ecosystem relationships across taxonomic groups and ecological processes (Appendix S1: Fig. S1).

Asymptotic and nonasymptotic ecological thresholds

We calculated the densities of salmon required to achieve 75% and 90% of the maximum ecological or

isotopic response for each relationship, based on its “best model.” Most relationships reached the thresholds at low densities of salmon relative to those tested in the studies (Fig. 7; Appendix S1: Fig. S2). There was little overall difference in the predicted salmon densities to reach the 75% or 90% thresholds, though this was influenced by the steepness of each curve. Most relationships reached 90% thresholds at $<3 \text{ kg/m}^2$ of salmon (Fig. 7a, b left panels; Data S2). However, bears and freshwater fish required much higher densities of salmon to reach their 90% thresholds: food provision for bears (9.2 kg/m^2 , Quinn et al. 2003) and freshwater fish abundance (7.3 kg/m^2 , Swain and Reynolds 2015; Fig. 7a left panel). For relationships that measured salmon density by length of stream (kg/m), we found that plants and small terrestrial invertebrates required higher levels of salmon biomass to reach their maximum level of marine-derived stable isotopes (max = 106.1 kg/m , Fig. 7a, b center panels), from Hocking and Reimchen (2009). For studies that measured total biomass of salmon in a stream (kg), bears required the most salmon to reach their ecological response maximum for food provision, $3.9 \times 10^5 \text{ kg}$ of salmon for 90% the asymptote (Fig. 7, i.e., number of salmon killed in 27 streams with an average width of 8.0 m [$\text{SD} = 10.1 \text{ m}$], Quinn et al. 2017).

DISCUSSION

Salmon have a diversity of impacts across multiple ecological boundaries, including estuaries, streams, lakes, and forests. Here we synthesized 172 relationships from 31 published studies to quantify and classify the directions, magnitudes, and shapes of these relationships. We also identified possible indicator taxa and their “saturation” levels of Pacific salmon, which can be used to inform ecosystem-based fisheries management, responding to calls for an assessment of the requirements of salmon for wildlife and ecological processes (Hilderbrand et al. 2004, Hill et al. 2010, Richardson and Wipfli 2016). We aimed to test how salmon density or abundance influences ecological structure and function; however, we found that many metrics—such as isotopes—used in the existing studies were weak proxies and their correlational study designs made it difficult to attribute causality of salmon to these relationships. Furthermore, the diversity of metrics used and the sometimes conflicting directions of the relationships reduced our ability to generalize results across and within ecosystem processes and taxonomic groups.

Complexity and context of isotopic and ecological responses

Many isotopic analyses have been interpreted to suggest that marine-derived nutrients are present at higher concentrations in streams and riparian forest ecosystems with higher densities of salmon than ecosystems with low salmon densities (Fig. 4). Studies demonstrating this

link exist for most aquatic and terrestrial taxonomic groups, except birds, mammals, and fungi (Fig. 1). However, confounding factors, such as geomorphology or soil moisture, which can lead to higher rates of denitrification in open floodplains, could contribute to these higher concentrations of isotopes in high salmon spawning streams (Schindler and Smits 2017). This could be problematic if the hypothesized pathway of nutrient transfer is through fertilization of the soil, for example, for plants. These effects are difficult to separate out in observational studies, though a study by Hocking and Reynolds (2011) found elevated $\delta^{15}\text{N}$ in leaves of plants on high-density salmon streams even when an index of soil moisture was included in the analyses. Even if isotopes can be used to trace mechanistic links between salmon and ecosystem attributes, accumulation of marine-derived isotopes may not reflect changes to the ecosystem structure or function, and may not be reliable predictors of ecological responses. For example, a recent study found that there was no relationship between isotopes and C:N ratio of riparian sedges (*Carex* spp.), nor indices of body condition of ants (*Formica* spp.) or spiders (*Pardosa* spp.; Vizza et al. 2017).

Density (or abundance) of salmon is a critical driver of the magnitude of impact on some, but not all, ecological responses. We found very limited evidence about the effect of salmon density on structural diversity or overall ecosystem function (such as decomposition, primary production; Fig. 2). However, from the 104 individual nonisotopic ecological relationships (from 30 papers), we can begin to piece together a broader understanding of how salmon density influences individual organisms and populations across taxonomic groups. Several consistent patterns emerge, including strong positive relationships between salmon density and food provision of bears and freshwater fish (Fig. 5), abundance of scavenger birds and passerines (positive, Fig. 6), proportional change of stream invertebrate and algal biomass during and after spawning (negative, Fig. 6), and organism growth rate and size of freshwater fish (positive; Table 1). In contrast, biomass of biofilm, algae, and periphyton during spawning, and diversity of stream macroinvertebrates and vegetation structure were not often correlated with salmon density in our analysis (Table 1, Data S2). This suggests that proportional change in biomass between fall and spring may be a more reliable measure of the effect of salmon on stream invertebrates and biofilm, than simply measuring biomass during spawning in fall.

We found a range of immediate, seasonal, and legacy temporal effects of salmon density. Some studies reported that immediate positive nutrient effects of spawning were only temporary and not observed a few months before or after spawning (e.g., biofilm, Holtgrieve et al. 2010, and juvenile coho salmon, Nelson and Reynolds 2014). Other studies found longer-term benefits of high salmon densities in the following spring or summer after spawning, such as faster growth (Nelson

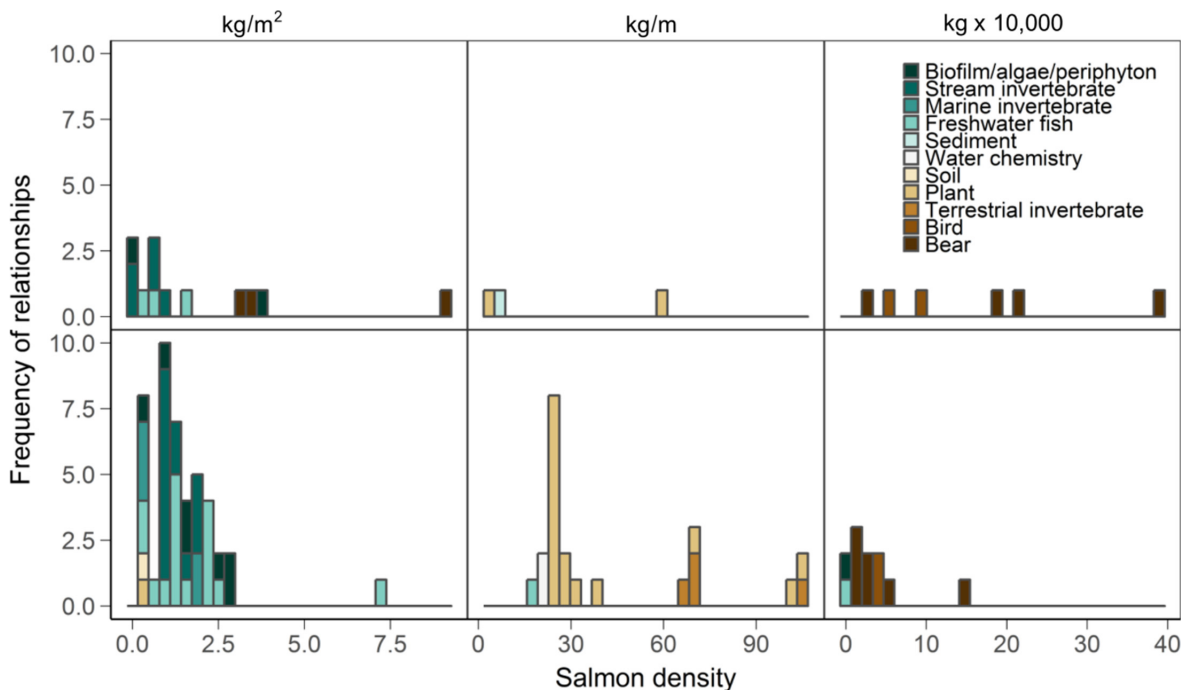
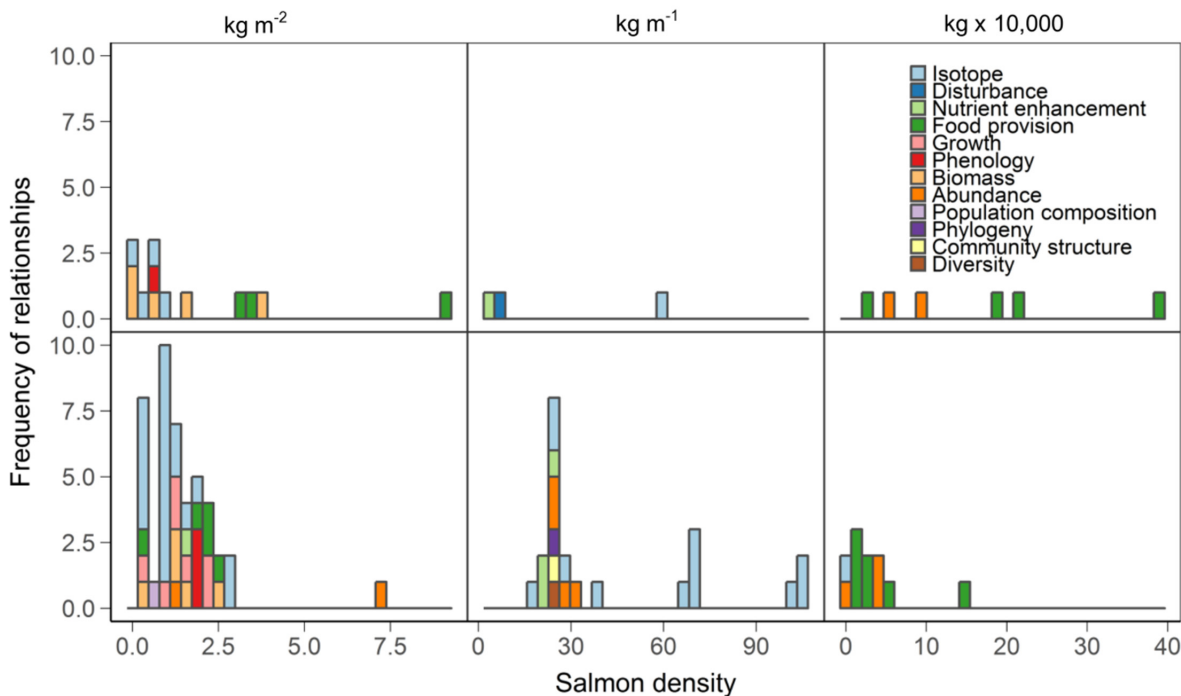
(a) Taxonomic group**(b) Ecological response**

FIG. 7. Histograms showing the salmon densities (or abundances) required to reach 90% of the maximum ecological or isotopic responses across all data sets, where the best model was an asymptotic function (top panels, $n = 22$) and where the best model was a linear or convex function (bottom panels, $n = 79$): (a) Showing distribution across taxonomic groups or abiotic factors; (b) Showing distribution across types of ecological or isotopic response. Relationships with null responses are not shown ($n = 71$). Relationships are presented in the unit of salmon density used in the original studies (kg, kg/m, and kg/m²).

and Reynolds 2015), and increases in freshwater fish populations (Swain and Reynolds 2015). Finally, longer-term responses such as changes in habitat and vegetation structure could take multiple years to be observed (Hocking and Reynolds 2011) and would be influenced by accumulation of nutrients from salmon and other sources in the soil.

Implications for ecosystem-based management

Ideally, decision makers would have information about how many salmon are required to maintain—or restore—structure and function in stream and riparian ecosystems, and the ecological, social, and economic consequences of different management scenarios. The substantial variation we observed in the shapes, directions, and thresholds among ecological or isotopic responses demonstrates that ecosystem-based management requires more than blanket assumptions about how ecological processes respond to nutrient subsidies and disturbance from salmon.

Some of the relationships and thresholds we have quantified in this study could be used as starting points to guide ecosystem-based fisheries management targets. Bears have been suggested as good indicators for ecosystem-based management, because they are top predators, have large home ranges, and are culturally important (Hilderbrand et al. 2004, Levi et al. 2012, Housty et al. 2014). Our results confirm that they require some of the highest densities of salmon to reach their maximum number of fish killed (9.2 kg/m^2 of salmon). As apex predators, this suggests that the lower nutrient requirements of other species may be accounted for, if ecosystem-based management targets focus on bears. This synthesis shows that freshwater fish or birds are also potential indicator species, given their relatively consistent ecological responses to increases in salmon density (Fig. 7).

However, the aim of ecosystem-based management is not to maximize responses for all possible taxonomic groups, but to understand trade-offs between different ecological scenarios. Alternatively, indicators across taxonomic groups at different trophic levels could be chosen (e.g., bears, freshwater fish, birds, and invertebrates), in combination with indicators with consistently steep curves that quickly detect large ecological changes (e.g., proportional decrease in stream invertebrate or algal biomass between spring and peak salmon spawning—Figs. 6, 7). The salmon densities required to reach these 90% thresholds would be $2.7\text{--}3.8 \text{ kg/m}^2$ for algal biomass ($n = 2$ relationships from two studies), and an average 0.6 kg/m^2 across stream invertebrate taxa ($SD = 0.6$, $n = 5$ relationships from one study; Data S2). Even for the relationships with consistent shapes and directions, the densities of salmon that are associated with an ecological threshold are likely to vary over space and time. When setting regional ecosystem benchmarks, this variation could be accounted for by using models that predict

how the salmon thresholds would change under different environmental conditions, or by applying large precautionary buffers to benchmarks.

Ultimately, appropriate indicators for ecosystem-based management would be those that have consistent asymptotic relationships with salmon densities (i.e., a predictable shape, direction, and corresponding salmon threshold over space and time); are simple, easy, and cheap to measure; and provide precautionary salmon density thresholds that would represent other important ecosystem components or functions. Several knowledge gaps and shortcomings of existing studies make it difficult to assess whether the ecological relationships presented within this study would be the most suitable indicators. We discuss how these challenges could be improved in future research.

First, the response variables used in past studies may not be the most appropriate metrics for assessing ecological thresholds associated with salmon densities. Isotopic concentrations were the most common response variables, even though they may not reflect ecosystem function, structure, or condition and are not likely to be relevant when developing ecosystem-based metrics and indicators. Freshwater fish were the only taxonomic group that had studies measuring metrics relevant for mechanistic population modeling, such as growth and mortality (Fig. 1). New research might focus on how salmon density affects ecological responses that are relevant to management decisions, such as biomass, abundance, growth, survival, diversity of species, and ecosystem-level processes, such as the resilience and functioning of nutrient cycles and other ecosystem services. Studies that estimate the influence of salmon density on growth parameters and population abundance for producers and consumers could provide more appropriate metrics to predict the ecological impacts of salmon fisheries and other management strategies.

Second, most studies in this review were observational, where comparisons are made across streams with different salmon densities. These correlational studies make it difficult to determine if confounding variables are driving salmon density and responses of other taxonomic groups. For almost half of all the relationships included in this analysis (45%, 78 of 172), the salmon density had been tested alongside covariates in a statistical model in the original studies. Salmon was one of the important explanatory variables (i.e., in top model/s) in 94% of these relationships, though publication bias may affect this result. Path analyses could be an alternative method to evaluate the causality of the relationships between salmon and their environments, while accounting for other confounding factors, such as hydrology, nutrient cycling, and other environmental variables influencing the forest and stream biota. Quasi-experimental designs such as matching analyses, or within-stream above/below waterfall comparisons may provide suitable control streams to reduce the effect of confounding factors (Janetski et al. 2009).

Third, it is unclear how the saturating thresholds across the different units of salmon density or abundance (kg, kg/m, kg/m²) can be compared. Their applicability across different catchments should be verified before they are incorporated into management decisions. Salmon thresholds measured as total abundance (kg) need to be converted to a density before extrapolating to other regions, as most ecological responses would be relative to the size of the stream or river. For example, many of the bear studies measured salmon density as total biomass (kg) along a stream (Fig. 7, right panels), rather than salmon density (kg/m²), making it challenging to convert these thresholds into meaningful numbers for ecosystem-based management targets. Although total salmon abundance may be an appropriate unit for an original study, we recommend that raw data for each stream, such as stream width and length and other covariates, are routinely published, so that the salmon density measures can be calculated if required.

Other knowledge gaps include geographic distribution of studies and possible interactions between ecological components. Most studies that were eligible for inclusion in our analysis were conducted on the central coast of British Columbia and in Alaska. Several studies from Japan, Washington, Idaho, and Oregon were excluded. This geographic bias is confounded by the large declines of salmon and higher urban development in the United States outside Alaska, making it difficult to estimate the potential loss of ecosystem composition, structure, and function that has already occurred in these regions. Very few studies focused on interactions (e.g., between salmon density, bears, and soil nutrient cycles; Holtgrieve et al. 2009), trophic cascades (as shown by Klemmer and Richardson 2013), or behavioral or evolutionary changes. These could be avenues of future research.

Caveats and limitations

The correlative relationships included in this review are inherently biased towards ecological and isotopic responses that are of interest or are easy to measure. We can expect a bias towards publishing positive results, and therefore, many nonresults (i.e., null relationships) or negative results are likely to have been excluded from this synthesis. The covariates that were found to influence the salmon–ecological responses significantly in the original studies could not be included in a systematic way in this study, making it difficult to incorporate potentially confounding factors, such as slope of bank, watershed, or catchment area or stream width, and capacity of the stream to retain carcasses. This may be a potential reason why 41% of the tested relationships found no effect of salmon (i.e., the null model had the lowest AIC_c). Other reasons for the high number of null relationships could be that the response variables may genuinely not be sensitive to salmon densities, the range of salmon densities tested were not high enough to cause an effect, or we may have been unable to detect an effect because of low power.

Finally, the large number of studies included in our synthesis led us to automate many of the modeling steps, which precluded accounting for different variance structures, covariates, random effects, or model sensitivity, and may not have produced optimal models. As the raw data were not available, we used the published means, digitized from figures, which excluded any measures of variation shown by confidence intervals in the original studies.

CONCLUSION

Our review illustrates the complexities associated with setting targets for ecosystem-based fisheries management and demonstrates why quantifying the shape, direction, and steepness of the salmon–ecological relationships across terrestrial and aquatic ecosystems is crucial when choosing appropriate indicators and benchmarks. There is no simple answer to the question of how many salmon a stream needs. Instead, indicators could focus on specific ecosystem components that require high salmon densities to reach saturation, are valued by society, and are easy to measure and adapt across time and space. This review provides a summary of the diversity of salmon–ecological relationships studied to date, and it highlights some potential indicators that decision makers could use (such as bear food consumption) when setting fisheries targets to maintain or enhance overall functioning of coastal ecosystems. In addition, we show that nonlinear relationships need to be accounted for when determining the extent of ecological (and indirectly social and economic) trade-offs of ecosystem-based management.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3060/supinfo>