Received: 21 February 2023 | Revised: 19 June 2023 | Accepted: 26 June 2023
DOI: 10.1111/fme.12643

REVIEW

Fisheries Management and Ecology WILEY

A global synthesis of peer-reviewed research on the effects of hatchery salmonids on wild salmonids

John R. McMillan[1] | Brian Morrison[2] | Nick Chambers[3] | Greg Ruggerone[4] | Louis Bernatchez[5] | Jack Stanford[6] | Helen Neville[1]

[1]Trout Unlimited, Arlington, Virginia, USA
[2]Brian Morrison Consulting, Peterborough, Ontario, Canada
[3]School of Aquatic & Fishery Sciences, University of Washington, Seattle, Washington, USA
[4]Natural Resources Consultants, Seattle, Washington, USA
[5]IBIS (Institut de Biologie Intégrative et des Systèmes), Université Laval, Québec City, Québec, Canada
[6]Flathead Lake Biological Station, University of Montana, Polson, Montana, USA

Correspondence
John R. McMillan, The Conservation Angler, 16430 72nd Ave W, Edmonds, WA 98026, USA.
Email: john@theconservationangler.org

Abstract
Hatcheries have long produced salmonids for fisheries and mitigation, though their widespread use is increasingly controversial because of potential impacts to wild salmonids. We conducted a global literature search of peer-reviewed publications (1970–2021) evaluating how hatchery salmonids affected wild salmonids, developed a publicly available database, and synthesized results. Two hundred six publications met our search criteria, with 83% reporting adverse/minimally adverse effects on wild salmonids. Adverse genetic effects on diversity were most common, followed by effects on productivity and abundance via ecological and genetic processes. Few publications (3%) reported beneficial hatchery effects on wild salmonids, nearly all from intensive recovery programs used to bolster highly depleted wild populations. Our review suggests hatcheries commonly have adverse impacts on wild salmonids in freshwater and marine environments. Future research on less studied effects—such as epigenetics—could improve knowledge and management of the full extent of hatchery impacts.

KEYWORDS
artificial propagation, hatchery salmonids, hatchery supplementation, salmonid captive-breeding, salmonid enhancement, salmonid stocking

1 | INTRODUCTION

For over one hundred years, hatcheries have been used to propagate and release salmonids across the globe (Jonsson, 1997; Waples, 1991; Zaporozhets & Zaporozhets, 2004), largely to subsidize fisheries, attempt to mitigate for habitat loss and overexploitation (Araki & Schmid, 2010; Hilborn, 1992; Maynard & Trial, 2014) and, more recently, to try to rebuild depleted populations of wild salmonids (Berejikian & Van Doornik, 2018; Hagen et al., 2021; Hess et al., 2012). Hatchery salmonids currently underpin many recreational, commercial, and (in the lower-48 of the United States in particular) legally obligated mitigation and tribal treaty fisheries, but the pervasive reliance on hatcheries remains contentious (Claussen & Philipp, 2022; Harrison et al., 2019; Kleiss, 2004). Although there is substantial evidence that hatchery salmonids generally have lower relative fitness than wild salmonids (Bouchard et al., 2022; Christie et al., 2014; Milot et al., 2013), continuing debate centers on the broad potential effects of releasing hatchery salmonids into nature and their potential impacts on sympatric wild salmonids (see Section 2 and Figure 1 for the definition of effect and impact), particularly when it comes to recovery of threatened and endangered populations (Araki & Schmid, 2010; Paquet et al., 2011; Young, 2013).

Evaluating and synthesizing the breadth of potential hatchery effects is complicated, however, because results may depend on several factors. For instance, while adverse effects on wild salmonids have been commonly reported, others have found beneficial effects (Maynard & Trial, 2014; Miller et al., 1990; Naish et al., 2007), and publications cover a range of potential effects on different "Viable Salmonid Population parameters" (VSP: McElhany et al., 2000)—distribution (Laffaille, 2011), diversity (Bernaś et al., 2014), abundance (Willmes et al., 2018), and productivity of wild salmonids (Nickelson, 2003)—that may occur through different pathways such as ecological or genetic processes (Allendorf, 1991; Flagg et al., 2000; Neff et al., 2011), disease (Lamaze et al., 2014), or fishing (Hilborn & Eggers, 2000; Naish et al., 2007). Further, responses can differ among species (Araki & Schmid, 2010); the existing body of literature encompasses numerous salmonid species, and within species, there can be very different life histories such as individuals that migrate to the ocean and back (anadromous) or remain and mature in freshwater (resident) (Gossieaux et al., 2019; Maynard & Trial, 2014; Naish et al., 2007).

The source broodstock and intent of the hatchery program could also influence the type and magnitude of effects on wild fish. Traditional "production" type hatchery programs generally breed only hatchery individuals, often from a non-local source, and stock them to provide fisheries, and consequently, their effects could differ from modern "supplementation" programs that integrate some wild fish into their broodstock (to reduce genetic impacts) and release fish to enhance fisheries and the number of naturally spawning adults (Araki & Schmid, 2010; HSRG, 2015; Naish et al., 2007, Table 1). Moreover, smaller-scale "recovery" programs, including some captive breeding efforts, that rely solely on wild fish as broodstock to provide a short-term, conservation boost to highly depleted wild populations (Berejikian & Van Doornik, 2018; Janowitz-Koch et al., 2019) may offer more conservation benefits to wild salmonids than longer running supplementation programs that try to achieve multiple goals (Bowlby & Gibson, 2011; Naish et al., 2007).

Finally, large releases of hatchery salmonids also raise the potential for ecological effects in the North Pacific Ocean (Ruggerone & Irvine, 2018). An emerging body of research suggests hatchery salmon have triggered density-dependent responses in several co-mingling populations of wild salmonids, including but not limited to, reduced survival (Fukuwaka & Suzuki, 2000; Cunningham et al., 2018), growth (Kaeriyama et al., 2011), fecundity (Shaul & Geiger, 2016), and body size and abundance (Ruggerone et al., 2012).

The immense body of literature makes it difficult to interpret the information and results succinctly (Araki & Schmid, 2010). Research on the potential effects of hatchery salmonids on wild salmonids dates to the early-1900s and spans numerous species and three continents (Jonsson, 1997; Lichatowich, 2001; Maynard & Trial, 2014; Zaporozhets & Zaporozhets, 2004). In practice, scientists, managers, and policymakers may be familiar with studies in their region and on species they are tasked with managing and conserving but may be unaware of research outside their immediate scope of focus. For example, there have been numerous hatchery studies on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) that commonly reference one another (Horreo et al., 2014; Nilsson et al., 2008) and there are several publications on brook charr (*Salvelinus fontinalis*) (Bruce et al., 2020; Létourneau et al., 2018; Marie et al., 2010), yet those results are rarely cited or utilized in research on Pacific Salmon and vice-versa (e.g., Tatara & Berejikian, 2012; Wang et al., 2002). Accordingly, while several studies have reviewed hatchery effects on wild salmonids (Fraser, 2008; Naish et al., 2007), few have covered both *Oncorhynchus* and *Salmo* spp. (e.g., Araki & Schmid, 2010; Maynard & Trial, 2014), and to our knowledge, none have attempted to account for the entire breadth of publications for all species across the globe from freshwater to the ocean.

An evaluation of the overall body of peer-reviewed literature seems particularly valuable given the ongoing debate over hatchery practices in the western United States and other regions where salmonid recovery efforts are underway. A synthesis of publications from across the globe, covering various species and spanning freshwater and saltwater ecosystems would consolidate a broad array of literature and findings, and offer comprehensive insight into the patterns and processes of how hatchery salmonids potentially affect wild salmonids (Figure 1). For example, a synthesis could help determine: (1) How many studies have been published and how is the research distributed by year, country, species, and life history? (2) What proportion of publications reported adverse or beneficial hatchery effects on wild fish and how did those results vary by year, country, species, and life history? (3) Do potential effects differ based on the type of hatchery program? (4) Which VSP parameters (abundance, productivity, diversity, spatial distribution: McElhany et al., 2000) are most affected and what are the most common pathways of hatchery influence, such as genetic or ecological processes? and, (5) How many publications have evaluated potential hatchery effects in the open ocean and what are the general results so far? In turn, such an effort would help illuminate gaps in knowledge and areas for future research, increase the breadth of information available to decision-makers, and improve opportunities for collaborative research among scientists across different regions and countries.

2 | METHODS AND SYNTHESIS

2.1 | Objective and focus

Our objective was to collate all relevant peer-reviewed publications from across the globe and synthesize the main results—as presented by the authors—to answer broad-scale questions that are important to those tasked with researching, managing, and conserving salmonids (Figure 1). We also sought to incorporate the publications into an easily accessible database that can serve as a standing resource and be updated by scientists as new information comes to light (Appendix S1). In this effort, we reviewed only publications that explicitly and quantitatively evaluated whether stocking of hatchery salmonids affected the diversity, abundance, productivity (including effects on growth and survival as components of productivity), and distribution of wild salmonids via genetics, ecology, fishing, or disease (e.g., Berejikian & Van

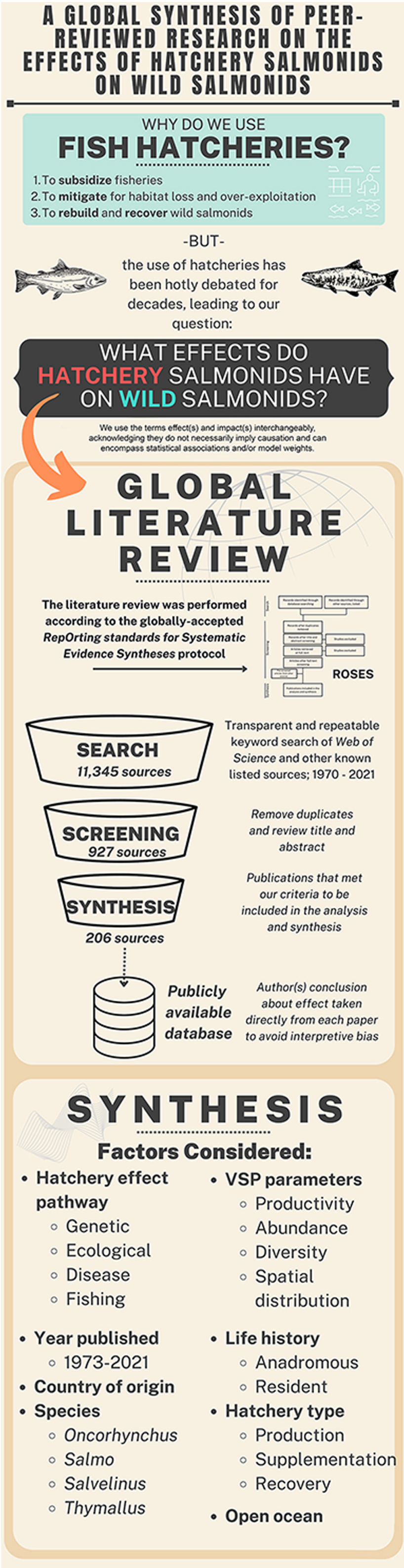

FIGURE 1 Infographic displaying the rationale for the synthesis of research on how hatchery salmonids affect wild salmonids, how we define the terms effect(s) and impact(s), the literature search process, and the factors we considered when evaluating results from each publication. Although we identified 206 total publications, there are 207 total entries because Levin and Williams (2002) was counted twice, once for an adverse effect and once for no effect.

Doornik, 2018; Reisenbichler & Rubin, 1999). We did not seek to review publications that only compared *differences* between hatchery and wild salmonids, such as studies on the relative fitness of hatchery and wild individuals (e.g., Christie et al., 2014) unless the research also directly evaluated whether those effects influenced the recipient wild population of salmonids (e.g., Araki et al., 2009). Similarly, though epigenetic influences (i.e., effects arising through altered gene expression rather than changes to the genetic code) are increasingly recognized as important mechanisms for domestication (Le Luyer et al., 2017), we did not include epigenetic studies here because so far they have not directly addressed impacts to VSP characteristics in wild populations (but see Section 4 for emphasis that this topic deserves greater attention, and future iterations of our database will incorporate relevant studies as they become available). Ours was not a formal meta-analysis of quantitative effects, nor an assessment of fisheries that hatcheries can provide unless the study also examined whether fisheries potentially affected wild salmonids. Last, we use the terms effect(s) and impact(s) interchangeably, acknowledging they do not necessarily imply causation and can encompass statistical associations and/or model weights.

2.2 | Literature search

We conducted a literature search of peer-reviewed global publications focused only on research that directly evaluated how releases of hatchery salmonids potentially affected VSP characteristics of wild salmonids (*Oncorhynchus*, *Salmo*, *Salvelinus*, *Thymallus*) living in nature. We did not find any relevant literature on *Hucho or Coregoninae*. We used a modified search strategy based on guidelines from the Collaboration for Environmental Evidence for conducting a literature synthesis (Haddaway et al., 2018; Pullin et al., 2022: Figure 2). We started our search date with 1970 because preliminary searches found few publications prior to 1970 that matched our criteria (Table 2). Primary publications from 1970 (capturing a ramping up of searchable, relevant research) through May 29, 2021, were discovered via two English language searches in Web of Science (WOS) (Figure 2). We then reviewed a broad suite of publications to identify appropriate search terms that were relevant to our topic of interest and covered the array of descriptors used to characterize potential effects of hatchery salmonids on wild salmonids. Based on this foundation, we conducted a topic search (TS) using the descriptors: TS=(((hatcher* OR supplement* OR stock* OR enhance* OR artificial production* OR captive born OR introduced) AND (salmon* OR salmoni* OR steelhead OR char OR trout OR Oncorhynchus OR Salvelinus OR Salmo OR Grayling)) AND (effect* OR affect* OR outcome* OR respon* OR result* OR reestablish* OR restor* OR recover* OR collaps* OR influence* OR impact* OR chang* OR alter* OR increas* OR decrease* OR strength* OR weak* OR prevent* OR eliminat* OR assist* OR improv* OR reduc* OR replace* OR benefit* OR differ* OR consequenc* OR implicat* OR contribut* OR compensat* OR imped*

TABLE 1 Definition, description, and alternative terms used to classify different types of hatchery programs found in the literature review.

Hatchery type	Source of broodstock	Intent	Also referred to as
Production	Uses all or nearly all hatchery fish for broodstock, often but not always founded on non-local or non-native stock	Produce fish to support fisheries; rarely have conservation intent	Traditional, stocking, planting, releasing, supplementation, ocean ranching
Supplementation	Uses a proportion of wild fish as broodstock to help integrate hatchery and wild gene pool	Enhance fishery and supplement wild/natural populations, often run indefinitely	Supplementation, enhancement, conservation, supportive breeding
Recovery	Uses all or almost all wild fish for broodstock to fully integrate hatchery and wild gene pool	Rebuild wild populations by providing boost in abundance, sometimes no fishery focus, and temporary	Supplementation, enhancement, supportive breeding, captive breeding, conservation

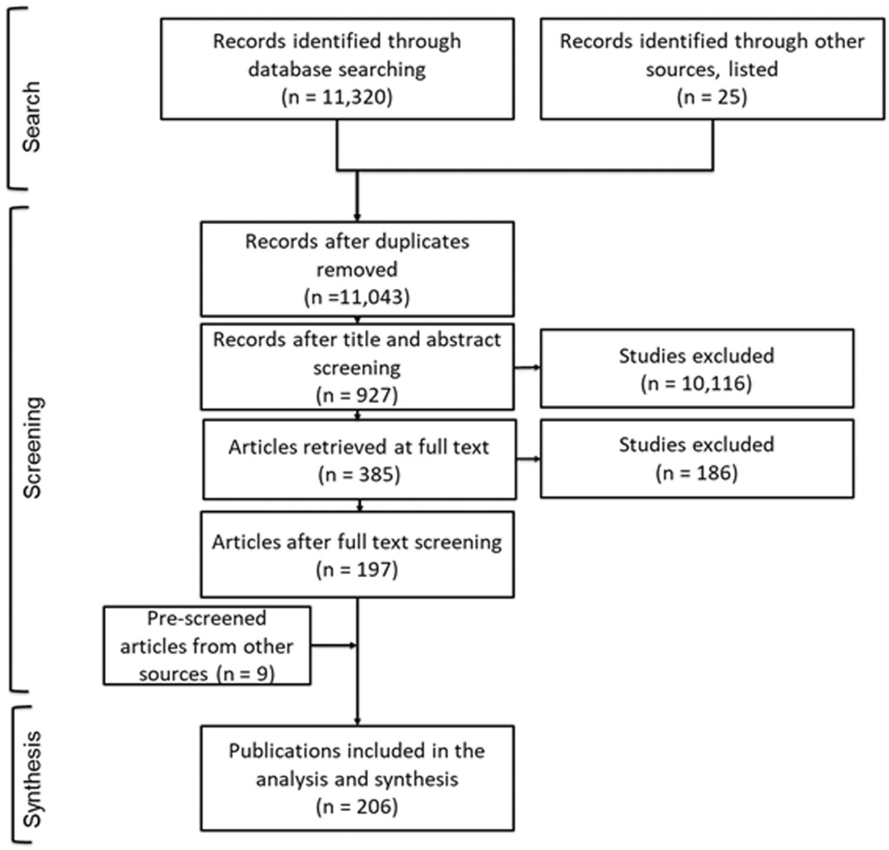

FIGURE 2 Flow diagram of the literature review process based on ROSES (RepOrting standards for Systematic Evidence Syntheses) flow diagram for systematic reviews (Collaboration for Environmental Evidence, 2018).

OR threat* OR caus* OR mask*) AND (gene* OR competition OR divers* OR producti* OR distribut* OR abundan* OR fitness OR demograph* OR evolution* OR ecolog* OR diverge* OR introgress* OR integrity* OR structure* OR life histor* OR portfolio OR size OR tim* OR space* OR spatial* OR densit* OR density dependen* OR growth OR surviv* OR predat* OR composit* OR interbreed* OR status OR trend OR hybrid* OR biomass OR disease* OR rate OR duration OR resilien* OR habitat* OR interspecific OR intraspecific OR regime OR manage*)). Next, we conducted a title search (TI) in WOS using the same descriptors.

2.3 | Selection process and criteria for inclusion

The WOS search revealed 11,320 potential publications, including 10,867 in the topic search and 453 in the title search (Figure 1). Following the decision tree outlined in Figure 2, duplicates were removed, and titles and abstracts were screened manually to identify publications that met the criteria to be eligible for our review (Table 2). To be included, first, the publication had to have been peer-reviewed and provide empirical data or a model that evaluated whether hatchery salmonids, via genetics, ecology,

TABLE 2 Criteria for inclusion of publications found during the search, including the type and year of the publication, hatchery type, the study focus, and review articles.

Criteria	Include	Exclude
Publication and years	Peer-reviewed in primary literature; 1970–2021	Non-peer-reviewed; prior to 1970
Hatchery type	Any production, supplementation, or recovery hatchery where fish are purposely released into nature	Net-pens where fish are not purposely released into nature
Study focus	Examined genetic, ecological, fishing, and/or disease effects of hatchery salmonids on wild salmonid abundance, productivity, diversity, and distribution	Examined how hatchery rearing and production affected wild salmonid performance, behavior, and traits (e.g., fitness of wild fish vs. hatchery fish)
Review publications	Contain new analyses, previously unpublished data	Summarize existing publications, no new analyses and/or data

TABLE 3 The sub-set of information for each publication that we used in our synthesis and summaries.

Attribute	Definition and/or classification
Year	Year study was published
Location	State, province, country of research
Hatchery species	Species of salmonid(s) that were studied
Life history	Did study focus on anadromous or freshwater resident (including freshwater migratory) species, or both
Habitat	Denotes whether study was conducted in freshwater or ocean or both
Hatchery type and intent	Hatchery classified as production, supplementation, recovery, or a combination thereof based on criteria in Table 1
Hatchery effect pathway	Denotes whether study examines, (1) genetic, (2) ecological, (3) fishing, or (4) disease effects, or combination thereof, on wild fish due to the presence of hatchery fish
Viable Salmonid Population parameter	Denotes whether study evaluates productivity, abundance, diversity, spatial distribution, or combination thereof
Genetic effect	Denotes which genetic attribute was analyzed, including diversity, population structure, effective population size, or a combination thereof
Effect on wild fish	Denotes whether hatchery effect on wild fish is adverse, minimally adverse, indeterminate, beneficial, or no effect if authors did not find any statistically significant effect

Note: See Table S1 in Appendix S1 for full description of all information included in the entire database.

fishing, or disease (i.e., hatchery effect process: Table 3), influenced VSP parameters that are fundamental to the viability of wild salmonids (McElhany et al., 2000). This also included publications that examined intra- and inter-species impacts of large releases of hatchery salmonids into the North Pacific Ocean (e.g., Frost et al., 2020; Ruggerone et al., 2012). Second, publications had to focus on hatchery programs that purposefully released fish into nature for fishing or conservation or both; we excluded publications on the effects of farmed salmon raised in net pens for direct consumption. Third, the search revealed numerous review articles. To minimize potential duplication, we only included reviews that contained new data or new analysis of previously collected data. Fourth, we excluded studies on inter-species impacts of introduced non-native resident salmonids, such as effects of non-native hatchery rainbow trout (*O. mykiss*) on native cutthroat trout (*O. clarkii*) in the United States' Intermountain West, because those results are clearly understood to be negative (Dunham et al., 2004; Hansen et al., 2019; Seiler & Keeley, 2009). Last, after reviewing papers on potential effects of hatchery salmonids in the open ocean, we identified and included an additional nine publications that were not found in the formal literature review (Figure 2).

2.4 | Classification and database of publications

We reviewed the full text of every publication that met our criteria with a strong focus on information that was most relevant to our synthesis, such as the study questions, the location and description of the hatchery programs, and the results of potential impacts on wild salmonids. Next, each publication was entered into a database created in R Core Team (2022), provided in Appendix S1, and classified according to several relevant basic attributes so that each article entry includes associated columns with the authors, year, journal, DOI, the abstract, country, hatchery species, species interaction (e.g., intra- or inter-species hatchery effect), habitat (freshwater or ocean), life history (anadromous or freshwater resident or both), and study approach, which denoted whether it was an observation, model, experiment, or combination thereof (Table S1), but we only used a subset of these attributes in our analysis (Table 3).

We then classified the hatchery type and intent as production, supplementation, or recovery because previous studies (e.g., Berejikian & Van Doornik, 2018; Bingham et al., 2014; Bowlby & Gibson, 2011) and reviews (Araki & Schmid, 2010; Maynard & Trial, 2014; Naish et al., 2007) suggest potential effects on wild salmonids may vary in relation to the goal and broodstock sources of the hatchery program. We used criteria in Table 1 to define: (a) production hatcheries as those that solely or mostly use hatchery fish for broodstock, often but not always consisting of non-local or non-native strains, to produce fish for fisheries; (b) supplementation hatcheries as those that use a mixture of wild and hatchery fish for broodstock to improve genetic integration of the two populations and produce fish both to enhance fisheries and supplement natural spawners (e.g., Naish et al., 2007); (c) recovery hatcheries as those that use all or almost all wild fish for broodstock, including some captive brood programs, and produce fish solely to rebuild depleted stocks of wild salmonids (e.g., Berejikian & Van Doornik, 2018). Less commonly, we classified studies as including a combination of the different types of hatchery programs, such as Chilcote et al. (2011) which evaluated multiple stocks with a mixture of supplementation and production hatcheries.

Classifying the hatchery types was not always clear-cut, however. For instance, some publications used the term supplementation to describe the intent of hatchery programs that used non-local strains to "supplement" fisheries (e.g., Baer & Brinker, 2010; Baillie et al., 2016). Because they used non-local stocks and the hatchery releases were focused on production for fisheries, we classified them as production programs to be consistent with our criteria. In others, it was not clear from where the hatchery brood originated, but it was clear the focus was on fisheries (e.g., Hilborn & Eggers, 2000). Accordingly, we were cautious when classifying publications as supplementation programs unless there was sufficient information on the source of broodstock and intent (e.g., Fernández-Cebrián et al., 2014).

Next, we recorded the pathway of hatchery effect (i.e., genetic, ecological, fishing, disease) and VSP parameter(s) studied. Given the number of genetic publications on diversity, we further classified those studies according to the attribute that was analyzed, including diversity (e.g., Williamson & May, 2005), genetic population structure (e.g., Bruce et al., 2020), effective population size (e.g., Berejikian & Van Doornik, 2018), or a combination thereof such as both population structure and effective population size (e.g., Almodóvar et al., 2020).

We classified the hatchery effect on wild salmonids as adverse, minimally adverse, indeterminate, no effect, or beneficial (Table 3). To avoid any interpretative bias, we recorded the effect(s) directly as declared by the author(s). *Adverse and beneficial* refer to publications where the hatchery effect was determined by the authors to be harmful or helpful to the wild population, respectively. Adverse effects could include but are not limited to evidence of reduced productivity or abundance (e.g., Chilcote et al., 2011), or reduced diversity (e.g., Williamson & May, 2005) via unintended genetic introgression with hatchery fish (e.g., Cordes et al., 2006) or reduced effective population size (e.g., Gossieaux et al., 2019). Beneficial could denote effects such as evidence of increased effective population size (e.g., Hedrick et al., 1995), a demographic boost (e.g., Janowitz-Koch et al., 2019), or increased diversity and abundance from a critical level (e.g., Berejikian & Van Doornik, 2018). *Minimally adverse* refers to publications that found some negative effects on wild fish, but where those negative effects were inconsistent or explicitly reported by the authors as being minimal or slight (e.g., Finnegan & Stevens, 2008), while *indeterminate* refers to publications where both negative and positive effects were found (e.g., Small et al., 2009). *No effect* means the authors did not find a statistically significant effect for their measurement of choice (e.g., Wishard et al., 1984).

Last, we included an *effect summary*, a single sentence that encapsulated how the hatchery effects impacted the wild fish in relation to the VSP parameter(s) of interest. For instance, an effect summary could conclude that hatchery salmonids had a beneficial effect on the wild populations via increased genetic diversity (Berejikian & Van Doornik, 2018) or an adverse effect due to decreased genetic diversity (Bernaś et al., 2014).

2.5 | Questions and synthesis of information

After consolidating the research into a database, we synthesized the distribution of publications from 1970 to 2021 to summarize existing knowledge about how hatchery salmonids affect wild salmonids in freshwater and marine environments across the globe. Although the database contains a range of information which we provide in Appendix S1, hereafter we focus our analysis and results on five specific objectives:

1. To understand how the research effort was distributed, we first summed the total number of publications by year, country, species, habitat type, and life history.
2. Second, to synthesize the overall body of literature on hatchery effects on wild salmonids we summed the number of publications that reported adverse, minimally adverse, indeterminate, no effect, or beneficial effects on wild salmonids, and then calculated the proportion of different potential hatchery effects by year, country, species, and life history.
3. Third, we calculated the proportion of studies for each hatchery effect in relation to the hatchery's source of broodstock and

intent, which was classified as production, supplementation, recovery, or a combination thereof.

4. Fourth, to understand the potential ways hatchery fish impacted wild salmonids, for each hatchery effect we summed the number of publications in relation to the processes that contributed to the hatchery effect (genetic, ecological, fishing, disease, or a combination thereof), the affected VSP parameters (productivity, diversity, spatial distribution, and abundance, or a combination thereof), and if relevant, the type of genetic effect (diversity, population structure, effective population size, or a combination thereof).
5. Fifth, we tallied the number of publications that evaluated hatchery effects in the ocean and summarized the general results.

After evaluating those results, we identified potential data gaps and highlighted areas for future research in the Section 4.

3 | RESULTS

3.1 | Number of publications and database

After eliminating duplicates and reviewing titles, abstracts, and then full papers, we identified 206 relevant articles published between 1970 and 2021 (Figure 2). The literature search accounted for 197 of the publications, while nine studies in the ocean were identified through citations in other publications. One publication, Levin and Williams (2002), was counted twice in each component of the synthesis because the authors found adverse effects on one species and no effects on another; hence, hereafter we refer to 207 as the number of publications. The articles cover a wide range of observational studies, models, and experiments focused on *Oncorhynchus*, *Salmo*, *Salvelinus*, *and Thymallus* species in North America, Europe, and Asia. We also identified 50 review publications on the effects of hatchery fish on wild fish that could provide useful context and discussion points for this synthesis, though only four (Hilborn & Eggers, 2000; Naman & Sharpe, 2011; Ruggerone & Nielsen, 2004; Zaporozhets & Zaporozhets, 2004) provided new data and were therefore included in our synthesis (Appendix S1).

3.2 | Distribution of research by year, country, species, habitat, and life history

Our summary of publications revealed several results about how research was distributed in relation to several factors ranging from time to VSP parameters. First, the number of publications on the effects of hatchery salmonids on wild salmonids was unequal over time (Figure 3a). Publications per year steadily increased from 1973 and peaked at 15 publications in 2012, after which the number of publications per year slightly declined until the end of May 2021, when our search was concluded.

Second, we found publications from 22 different countries (Figure 3b). Among those, over half ($n=113$) of the results focused on salmonid populations in the USA, followed by 20 in Canada, 11 in France, and 10 apiece in Spain and Norway (Figure 3b). Three to five publications each were found for the UK, Switzerland, Sweden, Poland, Russia, and Denmark.

Third, publications covered 15 species; among those, brown trout were the most researched with 39 publications, followed by steelhead ($n=33$), Chinook salmon ($n=28$), and Atlantic salmon ($n=19$), compared to 14 publications on chum salmon, 11 on brook charr, and nine apiece on pink and coho salmon (Figure 3c). We also classified 11 studies as *Oncorhynchus* species, either because the analyses were not species-specific (e.g., Goodman, 2005) or they covered three or more species (e.g., Chilcote et al., 2011). One study was classified as Pacific salmon because they focused on multiple species of salmon in the ocean (Bigler et al., 1996), and we found two studies on grayling and one apiece for Amago salmon (*O. masou*), Arctic charr (*S. alpinus*), cutthroat trout, and golden trout.

Fourth, 181 studies evaluated hatchery effects occurring in freshwater, 23 in the ocean, and three were classified as both because they considered impacts in freshwater and the estuary (Levin & Williams, 2002; Nickelson, 2003). And, twice as many publications focused on anadromous life histories ($n=132$) compared to resident life histories ($n=64$), while only 12 publications included data on both life histories (Figure 3d).

3.3 | Synthesis and distribution of hatchery effects on wild salmonids

3.3.1 | All publications combined

Reported hatchery effects on wild salmonids ranged from adverse to beneficial, but the majority were adverse: 144 (70%) studies reported an adverse effect on wild salmonids and another 26 articles (13%) reported a minimally adverse effect (Figure 4). Thus, 83% of studies reported some degree of adverse effects from hatcheries on wild salmonids. Only seven publications (3%) reported beneficial effects of hatchery salmonids on wild salmonids, while 17 studies (8%) reported no hatchery effects on wild salmonids, and 13 (6%) were classified as indeterminate.

3.3.2 | Hatchery effects by year, country, species, and life history

Adverse or minimally adverse effects predominated the distribution of research across time, space, species, and life history. From 1970 through 2021, most publications each year reported adverse or minimally adverse effects on wild salmonids, except for 1994–1995 (Figure 3a). The first publication to report a beneficial hatchery effect occurred in 1995 followed by another publication in 2006,

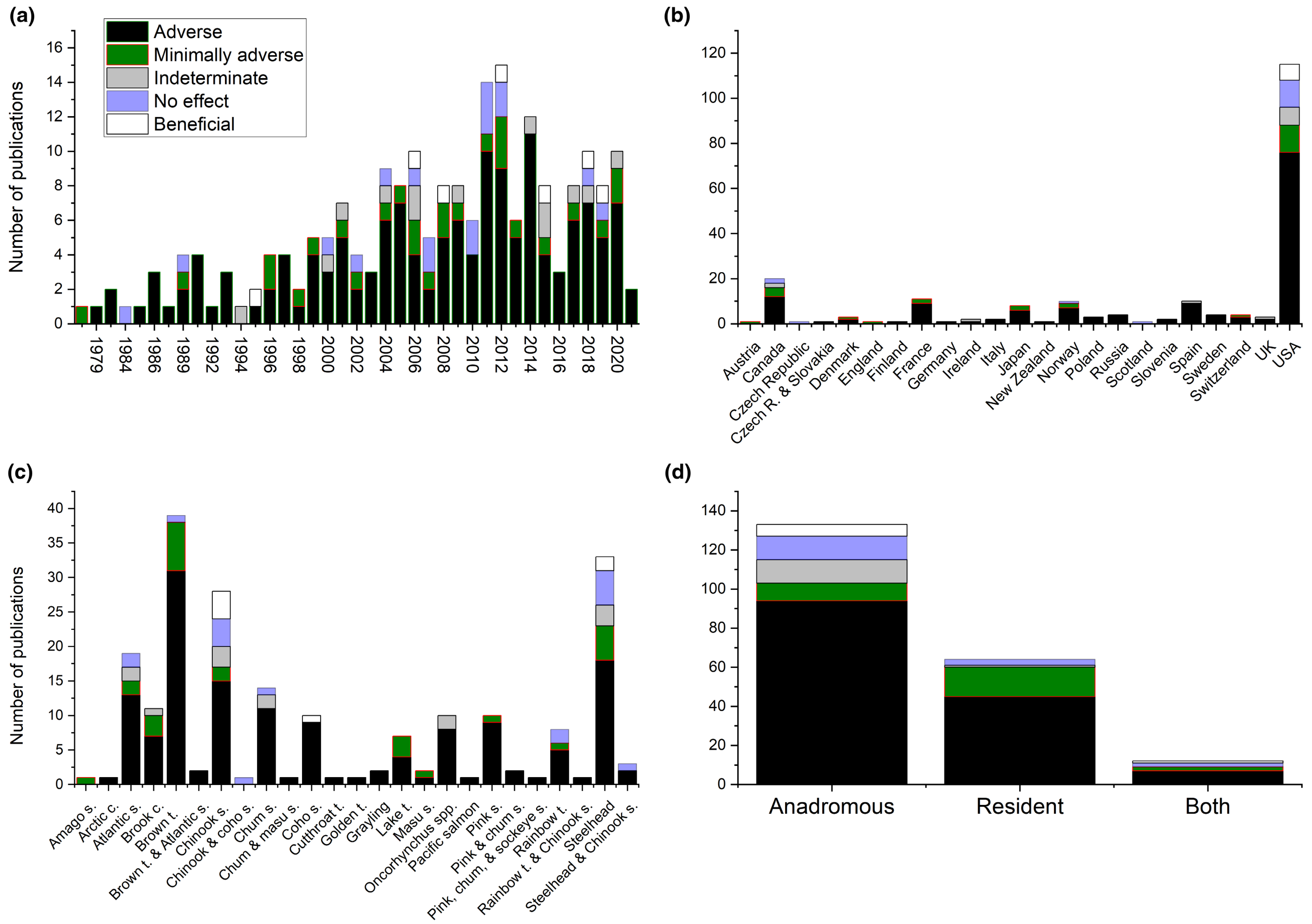

FIGURE 3 Distribution of publications by (a) year, (b) country, (c) species, and (d) life history in relation to the hatchery effect on wild fish, denoted as adverse, minimally adverse, indeterminate, no effect, or beneficial. Adverse and beneficial refer to publications where authors describe the hatchery effect as being negative or positive on the wild population, respectively. A minimally adverse effect refers to publications that found some negative effects on wild fish, but they were inconsistent, while indeterminate refers to publications where hatchery effects included aspects that had both negative and positive effects on the wild population or hatchery effects were almost immeasurable. No effect means that the authors did not find a significant hatchery effect on wild fish for the parameters they measured. In panel c., *Oncorhynchus* spp. refers to studies that focused on *Oncorhynchus* in general or included information on several species. There are 207 total entries because Levin and Williams (2002) was counted twice in each panel, once for an adverse effect on Chinook salmon and once for no effect on steelhead.

with the remaining five reports of beneficial effects being published thereafter as the number of publications increased.

Across the globe, 86 of 113 publications from the USA reported some type of adverse effect (adverse = 74, minimally adverse = 12), but it was also the only country to report beneficial effects (Figure 3b). In Canada and France, 12 of 20 studies and nine of 11 studies reported adverse effects, respectively, compared to nine of 10 in Spain and seven of 10 in Norway (Figure 3b). The Czech Republic and Scotland, with one study apiece finding no effect, were the only countries where an adverse or minimally adverse effect was not found, but overall, reports of no hatchery effect were rare outside North American countries.

For the most studied species, 37 of 38 brown trout publications reported adverse ($n = 31$) or minimally adverse hatchery effects ($n = 7$), compared to 17 of 28 for Chinook salmon (adverse = 15, minimally adverse = 2) and 15 of 19 studies on Atlantic salmon (adverse = 13, minimally adverse = 2: Figure 3c). For steelhead, 23 of 35 found adverse ($n = 18$) or minimally adverse effects ($n = 5$), including one study on "steelhead" from the Great Lakes where they are introduced (Bartron & Scribner, 2004); five of eight studies on resident rainbow trout also found adverse effects. Otherwise, 10 of 11 publications on brook charr and eight of nine each on pink and coho salmon reported adverse or minimally adverse effects, while beneficial hatchery effects were only reported for Chinook salmon, steelhead, and coho salmon.

Adverse and minimally adverse effects accounted for 102 of 132 publications on anadromous life histories and 60 of 64 publications on resident life histories (Figure 3d). Of the few publications that found a beneficial effect, six of seven were documented for the anadromous life history.

3.3.3 | Hatchery effect by hatchery type and intent

Most publications focused on production hatchery programs ($n = 143$) and more studies focused on supplementation programs ($n = 28$) than recovery programs ($n = 17$), while 19 studies accounted for a combination of production and supplementation hatcheries (Table 5). The proportion of studies reporting adverse effects on wild salmonids was 74% for production programs and 64% for supplementation programs. However, another 17% of the studies on production programs found minimally adverse impacts, while no minimally adverse effects were reported for supplementation programs (Table 5). On the contrary, 7% of the publications on supplementation programs found beneficial results and 17% indicated no effect, while 74% of the studies focused on both production and supplementation programs found adverse effects and 16% reported no effect.

For supplementation programs specifically, one publication reported a beneficial hatchery effect on abundance and productivity of natural-origin Chinook salmon (Fast et al., 2015) and another found releases of hatchery coho salmon increased abundance of naturally spawning fish without appearing to adversely affect wild productivity (Sharma et al., 2006). Nonetheless, adverse results from supplementation hatcheries were multiple and ranged from reduced diversity (Christie et al., 2012), productivity (Buhle et al., 2009), and abundance (Willmes et al., 2018) to altered run timing and spatial distribution (Hoffnagle et al., 2008).

The distribution of effects was more balanced for recovery programs, though the sample size was smaller (Table 5). Of the 17 studies on recovery hatcheries, the proportion of beneficial results (29%) was similar to the combined 30% of studies that found adverse (24%) and minimally adverse results (6%), respectively, while another 12% reported no effect and 29% were indeterminate. Of the five studies that reported beneficial effects from recovery hatcheries, four used all wild fish for broodstock, including two publications on the same long-term experiment on highly depleted populations of steelhead (Berejikian et al., 2008; Berejikian & Van Doornik, 2018) and the two on the same population of Chinook salmon (Hess et al., 2012; Janowitz-Koch et al., 2019). Adverse effects from recovery programs included decreased productivity in steelhead (Araki et al., 2009), reduced genetic structure (Lynch & O'Hely, 2001), and reduced diversity and productivity in Atlantic salmon (Bowlby & Gibson, 2011) and coho salmon (Willoughby & Christie, 2019).

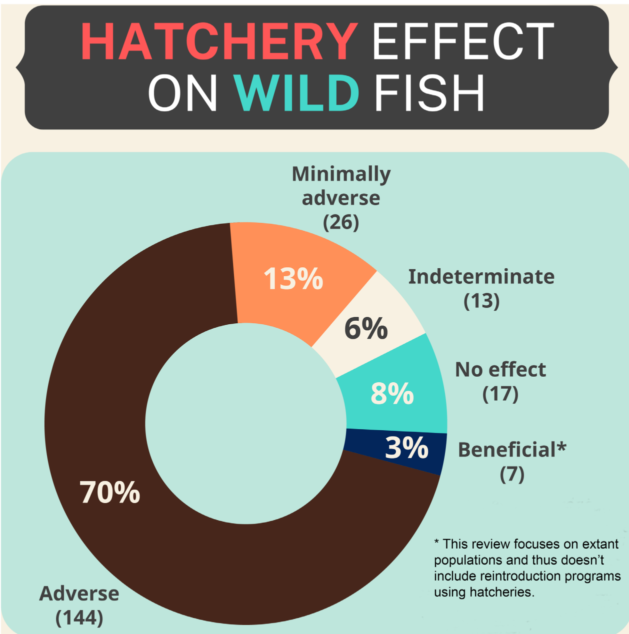

FIGURE 4 Donut plot displaying proportion (and number, in parentheses) of publications by the effect of hatchery salmonids on wild salmonids, including adverse, minimally adverse, indeterminate, no effect, and beneficial. There are 207 total entries because Levin and Williams (2002) was counted twice, once for an adverse effect and once for no effect.

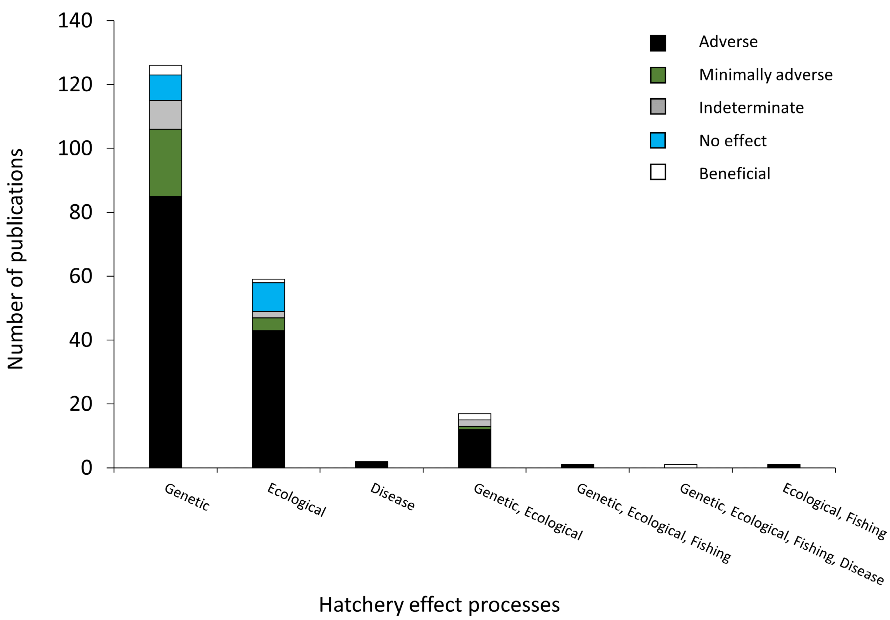

FIGURE 5 Distribution of publications in relation to the different processes through which hatchery fish affected wild salmonids, including ecological, genetic, fishing, disease, or some combination thereof in relation to the hatchery effect on wild population, denoted as adverse, minimally adverse, indeterminate, no effect, or beneficial. There are 207 total entries because Levin and Williams (2002) was counted twice in the ecological category, once for an adverse effect and once for no effect.

TABLE 4 Number of publications by their respective hatchery effect (adverse, minimally adverse, indeterminate, no effect, beneficial) on the Viable Salmon Population (VSP) parameter(s) of wild fish, including abundance (Abun.), distribution (Distr.), diversity (Diver.), productivity (Prod.), and various combinations thereof.

Effect on wild fish	Abun.	Distr.	Diver.	Prod.	Abun. & Distr.	Abun. & Diver.	Abun. & Prod.	Abun., Diver., and Prod.	Diver. & Distr.	Diver. & Prod.	Diver., Prod., & Distr.
Adverse	9 (1)	2	**66**	38 (14, 2)	1	3	14 (4)	4	1	4	1
Minimally adverse	2	1	**20**	3 (1)							
Indeterminate	1		**8**	2			2				
No effect		2	**7**	6 (4)	1		1				
Beneficial	1		1	**2**		**2**	1				
Total	13	5	**102**	51	2	5	18	5	1	3	1

Note: Adverse and beneficial refer to publications where authors describe the hatchery effect as being negative or positive on the wild population, respectively. A minimally adverse effect refers to publications that found some negative effects on wild fish, but they were inconsistent, while indeterminate refers to publications where hatchery effects included aspects that had both negative and positive effects on the wild population or hatchery effects were almost immeasurable. No effect means that the authors did not find a significant hatchery effect on wild fish for the parameters they measured. In cells with parentheses, the number refers to the number of studies in ocean, and if present, the second number after the comma refers to the number of studies in both the ocean and freshwater. Bolded and underlined values represent the VSP parameter with the greatest number of studies for each respective effect on wild fish. There are 207 total entries because Levin and Williams (2002) was counted twice in the productivity category, once for an adverse effect and once for no effect.

3.3.4 | Hatchery effect pathways and genetic effects

More publications ($n=126$) tested or evaluated how hatchery salmonids affected wild salmonids via genetics than other pathways, and most reported adverse ($n=85$) or minimally adverse effects ($n=21$), while fewer were indeterminate ($n=9$), found no effect ($n=8$), or reported a benefit ($n=3$) (Figure 5). Adverse effects also predominated ($n=44$) among the 60 ecological studies, and 12 of the 17 articles focused on a combination of genetic and ecological processes found adverse results. Potential disease and fishery effects were far less studied. Outside of a review by Naish et al. (2007), we found only two publications that evaluated potential effects of disease and parasites (Lamaze et al., 2014; Robinson et al., 2020) and three that included fishery effects as a component of their research (Baer & Brinker, 2010; Fast et al., 2015; Hilborn & Eggers, 2000).

The strong genetic focus is why one VSP parameter, diversity, was also commonly represented in 102 publications, 86 of which reported adverse ($n=66$) or minimally adverse effects ($n=20$) (Table 4). This was particularly true for brown trout, where 35 of 39 publications focused on diversity. An additional 13 studies included genetic diversity as a component and 12 found adverse effects. Of the 115 genetic-centric studies, most focused on potential effects on population structure ($n=59$), followed by various measures of genotypic/allelic diversity ($n=25$) and effective population size ($n=7$). The remaining 10 genetic articles were combinations of population structure, diversity, and effective population size.

Examples of adverse genetic effects included, but were not limited to, changes in population structure (Ayllon et al., 2006; Thaulow et al., 2012) stemming from an increased frequency of hatchery-origin alleles in wild populations (Caudron et al., 2009; Létourneau et al., 2018), reduced effective population size in wild populations with hatchery releases (Almodóvar et al., 2020; Hagen et al., 2021), replacement of wild salmonids by hatchery salmonids (e.g., Quiñones et al., 2013; Reisenbichler & Rubin, 1999), and reduced resistance to parasitic infections (Lamaze et al., 2014). In the single beneficial publication on diversity, a recovery hatchery program increased the effective population size in an endangered population of salmon (Hedrick et al., 1995), although as mentioned below, benefits to diversity were found in other publications that measured multiple VSP parameters.

After diversity, most publications focused on productivity, abundance, and a combination of productivity and abundance (Table 4). Of the publications on productivity, 30 were conducted in freshwater, 18 in the ocean, and three in both freshwater and an estuary. In freshwater, 22 of 30 studies found adverse effects on the productivity of wild salmonid populations (e.g., Chilcote et al., 2011; Jonsson et al., 2019; Skaala et al., 1996), while two apiece found no effect (e.g., Courter et al., 2019) or were indeterminate (e.g., Riley et al., 2005). In addition, nine of 13 studies on abundance and 14 of 18 studies on productivity and abundance in freshwater reported adverse effects, such as reduced productivity and abundance of wild salmonid populations (e.g., Byrne et al., 1992; Young, 2013) and reduced abundance and individual

TABLE 5 Number of publications (proportion in parentheses) and hatchery effect on wild fish by hatchery type.

Hatchery type	Adverse	Minimally adverse	Indeterminate	No effect	Beneficial
Production	108 (75%)	24 (17%)	4 (3%)	7 (5%)	0 (0%)
Supplementation	15 (64%)	0 (0%)	3 (11%)	5 (18%)	2 (7%)
Recovery	4 (24%)	1 (6%)	5 (29%)	2 (12%)	5 (29%)
Production, supplementation	14 (74%)	1 (5%)	1 (5%)	3 (16%)	0 (0%)

Note: Hatchery types include: production, supplementation, recovery, or a combination of production and supplementation or supplementation and recovery. Production refers to hatcheries that use all or nearly all hatchery fish for broodstock, which are often from a non-local source, and focus on producing fish for fisheries; supplementation refers to programs that integrate local wild and hatchery fish for broodstock to enhance fisheries and supplement wild populations; and a recovery program focuses strongly on conservation and uses mostly or all wild fish (fully integrated) to try and rebuild wild populations by providing a boost in abundance (often temporary). There are 207 total entries because Levin and Williams (2002) was counted twice in the production and supplementation category, once for an adverse effect and once for no effect.

condition of wild juveniles (Noble, 1991). The six remaining publications that reported benefits to abundance and productivity or a combination thereof all occurred in freshwater (e.g., Berejikian & Van Doornik, 2018; Janowitz-Koch et al., 2019). Effects on distribution and combinations of parameters including distribution were less represented than the other three VSP parameters (e.g., Hoffnagle et al., 2008; Love Stowell et al., 2015; Table 4).

3.3.5 | Hatchery effects in ocean

Hatchery effects on salmonids in the ocean involve competition for prey, potentially leading to reduced growth, body size and fecundity, delayed maturation, lower productivity, and fewer wild salmon. We found 23 studies on potential hatchery effects. Thirteen of those examined hatchery effects on local populations of wild salmon in the ocean, of which nine (69%) were adverse, one (8%) was minimally adverse, and three (23%) found no effect (Table S2). One of the three no-effect publications focused explicitly on potential juvenile competition in nearshore habitats during early marine residence (Sturdevant et al., 2011), while the other two focused on adult hatchery Chinook salmon production (Ohlberger et al., 2018; Nelson et al., 2019). Most other publications examined correlations between hatchery chum salmon and pink salmon and the productivity and growth wild adult salmon in the ocean (e.g., Cunningham et al., 2018; Frost et al., 2020; Ward et al., 2017).

We also included 10 studies that examined total salmon density effects on wild salmon in which hatchery salmon were an important component (additional studies involving density dependence at sea are available); nine (90%) of these studies reported adverse effects of density dependence on wild salmon while inferring an adverse effect of abundant hatchery salmon stemming from production hatcheries in Asia and North America (Table S2). Declines in the growth of all salmon species across most of their range are the most commonly observed effect of density dependence, including hatchery production (Bigler et al., 1996; Oke et al., 2020). Though not included in our analyses because it did not explicitly evaluate hatchery fish and in contrast to most results, Shuntov et al. (2019, 2020) argued that competition for prey at sea is minimal because prey biomass is exceptional and because salmon consume a small fraction of the available prey. However, this assessment cannot explain the density-dependent biennial patterns observed in Pacific salmon metrics (growth, abundance, productivity, maturation) in response to the biennial abundances of highly abundant pink salmon (Ruggerone et al., in press; Ruggerone & Connors, 2015; Ruggerone & Nielsen, 2004), of which many are hatchery fish (Ruggerone & Irvine, 2018).

4 | DISCUSSION

Hatcheries are used worldwide to produce salmonids for purposes ranging from providing fish for harvest to rebuilding endangered stocks and meeting Treaty responsibilities (Araki & Schmid, 2010; Maynard & Trial, 2014; Naish et al., 2007), but a strong dependence on hatcheries has also generated controversy and debate (Brannon et al., 2004; Claussen & Philipp, 2022; Harrison et al., 2019; Holt et al., 2008). Clarity in this discourse is partly obscured, however, by the sheer volume of complex research that dates back several decades, covers numerous species, and spans three continents, which makes it difficult to interpret succinctly the existing weight of evidence. We sought to provide a transparent, reproducible, and updatable synthesis and database of the current global research evaluating the impacts of hatcheries on wild populations, while purposefully not delving into the complex social and political desires or tribal Treaty and mitigation legal obligations surrounding hatcheries. Our review of over 50 years of peer-reviewed publications on how hatchery salmonids affect wild salmonids found most research reported adverse or minimally adverse hatchery effects across time, species, and countries, even for supplementation-type hatcheries, while reports of beneficial effects on wild salmonids were scarce except for a few very specific situations (e.g., Berejikian & Van Doornik, 2018; Hess et al., 2012). We hope this database serves as a useful standing resource that can be used and built upon to improve the breadth of science incorporated into decision-making.

Prior reviews have summarized overarching hatchery practices and processes, identified potential adverse impacts, and evaluated the role of hatcheries in salmonid fisheries and recovery (Fraser, 2008; Jonsson, 1997; Maynard & Trial, 2014; Naish et al., 2007). More similar to Miller et al. (1990) and Araki and Schmid (2010), we attempted to census the balance of existing peer-reviewed literature and provide summaries of each publication (Appendix S1). Miller et al. (1990) reviewed 316 hatchery projects, including numerous supplementation programs, across the western USA and Canada and in New England states working with Atlantic salmon. Of those, only 25 projects, or 8%, successfully supplemented existing runs of wild salmonids, and while adverse impacts to wild stocks were reported or postulated for almost every type of hatchery situation where the intent was to rebuild wild runs. The authors also suggested a bias toward not reporting negative or unsuccessful results. Two decades later, Araki and Schmid (2010) synthesized 266 hatchery case studies covering several species of fish, including 70 on salmonids, 51 of which (72%) reported adverse impacts ranging from deleterious effects of hatchery rearing on fitness in nature to reduced genetic variation in populations of hatchery fish. Our review of 208 publications found 70% reported adverse hatchery effects and another 13% found minimally adverse effects, while just 3% reported beneficial effects. Although we likely missed some relevant publications despite a transparent search process and did not include research on reintroductions using hatchery salmon (e.g., Liermann et al., 2017) or domestication effects on wild fish reared in hatcheries (e.g., Christie et al., 2016), the overall balance of results across three reviews and hundreds of studies appear relatively similar.

One possible reason for the preponderance of adverse effects across time, space, and species is most publications in our review assessed traditional, production hatcheries that focused on producing fish for fisheries, often but not always from non-local broodstock. Adverse effects on wild salmonids from such programs are well documented (Almodóvar et al., 2020; García-Marín et al., 1999; Marie et al., 2010). This was particularly true for brown trout, the most studied species, where many publications evaluated possible genetic effects of non-local hatchery stocks across Europe, often finding adverse genetic impacts (Araguas et al., 2017; Hansen et al., 2009; Thaulow et al., 2012). However, adverse effects also accounted for 63% of the publications that evaluated potential impacts from supplementation programs that use some or mostly wild fish and frequently employ breeding protocols to try to reduce deleterious genetic effects (Hutchings, 2014; Neff et al., 2011; Pinter et al., 2019).

Adverse effects from supplementation programs could be related to a suite of factors that are not dissimilar from production programs. For example, supplementation broodstock is generally derived from local populations to reduce potential genetic impacts; however, a review of 51 estimates of annual productivity from six studies on four salmon species found the relative fitness of early-generation hatchery individuals was about half that of wild fish (Christie et al., 2014), while another found hatchery salmonids displayed lower genetic variation than wild populations (Araki & Schmid, 2010). Interbreeding with individuals that have lower fitness and less diversity, among other differences, can reduce the diversity (Hagen et al., 2021), effective population size (Christie et al., 2012; Hagen et al., 2021), and productivity of wild populations (Goodman, 2005; Jonsson et al., 2019; Reisenbichler & Rubin, 1999). Depending on the intensity and duration of stocking, the gene pool of the wild population may eventually be compromised by high levels of hatchery influence, as evidenced by studies on brown trout in Europe (Fernández-Cebrián et al., 2014; Hauser et al., 1991; Pustovrh et al., 2012) and brook charr in North American (Létourneau et al., 2018); in the extreme, hatchery salmonids may replace wild fish (Largiadèr & Scholl, 1996; Quiñones et al., 2013).

In addition, although a key goal of supplementation hatcheries is to enhance opportunities for harvest, in some populations and years large numbers of returning hatchery salmon escape fisheries or are allowed intentionally to spawn, leading to many more total salmon than can be supported by the habitat and heighten density-dependent effects (HSRG, 2020; ISAB, 2015). We found studies where hatchery juveniles reduced the abundance and productivity of wild juveniles (Nickelson et al., 1986; Warren et al., 2014). Competition for habitat likely contributed to declines in wild coho salmon on the Oregon coast, USA, where density-dependent effects were five times greater for hatchery salmon than wild salmon and the productivity of several wild populations decreased as hatchery releases increased (Buhle et al., 2009; Nickelson, 2003). Adverse effects may thus depend on genetic and ecological pathways and the intensity of stocking, and such effects may be more common than anticipated if supplementation programs do not meet their own goals for reducing risk (e.g., targeted levels of wild integration into broodstock) and limitations of habitat capacity are not considered (Anderson et al., 2020). Regardless, interbreeding with less fit individuals and increased competition for habitat may help explain why both production and supplementation programs negatively influenced productivity of several populations of wild steelhead (Chilcote et al., 2011), and why a long-term effort to increase natural-origin Chinook salmon did not find a positive effect on abundance after releases were ceased (Scheuerell et al., 2015; Venditti et al., 2018).

Hatcheries can also benefit wild salmonids, though the situations appear nuanced. For instance, hatcheries have helped re-establish extirpated populations of salmonids (Galbreath et al., 2014), prevent extinction (Kline & Flagg, 2014), and jump-start recolonization following dam removal (Liermann et al., 2017). While those efforts did not meet the criteria for inclusion in our synthesis (e.g., effects on wild fish could not, or were not, evaluated due to extirpation or near extinction levels of abundance), in the publications we reviewed nearly all benefits occurred when recovery-type programs were used to provide a demographic boost to endangered populations of salmonids. Examples include small releases of hatchery smolts from a short-term, temporary captive-broodstock program to increase abundance and diversity of steelhead populations that were almost extirpated (Berejikian et al., 2008; Berejikian & Van Doornik, 2018), and a carefully controlled hatchery program that bred only wild fish to boost abundance of a highly depleted population of Chinook salmon (Hess et al., 2012; Janowitz-Koch et al., 2019). However, two of the four beneficial studies reported on the same populations, which tilts the proportion of results given the relatively small number of publications, and other publications warn that even improved hatchery practices can still pose significant ecological and genetic risks to wild fish over the long term (Oosterhout et al., 2005), such as competition for food and habitat (ISAB, 2015) and reduced genetic diversity and divergence from the wild population (Bingham et al., 2014). Consequently, beyond 4–6 generations a loss in fitness can outweigh any increase in abundance from hatchery production and cause the population to decline (Bowlby & Gibson, 2011). Nonetheless, our review, like others (Maynard & Trial, 2014; Naish et al., 2007), suggests the balance of effects for recovery hatcheries is less skewed, with as many studies reporting beneficial or no effects as adverse ones.

Within the array of publications we reviewed, most research focused on hatchery effects that occurred via genetic interactions and found adverse impacts on wild salmonids, such as reduced diversity (García-Marín et al., 1999; Perrier et al., 2013; Willoughby & Christie, 2019) and altered genetic structure of wild populations (Valiquette et al., 2014; Weigel et al., 2019; Wenne et al., 2016), though adverse effects on growth (Hasegawa et al., 2014, 2018; McMichael et al., 1997), productivity (Buhle et al., 2009; Nickelson, 2003) and abundance (Nickelson et al., 1986; Quiñones et al., 2013; Willmes et al., 2018) via ecological or both ecological and genetic processes were also reported. The frequency of adverse genetic impacts may have consequences for the resilience of wild fish moving forward. As an example, research on brown trout found long-term supplementation significantly reduced genetic diversity among locations and compromised the conservation of local genetic variation (Fernández-Cebrián et al., 2014), which threatened biodiversity in their southern range (Cagigas et al., 1999; Horreo et al., 2014; Splendiani et al., 2019). A tremendous amount of money and effort has been invested in restoring habitat to improve population productivity and increase carrying capacity (ISAB, 2015), and help offset future effects from climate change (Beechie et al., 2013; Bilby et al., 2022), an action demonstrated to increase wild fish abundance more effectively than species-specific stocking efforts (Radinger et al., 2023). Because the resilience of salmonids also depends on their functional genetic capacity to survive and reproduce in a changing environment (Kardos et al., 2021), future research could help illuminate the extent to which, if any, alterations to genetic diversity may influence returns on habitat investments where both hatchery and wild fish co-exist.

Our literature review also revealed an extensive body of research focused on potential effects of annual releases of 4.5 billion hatchery Pacific salmon into the North Pacific Ocean, which represents 40% of the total mature and immature salmon biomass in the North Pacific Ocean (Ruggerone & Irvine, 2018). The combination of publications on the specific abundance of hatchery salmon and overall abundance of hatchery and wild salmon at sea suggest heightened abundances, particularly of hatchery chum salmon and pink salmon, have triggered density-dependent effects in wild populations resulting in reduced growth, body size, fecundity, productivity, and abundance, and delayed maturation (Table S2). For example, research has found adverse effects of hatchery or total chum salmon abundance on the growth, productivity, and abundance of wild chum salmon (Frost et al., 2020; Kaeriyama et al., 2011; Ruggerone et al., 2012), of total hatchery and wild pink salmon and chum salmon on body size, age, productivity, and abundance of Chinook salmon across their range (Cunningham et al., 2018; Oke et al., 2020; Ruggerone et al., in press), and of hatchery pink salmon on productivity of wild sockeye salmon populations in British Columbia and Alaska (Connors et al., 2020). While it is difficult to disentangle correlation and causation, the strong biennial patterns in abundant pink salmon cannot be explained by the environment alone (Batten et al., 2018; Ruggerone & Connors, 2015; Ruggerone et al., in press) and, consequently, concerns for wild salmon have led scientists to call for international discussions, limits on hatchery production, and hatchery taxes (Holt et al., 2008; Malick et al., 2017; Peterman et al., 2012).

Considering the balance of the research herein, we selected four topics that remain underrepresented and seem important to clarifying science and management opportunities moving forward. First, effects on genetic diversity of wild salmonids are well studied but investigation of epigenetic effects as a possible biological pathway for these (and other) effects has only begun (Koch et al., 2022). Christie et al. (2016) found a single generation in a hatchery environment altered the expression of over 700 genes in steelhead. Other research has found similar results (Leitwein et al., 2022), even in the absence of genetic differentiation between wild and hatchery populations (Le Luyer et al., 2017), and the potential for the epigenetic changes to be passed along to offspring (Leitwein et al., 2021; Venney et al., 2023). Though the duration of impacts remains unclear it is hypothesized that heritable epigenetic effects may alter the evolutionary trajectory of wild populations, which is a critical issue to evaluate where hatchery salmonids are allowed to or are able to breed with wild salmonids (Skinner & Nilsson, 2021). Second, future research could illuminate the adaptive consequences of genetic changes sustained by wild salmonids (Neff et al., 2011) and whether accumulated effects inhibit their capacity to keep pace with climate change (e.g., Munsch et al., 2022) or respond positively to habitat restoration efforts. Third, large-scale experiments that evaluate multiple VSP parameters before, during, and after supplementation, such as Berejikian and Van Doornik (2018), are scarce, but well-designed experiments could help parse out natural spatial and temporal variability in environmental capacity from hatchery effects and offer greater clarity regarding the risks and benefits of hatchery programs.

Last, few publications evaluated disease or fishery effects despite demonstrated mechanisms of influence, such as decreased resilience to parasites associated with hatchery genotypes (see, Lamaze et al., 2014) and mixed stock fisheries on abundant hatchery stocks that are unsustainable for wild stocks (Naish et al., 2007). It is possible our search string did not fully capture the breadth of literature on fishery effects, or such analyses are less frequently published in peer-reviewed journals. Naish et al. (2007) analyzed fishery data from management reports and described a long history of overharvesting weaker wild stocks in intensive hatchery fisheries, which ultimately led to changes in fishery policy in the United States, but direct references to studies that met our criteria were rare. Understanding how such impacts have and continue to affect wild stocks could provide further insight, though in some cases identifying potential changes to wild populations may require a longer-term perspective using historical data (e.g., McMillan et al., 2022).

5 | CONCLUSION

We created an easily accessible database focused on publications that examined potential effects of hatchery salmonids on wild salmonids, and then synthesized the large body of research to better understand how studies and potential hatchery impacts were distributed in relation to time, space, species, habitat, hatchery type, and other factors. Except in a few specific situations when recovery hatcheries were used to boost the abundance of wild salmonids threatened with extinction, hatchery effects on wild salmon were predominantly adverse across time, species, and countries, even when using more modern supplementation hatchery programs and practices. In addition, evidence indicates large releases of hatchery chum and pink salmon in the North Pacific Ocean alter the growth, survival, and abundance of wild salmonids that rely on the same common pool prey resource. These results have implications for conserving and sustaining wild salmonids and for extensive investments in salmon recovery across the globe. In conclusion, while there is a long history of debate over the widespread use of hatcheries, our results were consistent with prior reviews by Miller et al. (1990) and Araki and Schmid (2010), the combination of which clearly indicate that, from a scientific standpoint, hatcheries typically pose numerous risks that commonly result in negative impacts to the diversity, productivity, and abundance of wild salmonid populations. These negative impacts likely limit the efficacy of habitat restoration efforts aimed at rebuilding wild salmonid populations and the adaptive capacity of wild salmonids to keep pace with a changing environment, especially climate warming.

ACKNOWLEDGMENTS

The vast majority of project funding for the lead author was provided by Trout Unlimited, with additional funding via the Wild Steelhead Coalition and The Conservation Angler. We extend sincere thanks to Matt Mayfield for Figure 1, Craig Busack for early discussions and comments, Martin Liermann for assistance with R in generating an accessible database, and two anonymous reviewers for their constructive criticisms.

CONFLICT OF INTEREST STATEMENT

The authors declare there are no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article in the database provided in Appendix S2.

ETHICS STATEMENT

The manuscript has not been submitted for publication or published in another journal and because the manuscript is a review of prior publications on fish, information on ethical treatment of humans and animals is not applicable.

REFERENCES

Allendorf, F.W. (1991) Ecological and genetic effects of fish introductions: synthesis and recommendations. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 178–181.

Almodóvar, A., Leal, S., Nicola, G.G., Hórreo, J.L., García-Vázquez, E. & Elvira, B. (2020) Long-term stocking practices threaten the original genetic diversity of the southernmost European populations of Atlantic salmon *Salmo salar*. *Endangered Species Research*, 41, 303–317.

Anderson, J.H., Warheit, K.I., Craig, B.E., Seamons, T.R. & Haukenes, A.H. (2020) *A review of hatchery reform science in Washington State. Final report to the Washington Fish and Wildlife Commission*. Olympia, WA: Washington Department of Fish and Wildlife.

Araguas, R.M., Vera, M., Aparicio, E., Sanz, N., Fernández-Cebrián, R., Marchante, C. et al. (2017) Current status of the brown trout (*Salmo trutta*) populations within eastern Pyrenees genetic refuges. *Ecology of Freshwater Fish*, 26, 120–132.

Araki, H., Cooper, B. & Blouin, M.S. (2009) Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biological Letters*, 5, 621–624.

Araki, H. & Schmid, C. (2010) Is hatchery stocking a help or harm?: evidence, limitations and future directions in ecological and genetic surveys. *Aquaculture*, 308, S2–S11.

Ayllon, F., Martinez, J.L. & Garcia-Vazquez, E. (2006) Loss of regional population structure in Atlantic salmon, *Salmo salar* L., following stocking. *ICES Journal of Marine Science*, 63, 1269–1273.

Baer, J. & Brinker, A. (2010) The response of a brown trout stocks and perception of anglers to cessation of brown trout stocking. *Fisheries Management and Ecology*, 17, 157–164.

Baillie, S.M., Muir, A.M., Scribner, K., Bentzen, P. & Krueger, C.C. (2016) Loss of genetic diversity and reduction of genetic distance among lake trout *Salvelinus namaycush* ecomorphs, Lake Superior 1959 to 2013. *Journal of Great Lakes Research*, 42, 204–216.

Bartron, M.L. & Scribner, K.T. (2004) Temporal comparisons of genetic diversity in Lake Michigan Steelhead, *Oncorhynchus mykiss*, populations: effects of hatchery supplementation. *Environmental Biology of Fishes*, 69, 395–407.

Batten, S.D., Ruggerone, G.T. & Ortiz, I. (2018) Pink salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. *Fisheries Oceanography*, 27, 548–559.

Beechie, T., Imaki, H., Greene, J., Wade, A., Wu, H., Pess, G. et al. (2013) Restoring salmon habitat for a changing climate. *River Research and Applications*, 29, 939–960.

Berejikian, B.A., Johnson, T., Endicott, R.S. & Lee-Waltermire, J. (2008) Increases in steelhead (*Oncorhynchus mykiss*) redd abundance resulting from two conservation hatchery strategies in the Hamma Hamma River, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 754–764.

Berejikian, B.A. & Van Doornik, D.M. (2018) Increased natural reproduction and genetic diversity one generation after cessation of a steelhead trout (*Oncorhynchus mykiss*) conservation hatchery program. *PLoS One*, 13, e0190799.

Bernaś, R., Burzyński, A., Dębowski, P., Poćwierz-Kotus, A. & Wenne, R. (2014) Genetic diversity within sea trout population from an intensively stocked southern Baltic river, based on microsatellite DNA analysis. *Fisheries Management and Ecology*, 21, 398–409.

Bigler, B.S., Welch, D.W. & Helle, J.H. (1996) A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 455–465.

Bilby, R., Johnson, A., Foltz, J.R. & Puls, A.L. (2022) *Management implications from Pacific Northwest intensively monitored watersheds*. Available from: https://www.pnamp.org/document/15207:99. [Accessed 23rd April 2019].

Bingham, D.M., Kennedy, B.M., Hanson, K.C. & Smith, C.T. (2014) Loss of genetic integrity in hatchery steelhead produced by juvenile-based broodstock and wild integration: conflicts in production and conservation goals. *North American Journal of Fisheries Management*, 34, 609–620.

Bouchard, R., Wellband, K., Lecomte, L., Bernatchez, L. & April, J. (2022) Effects of stocking at the parr stage on the reproductive fitness and genetic diversity of a wild population of Atlantic salmon (*Salmo salar* L.). *Evolutionary Applications*, 15, 838–852.

Bowlby, H.D. & Gibson, A. (2011) Reduction in fitness limits the useful duration of supplementary rearing in an endangered salmon population. *Ecological Applications*, 21, 3032–3048.

Brannon, E.L., Amend, D.F., Cronin, M.A., Lannan, J.E., LaPatra, S., McNeil, W.J. et al. (2004) The controversy about salmon hatcheries. *Fisheries*, 29, 12–31.

Bruce, S.A., Kutsumi, Y., Van Maaren, C. & Hare, M.P. (2020) Stocked-fish introgression into wild brook trout populations depends on habitat. *Transactions of the American Fisheries Society*, 149, 427–442.

Buhle, E.R., Holsman, K.K., Scheuerell, M.D. & Albaugh, A. (2009) Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. *Biological Conservation*, 142, 2449–2455.

Byrne, A., Bjornn, T. & McIntyre, J. (1992) Modeling the response of native steelhead to hatchery supplementation programs in an Idaho river. *North American Journal of Fisheries Management*, 12, 62–78.

Cagigas, M., Vazquez, E., Blanco, G. & Sanchez, J. (1999) Genetic effects of introduced hatchery stocks on indigenous brown trout (*Salmo trutta* L.) populations in Spain. *Ecology of Freshwater Fish*, 8, 141–150.

Caudron, A., Champigneulle, A. & Guyomard, R. (2009) Evidence of two contrasting brown trout *Salmo trutta* populations spatially separated in the River Borne (France) and shift in management towards conservation of the native lineage. *Journal of Fish Biology*, 74, 1070–1085.

Chilcote, M.W., Fleming, I., Goodson, K.W. & Falcy, M.R. (2011) Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 511–522.

Christie, M.R., Ford, M.J. & Blouin, M.S. (2014) On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications*, 7, 883–896.

Christie, M.R., Marine, M.L., Fox, S.E., French, R.A. & Blouin, M.S. (2016) A single generation of domestication heritably alters the expression of hundreds of genes. *Nature Communications*, 7, 10676.

Christie, M.R., Marine, M.L., French, R.A., Waples, R.S. & Blouin, M.S. (2012) Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. *Heredity*, 109, 254–260.

Claussen, J.E. & Philipp, D.P. (2022) Assessing the role of supplementation stocking: a perspective. *Fisheries Management and Ecology*. Advanced online publication. Available from: https://doi.org/10.1111/fme.12573

Collaboration for Environmental Evidence (CEE). (2018) Guidelines and Standards for Evidence synthesis in Environmental Management. Version 5.0 (A.S. Pullin, G.K. Frampton, B. Livoreil & G. Petrokofsky, Eds). Available from: www.environmentalevidence.org/information-for-authors. [Accessed online 23rd March 2019].

Connors, B., Malick, M.J., Ruggerone, G.T., Rand, P., Adkison, M., Irvine, J.R. et al. (2020) Climate and competition influence sockeye salmon population dynamics across the Northeast Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 943–949.

Cordes, J.F., Stephens, M.R., Blumberg, M.A. & May, B. (2006) Identifying introgressive hybridization in native populations of California golden trout based on molecular markers. *Transactions of the American Fisheries Society*, 135, 110–128.

Courter, I.I., Wyatt, G.J., Perry, R.W., Plumb, J.M., Carpenter, F.M., Ackerman, N.K. et al. (2019) A natural-origin steelhead population's response to exclusion of hatchery fish. *Transactions of the American Fisheries Society*, 148, 339–351.

Cunningham, C.J., Westley, P.A.H. & Adkison, M.D. (2018) Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. *Global Change Biology*, 24, 4399–4416.

Dunham, J.B., Pilliod, D.S. & Young, M.K. (2004) Assessing the consequences of nonnative trout in headwater ecosystems in western North America. *Fisheries*, 29, 18–26.

Fast, D.E., Bosch, W.J., Johnston, M.V., Strom, C.R., Knudsen, C.M., Fritts, A.L. et al. (2015) A synthesis of findings from an integrated hatchery program after three generations of spawning in the natural environment. *North American Journal of Aquaculture*, 77, 377–395.

Fernández-Cebrián, R., Araguas, R.M., Sanz, N., García-Marín, J.L. & Fraser, D. (2014) Genetic risks of supplementing trout populations with native stocks: a simulation case study from current Pyrenean populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 1243–1255.

Finnegan, A.K. & Stevens, J.R. (2008) Assessing the long-term genetic impact of historical stocking events on contemporary populations of Atlantic salmon,*Salmo salar*. *Fisheries Management and Ecology*, 15, 315–326.

Flagg, T.A., Berejikian, B.A., Colt, J., Dickhoff, W.W., Harrell, L.W., Maynard, D.J. et al. (2000) *Ecological and behavioral impacts of artificial production strategies on the abundance of wild salmon populations: a review of practices in the Pacific Northwest*.

Fraser, D.J. (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, 1, 535–586.

Frost, T.J., Yasumiishi, E.M., Agler, B.A., Adkison, M.D. & McPhee, M.V. (2020) Density-dependent effects of eastern Kamchatka pink salmon (*Oncorhynchus gorbuscha*) and Japanese chum salmon (*O. keta*) on age-specific growth of western Alaska chum salmon. *Fisheries Oceanography*, 30, 99–109.

Fukuwaka, M. & Suzuki, T. (2000) Density-dependence of chum salmon in coastal waters of the Japan Sea. *North Pacific Anadromous Fish Commission Bulletin*, 2, 75–81.

Galbreath, P.F., Bisbee, M.A., Jr., Dompier, D.W., Kamphaus, C.M. & Newsome, T.H. (2014) Extirpation and tribal reintroduction of coho salmon to the interior Columbia River basin. *Fisheries*, 39, 77–87.

García-Marín, J., Sanz, N. & Pla, C. (1999) Erosion of the native genetic resources of brown trout in Spain. *Ecology of Freshwater Fish*, 8, 151–158.

Goodman, D. (2005) Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 374–389.

Gossieaux, P., Bernatchez, L., Sirois, P. & Garant, D. (2019) Impacts of stocking and its intensity on effective population size in Brook Charr (*Salvelinus fontinalis*) populations. *Conservation Genetics*, 20, 729–742.

Haddaway, N.R., Macura, B., Whaley, P. & Pullin, A.S. (2018) ROSES RepOrting standards for Systematic Evidence Syntheses: pro forma, flow-diagram and descriptive summary of the plan and conduct of environmental systematic reviews and systematic maps. *Environmental Evidence*, 7, 7.

Hagen, I.J., Ugedal, O., Jensen, A.J., Lo, H., Holthe, E., Bjøru, B. et al. (2021) Evaluation of genetic effects on wild salmon populations from stock enhancement. *ICES Journal of Marine Science*, 78, 900–909.

Hansen, M.J., Guy, C.S., Budy, P. & McMahon, T.E. (2019) Trout as native and nonnative species: a management paradox. In: Kershner, J.L., Williams, J.E., Gresswell, R.E. & Lobon-Cervia, J. (Eds.) *Trout and char of the world*. Bethesda, MD: American Fisheries Society, pp. 645–684.

Hansen, M.M., Fraser, D.J., Meier, K. & Mensberg, K.L. (2009) Sixty years of anthropogenic pressure: a spatio-temporal genetic analysis of

brown trout populations subject to stocking and population declines. *Molecular Ecology*, 18, 2549–2562.
Harrison, H.L., Hauer, J., Nielsen, J.Ø. & Aas, Ø. (2019) Disputing nature in the Anthropocene: technology as friend and foe in the struggle to conserve wild Atlantic salmon (*Salmo salar*). *Ecology and Society*, 24, 13.
Hasegawa, K., Morita, K., Ohkuma, K., Ohnuki, T. & Okamoto, Y. (2014) Effects of hatchery chum salmon fry on density-dependent intra-and interspecific competition between wild chum and masu salmon fry. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 1475–1482.
Hasegawa, K., Ohta, T. & Takahashi, S. (2018) Are hatchery chum salmon fry a native invader? Direct and indirect effects of stocking salmon fry on stream organisms. *Hydrobiologia*, 806, 111–121.
Hatchery Scientific Review Group (HSRG). (2015) *Annual report to Congress on the science of hatcheries, 2015: a report on the application of up-to-date science in the management of salmon and steelhead hatcheries in the Pacific Northwest*.
Hatchery Scientific Review Group (HSRG). (2020) *Developing recovery objectives and phase triggers for salmonid populations*.
Hauser, L., Beaumont, A., Marshall, G. & Wyatt, R. (1991) Effects of sea trout stocking on the population genetics of landlocked brown trout, *Salmo trutta* L., in the Conwy River system, North Wales, UK. *Journal of Fish Biology*, 39, 109–116.
Hedrick, P.W., Hedgecock, D. & Hamelberg, S. (1995) Effective population size in winter-run Chinook salmon. *Conservation Biology*, 9, 615–624.
Hess, M.A., Rabe, C.D., Vogel, J.L., Stephenson, J.J., Nelson, D.D. & Narum, S.R. (2012) Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon. *Molecular Ecology*, 21, 5236–5250.
Hilborn, R. (1992) Hatcheries and the future of salmon in the northwest. *Fisheries*, 17, 5–8.
Hilborn, R. & Eggers, D. (2000) A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society*, 129, 333–350.
Hoffnagle, T.L., Carmichael, R.W., Frenyea, K.A. & Keniry, P.J. (2008) Run timing, spawn timing, and spawning distribution of hatchery- and natural-origin spring Chinook salmon in the Imnaha River, Oregon. *North American Journal of Fisheries Management*, 28, 148–164.
Holt, C.A., Rutherford, M.B. & Peterman, R.M. (2008) International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. *Marine Policy*, 32, 607–617.
Horreo, J.L., Machado-Schiaffino, G., Griffiths, A.M., Bright, D., Stevens, J.R. & Garcia-Vazquez, E. (2014) Long-term effects of stock transfers: synergistic introgression of allochthonous genomes in salmonids. *Journal of Fish Biology*, 85, 292–306.
Hutchings, J.A. (2014) Unintentional selection, unanticipated insights: introductions, stocking and the evolutionary ecology of fishes. *Journal of Fish Biology*, 85, 1907–1926.
Independent Scientific Advisory Board (ISAB). (2015) *Density dependence and its implications for fish management and restoration in the Columbia river basin*. Independent Scientific Advisory Board for the Northwest Power and Conservation Council, Columbia River Basin Indian Tribes, and National Marine Fisheries Service. ISAB 2015-1.
Janowitz-Koch, I., Rabe, C., Kinzer, R., Nelson, D., Hess, M.A. & Narum, S.R. (2019) Long-term evaluation of fitness and demographic effects of a Chinook Salmon supplementation program. *Evolutionary Applications*, 12, 456–469.
Jonsson, B. (1997) A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science*, 54, 1031–1039.
Jonsson, B., Jonsson, N. & Jonsson, M. (2019) Supportive breeders of Atlantic salmon *Salmo salar* have reduced fitness in nature. *Conservation Science and Practice*, 1, e85.
Kaeriyama, M., Seo, H., Kudo, H. & Nagata, M. (2011) Perspectives on wild and hatchery salmon interactions at sea, potential climate effects on Japanese chum salmon, and the need for sustainable salmon fishery management reform in Japan. *Environmental Biology of Fishes*, 94, 165–177.
Kardos, M., Armstrong, E.E., Fitzpatrick, S.W., Hauser, S., Hedrick, P.W., Miller, J.M. et al. (2021) The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2104642118.
Kleiss, M.E. (2004) The salmon hatchery myth: when bad policy happens to good science. *Minnesota Journal of Law, Science & Technology*, 6, 431.
Kline, P.A. & Flagg, T.A. (2014) Putting the red back in redfish Lake, 20 years of progress toward saving the Pacific Northwest's most endangered salmon population. *Fisheries*, 39, 488–500.
Koch, I.J., Nuetzel, H.M., & Narum, S.R. (2022) Epigenetic effects associated with salmonid supplementation and domestication. *Environmental Biology of Fishes*, 106, 1093–1111.
Laffaille, P. (2011) Impact of stocked Atlantic salmon (*Salmo salar* L.) on habitat use by the wild population. *Ecology of Freshwater Fish*, 20, 67–73.
Lamaze, F.C., Pavey, S.A., Normandeau, E., Roy, G., Garant, D. & Bernatchez, L. (2014) Neutral and selective processes shape MHC gene diversity and expression in stocked brook charr populations (*Salvelinus fontinalis*). *Molecular Ecology*, 23, 1730–1748.
Largiadèr, C. & Scholl, A. (1996) Genetic introgression between native and introduced brown trout *Salmo trutta* L. populations in the Rhone River basin. *Molecular Ecology*, 5, 417–426.
Le Luyer, J., Laporte, M., Beacham, T.D., Kaukinen, K.H., Withler, R.E., Leong, J.S. et al. (2017) Parallel epigenetic modifications induced by hatchery rearing in a Pacific salmon. *Proceedings of the National Academy of Sciences*, 114, 12964–12969.
Leitwein, M., Laporte, M., Le Luyer, J., Mohns, K., Normandeau, E., Withler, R. et al. (2021) Epigenomic modifications induced by hatchery rearing persist in germ line cells of adult salmon after their oceanic migration. *Evolutionary Applications*, 14, 2402–2413.
Leitwein, M., Wellband, K., Cayuela, H., Le Luyer, J., Mohns, K., Withler, R. et al. (2022) Strong parallel differential gene expression induced by hatchery rearing weakly associated with methylation signals in adult Coho Salmon (*O. kisutch*). *Genome Biology and Evolution*, 14, evac036.
Létourneau, J., Ferchaud, A.L., Le Luyer, J., Laporte, M., Garant, D. & Bernatchez, L. (2018) Predicting the genetic impact of stocking in brook Charr (*Salvelinus fontinalis*) by combining RAD sequencing and modeling of explanatory variables. *Evolutionary Applications*, 11, 577–592.
Levin, P.S. & Williams, J.G. (2002) Interspecific effects of artifically propagated fish: an additional conservation risk for salmon. *Conservation Biology*, 16, 1581–1587.
Lichatowich, J.A. (2001) *Salmon without rivers: a history of the Pacific salmon crisis*. Washington: Island Press.
Liermann, M., Pess, G., McHenry, M., McMillan, J., Elofson, M., Bennett, T. et al. (2017) Relocation and recolonization of coho salmon in two tributaries to the Elwha River: implications for management and monitoring. *Transactions of the American Fisheries Society*, 146, 955–966.
Love Stowell, S.M., Kennedy, C.M., Beals, S.C., Metcalf, J.L., Martin, A.P. & Taylor, E. (2015) The genetic legacy of more than a century of stocking trout: a case study in Rocky Mountain National Park, Colorado, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1565–1574.
Lynch, M. & O'Hely, M. (2001) Captive breeding and the genetic fitness of natural populations. *Conservation Genetics*, 2, 363–378.
Malick, M.J., Rutherford, M.B. & Cox, S.P. (2017) Confronting challenges to integrating Pacific salmon into ecosystem-based management policies. *Marine Policy*, 85, 123–132.
Marie, A.D., Bernatchez, L. & Garant, D. (2010) Loss of genetic integrity correlates with stocking intensity in brook charr (*Salvelinus fontinalis*). *Molecular Ecology*, 19, 2025–2037.

Maynard, D.J. & Trial, J.G. (2014) The use of hatchery technology for the conservation of Pacific and Atlantic salmon. *Reviews in Fish Biology and Fisheries*, 24, 803–817.

McElhany, P., Rucklelshaus, M.H., Ford, M.J., Wainwright, T.C. & Bjorkstedt, E.P. (2000) *Viable salmonid populations and the recovery of evolutionarily significant units*. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-42, p. 156.

McMichael, G.A., Sharpe, C.S. & Pearsons, T.N. (1997) Effects of residual hatchery-reared steelhead on growth of wild rainbow trout and spring Chinook salmon. *Transactions of the American Fisheries Society*, 126, 230–239.

McMillan, J.R., Sloat, M.R., Liermann, M. & Pess, G. (2022) Historical records reveal changes to the migration timing and abundance of winter steelhead in Olympic Peninsula Rivers, Washington state, USA. *North American Journal of Fisheries Management*, 42, 3–23.

Miller, W.H., Coley, T.C. & Burge, H.L. (1990) *Analysis of salmon and steelhead supplementation, 1990 final report*. United States.

Milot, E., Perrier, C., Papillon, L., Dodson, J.J. & Bernatchez, L. (2013) Reduced fitness of Atlantic salmon released in the wild after one generation of captive breeding. *Evolutionary Applications*, 6, 472–485.

Munsch, S.H., Greene, C.M., Mantua, N.J. & Satterthwaite, W.H. (2022) One hundred-seventy years of stressors erode salmon fishery climate resilience in California's warming landscape. *Global Change Biology*, 28, 2183–2201.

Naish, K.A., Taylor, J.E., 3rd, Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D. et al. (2007) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, 53, 61–194.

Naman, S.W. & Sharpe, C.S. (2011) Predation by hatchery yearling salmonids on wild subyearling salmonids in the freshwater environment: a review of studies, two case histories, and implications for management. *Environmental Biology of Fishes*, 94, 21–28.

Neff, B.D., Garner, S.R. & Pitcher, T.E. (2011) Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1139–1154.

Nelson, B.W., Walters, C.J., Trites, A.W. & McAllister, M.K. (2019) Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 447–462.

Nickelson, T. (2003) The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences*, 60, 1050–1056.

Nickelson, T.E., Solazzi, M.F. & Johnson, S.L. (1986) Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 2443–2449.

Nilsson, J., Östergren, J., Lundqvist, H. & Carlsson, U. (2008) Genetic assessment of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta* stocking in a Baltic Sea river. *Journal of Fish Biology*, 73, 1201–1215.

Noble, S.M. (1991) *Impacts of earlier emerging steelhead fry of hatchery origin on the social structure, distribution, and growth of wild steelhead fry*. Thesis, Oregon State University.

Ohlberger, J., Ward, E.J., Schindler, D.E. & Lewis, B. (2018) Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, 19, 533–546.

Oke, K.B., Cunningham, C.J., Westley, P.A.H., Baskett, M.L., Carlson, S.M., Clark, J. et al. (2020) Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, 11, 4155.

Oosterhout, G.R., Huntington, C.W., Nickelson, T.E. & Lawson, P.W. (2005) Potential benefits of a conservation hatchery program for supplementing Oregon coast coho salmon (*Oncorhynchus kisutch*) populations: a stochastic model investigation. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1920–1935.

Paquet, P.J., Flagg, T., Appleby, A., Barr, J., Blankenship, L., Campton, D. et al. (2011) Hatcheries, conservation, and sustainable fisheries—achieving multiple goals: results of the Hatchery Scientific Review Group's Columbia River basin review. *Fisheries*, 36, 547–561.

Perrier, C., Bagliniere, J.L. & Evanno, G. (2013) Understanding admixture patterns in supplemented populations: a case study combining molecular analyses and temporally explicit simulations in Atlantic salmon. *Evolutionary Applications*, 6, 218–230.

Peterman, R.M., Holt, C.A. & Rutherford, M.R. (2012) *The need for international cooperation to reduce competition among salmon for a common pool of prey resources in the North Pacific Ocean*. North Pacific Anadromous Fish Commission Technical Report No. 8, 99–101.

Pinter, K., Epifanio, J. & Unfer, G. (2019) Release of hatchery-reared brown trout (Salmo trutta) as a threat to wild populations? A case study from Austria. *Fisheries Research*, 219, 105296.

Pullin, A.S., Cheng, S.H., Jackson, J.D.U., Eales, J., Envall, I., Fada, S.J. et al. (2022) Standards of conduct and reporting in evidence syntheses that could inform environmental policy and management decisions. *Environmental Evidence*, 11, 16.

Pustovrh, G., Sušnik Bajec, S. & Snoj, A. (2012) A set of SNPs for Salmo trutta and its application in supplementary breeding programs. *Aquaculture*, 370-371, 102–108.

Quiñones, R.M., Johnson, M.L. & Moyle, P.B. (2013) Hatchery practices may result in replacement of wild salmonids: adult trends in the Klamath basin, California. *Environmental Biology of Fishes*, 97, 233–246.

R Core Team. (2022) *R: a language and environment for statistical statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Radinger, J., Matern, S., Kleforth, T., Wolter, C., Feldhege, F., Monk, C.T. et al. (2023) Ecosystem-based management outperforms species-specific stocking for enhancing fish populations. *Science*, 379, 946–951.

Reisenbichler, R.R. & Rubin, S.P. (1999) Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES Journal of Marine Science*, 56, 459–466.

Riley, S.C., Tatara, C.P. & Scheurer, J.A. (2005) Aggression and feeding of hatchery-reared and naturally reared steelhead (*Oncorhynchus mykiss*) fry in a laboratory flume and a comparison with observations in natural streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1400–1409.

Robinson, H.E., Alexander, J.D., Hallett, S.L. & Som, N.A. (2020) Prevalence of infection in hatchery-origin chinook salmon correlates with abundance of Ceratonova Shasta spores: implications for management and disease risk. *North American Journal of Fisheries Management*, 40, 959–972.

Ruggerone, G.T., Agler, B.A. & Nielsen, J.L. (2012) Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environmental Biology of Fishes*, 94, 149–163.

Ruggerone, G.T. & Connors, B.M. (2015) Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 818–833.

Ruggerone, G.T. & Irvine, J.R. (2018) Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries*, 10, 152–168.

Ruggerone, G.T. & Nielsen, J.L. (2004) Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries*, 14, 371–390.

Ruggerone, G.T., Springer, A.M., van Vliet, G.B., Connors, B., Irvine, J.R., Shaul, L.D. et al. (in press) *From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems*. Marine Ecology Progress Series.
Shaul, L. & Geiger, H. (2016) Effects of climate and competition for offshore prey on growth, survival, and reproductive potential of Coho Salmon in Southeast Alaska. *North Pacific Anadromous Fish Commission Bulletin*, 6, 329–347.
Scheuerell, M.D., Buhle, E.R., Semmens, B.X., Ford, M.J., Cooney, T. & Carmichael, R.W. (2015) Analyzing large-scale conservation interventions with Bayesian hierarchical models: a case study of supplementing threatened Pacific salmon. *Ecology and Evolution*, 5, 2115–2125.
Seiler, S.M. & Keeley, E.R. (2009) Competition between native and introduced salmonid fishes: cutthroat trout have lower growth rate in the presence of cutthroat–rainbow trout hybrids. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 133–141.
Sharma, R., Morishima, G., Wang, S., Talbot, A. & Gilbertson, L. (2006) An evaluation of the Clearwater River supplementation program in western Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 423–437.
Shuntov, V.P., Ivanov, O.A. & Dulepova, E.P. (2019) Biological resources in the Sea of Okhotsk Large Marine ecosystem: their status and commercial use. *Deep Sea Research Part II: Topical Studies in Oceanography*, 163, 33–45.
Shuntov, V.P., Temnykh, O.S. & Naydenko, S.V. (2020) More on the factors that limit the abundance of Pacific Salmon (*Oncorhynchus* spp., Family Salmonidae) during the ocean phase of their life history. *Russian Journal of Marine Biology*, 45, 511–524.
Skaala, K.E., Jørstad, K.E. & Borgstrom, R. (1996) Genetic impact on two wild brown trout (*Salmo trutta*) populations after release of non-indigenous hatchery spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 2027–2035.
Skinner, M.K. & Nilsson, E.E. (2021) Role of environmentally induced epigenetic transgenerational inheritance in evolutionary biology: Unified Evolution Theory. *Environmental Epigenetics*, 7, dvab012.
Small, M.P., Taylor, E., Currens, K., Johnson, T.H., Frye, A.E. & Von Bargen, J.F. (2009) Impacts of supplementation: genetic diversity in supplemented and unsupplemented populations of summer chum salmon (*Oncorhynchus keta*) in Puget Sound (Washington, USA). *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1216–1229.
Splendiani, A., Giovannotti, M., Righi, T., Fioravanti, T., Cerioni, P.N., Lorenzoni, M. et al. (2019) Introgression despite protection: the case of native brown trout in Natura 2000 network in Italy. *Conservation Genetics*, 20, 343–356.
Sturdevant, M.V., Fergusson, E., Hillgruber, N., Reese, C., Orsi, J., Focht, R. et al. (2011) Lack of trophic competition among wild and hatchery juvenile chum salmon during early marine residence in Taku Inlet, Southeast Alaska. *Environmental Biology of Fishes*, 94, 101–116.
Tatara, C.P. & Berejikian, B.A. (2012) Mechanisms influencing competition between hatchery and wild juvenile anadromous Pacific salmonids in fresh water and their relative competitive abilities. *Environmental Biology of Fishes*, 94, 7–19.
Thaulow, J., Borgstrøm, R. & Heun, M. (2012) Brown trout population structure highly affected by multiple stocking and river diversion in a high mountain national park. *Conservation Genetics*, 14, 145–158.
Valiquette, E., Perrier, C., Thibault, I. & Bernatchez, L. (2014) Loss of genetic integrity in wild lake trout populations following stocking: insights from an exhaustive study of 72 lakes from Quebec, Canada. *Evolutionary Applications*, 7, 625–644.
Venditti, D.A., Kinzer, R.N., Apperson, K.A., Barnett, B., Belnap, M., Copeland, T. et al. (2018) Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 1495–1510.
Venney, C.J., Bouchard, R., April, J., Normandeau, E., Lecomte, L., Côté, G. et al. (2023) *Captive rearing effects on the methylome of Atlantic salmon after oceanic migration: sex-specificity and intergenerational stability*. bioRxiv:2022.2010.2003.510655.
Wang, S., Hard, J.J. & Utter, F. (2002) Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries*, 11, 301–319.
Waples, R.S. (1991) Genetic interactions between hatchery and wild salmonids: lessons from the Pacific northwest. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 124–133.
Ward, E.J., Adkison, M., Couture, J., Dressel, S.C., Litzow, M.A., Moffitt, S. et al. (2017) Evaluating signals of oil spill impacts, climate, and species interactions in Pacific herring and Pacific salmon populations in Prince William Sound and Copper River, Alaska. *PLoS One*, 12, e0172898.
Warren, D.R., Harvey, C.J., McClure, M.M. & Sanderson, B.L. (2014) Use of an ecosystem-based model to evaluate alternative conservation strategies for juvenile chinook salmon in a headwater stream. *North American Journal of Fisheries Management*, 34, 839–852.
Weigel, D.E., Adams, J.R., Jepson, M.A., Waits, L.P. & Caudill, C.C. (2019) Introgressive hybridization between native and non-local steelhead (*Oncorhynchus mykiss*) of hatchery origin. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 292–302.
Wenne, R., Bernaś, R., Poćwierz-Kotus, A., Drywa, A. & Wąs, A. (2016) Recent genetic changes in enhanced populations of sea trout (*Salmo trutta.trutta*) in the southern Baltic rivers revealed with SNP analysis. *Aquatic Living Resources*, 29, 103.
Williamson, K.S. & May, B. (2005) Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management*, 25, 993–1009.
Willmes, M., Hobbs, J.A., Sturrock, A.M., Bess, Z., Lewis, L.S., Glessner, J.J.G. et al. (2018) Fishery collapse, recovery, and the cryptic decline of wild salmon on a major California river. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 1836–1848.
Willoughby, J.R. & Christie, M.R. (2019) Long-term demographic and genetic effects of releasing captive-born individuals into the wild. *Conservation Biology*, 33, 377–388.
Wishard, L., Seeb, J., Utter, F. & Stefan, D. (1984) A genetic investigation of suspected redband trout populations. *Copeia*, 1984, 120–132.
Young, K.A. (2013) The balancing act of captive breeding programmes: salmon stocking and angler catch statistics. *Fisheries Management and Ecology*, 20, 434–444.
Zaporozhets, O. & Zaporozhets, G. (2004) Interaction between hatchery and wild Pacific salmon in the Far East of Russia: a review. *Reviews in Fish Biology and Fisheries*, 14, 305–319.

SUPPORTING INFORMATION

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

How to cite this article: McMillan, J.R., Morrison, B., Chambers, N., Ruggerone, G., Bernatchez, L., Stanford, J. et al. (2023) A global synthesis of peer-reviewed research on the effects of hatchery salmonids on wild salmonids. *Fisheries Management and Ecology*, 30, 446–463. Available from: https://doi.org/10.1111/fme.12643