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A Review of Habitat Connectivity Research for Pacific Salmon in Marine, Estuary, and Freshwater Environments

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Research Impact Statement: Science supporting Pacific salmon habitat connectivity is dominated by freshwater studies with limited marine and estuary work that is also critical for effective conservation planning.

ABSTRACT: Long-term conservation planning for diadromous fishes would benefit from a better understanding of both the role of connectivity among environments and habitat variability in the expression of life-history diversity. Most of the scientific knowledge on habitat fragmentation and connectivity has been developed in terrestrial systems in the discipline of landscape ecology. Research on habitat connectivity in aquatic systems (e.g., salmonid research that spans the spectrum of habitats from freshwater to the sea) is uncommon and largely focused on barriers to fish passage. Here, we present a review of the literature characterizing current research patterns on habitat connectivity within and among environments for Pacific salmon. We found this topic is still incipient: the literature is dominated by studies of freshwaters, with few articles focusing on habitat needs in estuary and marine systems. Pan-environment studies are rare, pointing to a gap in our understanding of complex habitat relationships that might be significant in the development of long-term conservation and restoration plans for Pacific salmon, particularly in light of the potential impact of climate change.

(KEYWORDS: Pacific salmon; habitat connectivity; freshwater; estuary; marine; complementarity; spatial arrangement; neighborhood effects.)

INTRODUCTION

Diadromous fishes (Myers 1949), such as Pacific salmon (*Oncorhynchus* spp.) in western North America, move through freshwater, estuary, and marine environments in order to complete their life cycle. For most Pacific salmon species, specific habitat types are required in each of these environments, and vary with life stage and life history (Figure 1) (Dadswell et al. 1987; Groot and Margolis 2003). Some species, such as Sockeye (*Oncorhynchus nerka*) and Masu (*O. masou*), spend similar amounts of time in freshwater and marine environments. This compares with species such as Chum (*O. keta*) and Pink (*O. gorbuscha*) whose life history tends to be more dominated by a marine environment (Groot and Margolis 2003). Thus, the connectivity among environments throughout the Pacific Rim is fundamental to long-term population persistence (Phelan 2003). Indeed, the dependence of Pacific salmon on multiple environments may complicate specific life-history strategies as climate change alters each environment in different ways (Crozier et al. 2008) and at potentially small spatial extents (Griffiths et al. 2014b). Further, changes in land and water uses (Poff et al. 1997; Graf 2006) may shift the location and distribution of available or connected habitats required for the completion of salmonid life histories (Sheer and Steel 2006), and may have already altered selection

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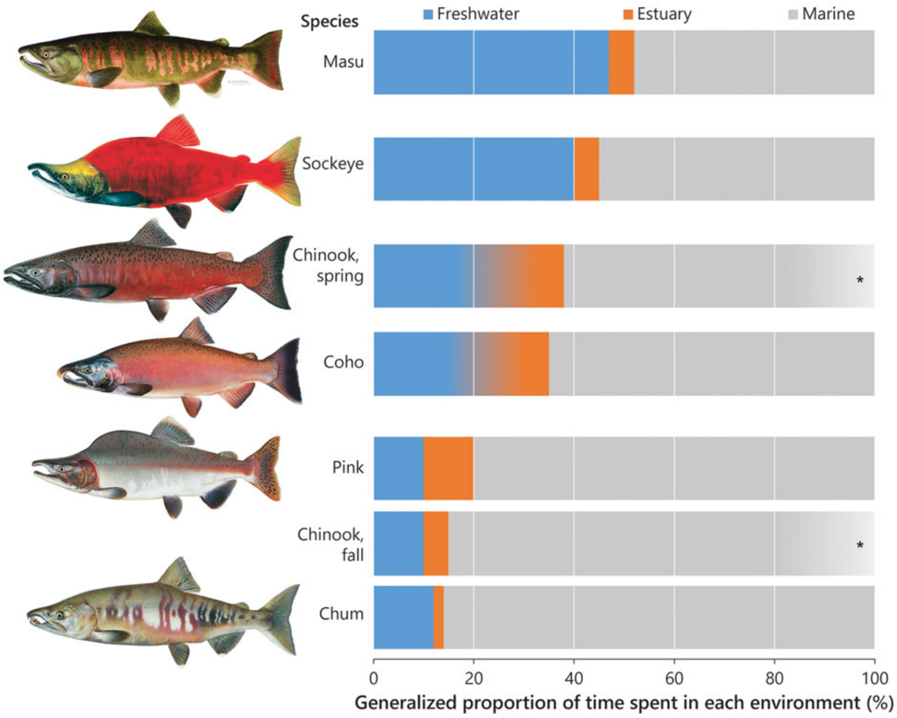

FIGURE 1. Generalized proportion of life cycle spent in environments by species of Pacific salmon. Variation in the amount of time spent in each environment depends on habitat, climate, latitude, and inherited local adaptation. Variation in freshwater and estuary residence times in Chinook and Coho Salmon is interpreted to reflect life-history diversity that confers population-scale resilience to dynamic conditions. (*designates variability in years of marine residence).

pressures on salmonids, resulting in evolutionary changes in their expression of life-history adaptation (Waples et al. 2007). These anthropogenic activities have the potential to affect population-scale resilience across fishes' range (Griffiths et al. 2014a).

The complex behavioral phenology — the linkage between timing of life stage expression of an organism and the environment — of Pacific salmon reflects the selective pressures of historical environmental conditions characteristic of the dynamic landscape processes from freshwater to the ocean. Although highly variable among species, events related to phenology have been linked to patterns of climate (e.g., Flitcroft et al. 2016) that are necessary for spawning and successful juvenile rearing (Quinn et al. 1997; Quinn 2005; Sykes et al. 2009). Estuary use by juvenile salmon provides important behavioral diversity and significantly contributes to population-scale survival and resilience (Reimers 1971; Ray 2005; Jones et al. 2014). Marine environments along the Pacific Coast of the Northern Hemisphere are highly productive for adult salmonids, but also strongly influenced by regional environmental conditions (Mueter et al. 2002). Broad-scale patterns of ocean-atmospheric climate have been associated with dramatic shifts in salmon productivity over time, from Alaska to California (Mantua et al. 1997). Thus, phenology defines how environments are connected, and may be vulnerable to changes in climate.

Although the importance of connectivity among habitats has been recognized (Schlosser 1991, 1995; Dunning et al. 1992; Schlosser and Angermeier 1995; Schofield et al. 2018), an empirical evaluation of habitat connectivity within or among the spectrum of habitats from freshwater to the sea for salmonids is scarce. As defined by Schlosser (1995), habitat *complementation* refers to species-specific habitat requirements that are not substitutable. This compares with habitat *supplementation*, in which species requirements for habitat may be substitutable across patches of habitat (Schlosser 1995). *Neighborhood effects* reflect the concept that fish movement is likely to occur into adjacent habitat patches rather than to distant patches (Schlosser 1995). Because of their need for habitats in multiple environments, restoration and long-term conservation planning for Pacific salmon would benefit from a clearer understanding of these concepts in the context of the multiple environments required for successful life-history completion.

In recent years, developments in modeling of river networks have enhanced the ability of researchers to graphically and statistically represent the configuration of habitats (Le Pichon et al. 2006, 2016; Erős et al. 2012; Isaak et al. 2014). For example, modeled metapopulations arrayed in habitats of dendritic river systems are susceptible to fragmentation (Fagan 2002). Carrara et al. (2012) found that headwater areas in constrained dendritic configurations were critical in maintaining regional biodiversity. Further, Carrara et al. (2014) found that clusters of habitat in the midpoint of a river network were associated with higher species richness. This builds on foundational conceptual work in freshwater environments describing predictable habitat configurations from the mouth to the headwaters from the River Continuum concept (Vannote et al. 1980), ideas regarding hierarchical organization of habitats (Frissell et al. 1986), and the Fausch et al. (2002) concept of the Riverscape. However, there is still much to be done, particularly in the development of analytical tools that capture the complexity of river network environments (e.g., Campbell Grant et al. 2007; Fullerton et al. 2010).

Habitat connectivity research has provided insights critical to conservation planning. For example, Thrush et al. (2008) explored the effect of habitat fragmentation and disturbance in estuary environments and showed that environmental conditions influence habitat recovery trajectories. Sogard (1992) found that different estuary habitats support different growth rates of marine-rearing fishes, contributing to the idea that understanding patterns of estuary habitat is important in fish conservation planning. In a recent review of seascape connectivity — landscape connectivity in the sea — Olds et al. (2016) saw stronger conservation outcomes resulting from greater seascape connectivity within marine reserves. Despite these findings, connectivity among habitats is not often a consideration in seascape research.

The effects of impaired connectivity within rivers due to physical barriers (roads and dams) have been studied intensively for migratory fishes (Pringle et al. 2000; Goodwin et al. 2014; Tullos et al. 2016). However, fewer studies have examined the importance of habitat connectivity among and within freshwater, estuary, and marine environments. Research on how habitats are used, the role of habitat complementarity and neighborhoods, and variability in habitat location over time, is critical to our understanding of the adaptive strategies of far-ranging and highly migratory species such as Pacific salmon. Such research is key to conservation planning and development of headwaters-to-the-ocean restoration strategies to bolster resilience in these species in the face of global environmental change.

Here, we explore current research on the topic of habitat connectivity within and among aquatic environments for Pacific salmon. We review what is known about connectivity, identify gaps in the published literature, and discuss how conservation planning might benefit from filling those gaps. We specifically excluded the topic of passage barriers, including dams and culverts. The immense body of literature on fish passage (or barriers to fish passage) in Pacific salmon alone would overwhelm any review of other types of research into habitat connectivity. For example, a Google Scholar Advanced Search using just the words “Pacific salmon” and “fish passage” returned over 21,800 articles between 1990 and 2018. Instead, we are particularly interested in research about the physical connectivity of habitats, rather than documenting fish passage, even though these topics are often interrelated. Thus, the focus of this review was at the intersection between studies of species movement, habitat descriptions, and the landscape/physical habitat template (Figure 2).

HABITAT CONNECTIVITY IN DIFFERENT ENVIRONMENTS

Freshwater Habitat Connectivity

For Pacific salmonids, spatial habitat relationships have been more thoroughly explored in freshwater environments than in the estuary or ocean. A search in Google Scholar found a predominance of publications

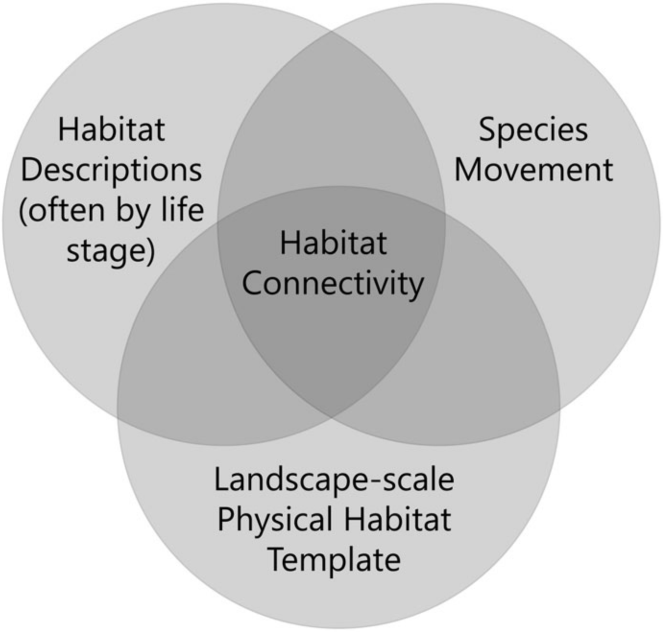

FIGURE 2. Venn diagram depicting the scope of this review on habitat connectivity that focuses at the nexus of research describing habitat, species movement, and the landscape-scale physical habitat template. These interrelated topics provide a foundation for understanding habitat connectivity in freshwater, estuary, marine, and combinations of environments.

on the topic of freshwater habitat connectivity compared with other habitat environments, or with pan-environment work (Appendix). In the freshwater literature, common research includes habitats for a single life stage, such as spawning, or for the diverse environments needed to complete the freshwater life stage.

Movement by individuals links habitat patches in freshwater systems. For example, juvenile Coho Salmon (*O. kisutch*) need different habitats at different life stages (Nickelson et al. 1992). Flitcroft et al. (2012, 2014) found that proximity between seasonal freshwater habitats is important in understanding interannual patterns of use, as habitat occupancy by juvenile fish occurred when seasonal habitats were close together, creating patches within stream networks that were consistently occupied over time. In another species, ecological neighborhoods (defined as habitat characteristics within 5 km) were the strongest predictor of anadromous Rainbow Trout (*O. mykiss*; Steelhead) spawning abundance in a study by Falke et al. (2013). Chinook Salmon consistently occupy patches of spawning habitat, but may expand out of core areas in years of larger population size (Isaak et al. 2007). Spatial distribution of spawning habitat may be important in modeling observed patterns of Chinook Salmon spawning (Carnie et al. 2016), and stream-channel bed mobility may be linked to species-specific spawning-site selection by salmonids (Montgomery et al. 1999). Anlauf-Dunn et al. (2014) showed that patterns of adult spawning Coho Salmon were best explained by the presence of connected seasonal habitats that support juvenile-rearing life stages. In Southeast Alaska, relative abundance of juvenile Rainbow Trout/Steelhead and Coho Salmon differs between mainstem and tributary habitats across seasons, with more fish using tributaries in the winter (Bramblett et al. 2002). In the Willamette River Basin, Oregon, life-history diversity among rearing juvenile Chinook Salmon (*O. tshawytscha*) contributed to population-scale resilience (Schroeder et al. 2016). In this large river system, juvenile fish that moved the longest distances (up to 100s of km) significantly contributed to production in the basin (Schroeder et al. 2016).

Movement among habitats in freshwater environments may also be a response to predicable food availability. Resident Rainbow Trout may move by as much as 7 km in a single summer in response to predictable patterns of food availability (Bentley et al. 2015). On the lower Sacramento River, floodplain habitats adjacent to the larger mainstem reaches may provide important food sources for rearing juvenile Chinook Salmon despite high temperatures during summer (Sommer et al. 2001).

River discharge and temperature have also been shown to be important in explaining patterns of habitat use for salmonids in freshwaters. Juvenile Coho Salmon respond to increased winter flows by moving between the fast-flowing mainstem and more protected tributary habitats (Ebersole et al. 2006; Hance et al. 2016), a response enabled by connectivity between habitats. LiDAR imagery, in conjunction with hydrologic monitoring, has been used to identify flow barriers for stream fishes (Grantham 2013). Stream power and depth are important in explaining interannual site occupancy patterns by spawning Chinook Salmon (Cram et al. 2017). Further, hydrologic variability in a managed flow system may result in higher smolt survival and outmigration success because it more closely mimics natural flow patterns and habitat connectivity (Zeug et al. 2014).

Thermal variability as well as physical habitat composition can be critical variables describing adult Chinook Salmon use of mainstem river habitats in spring (Torgersen et al. 1999). Further, thermal variability of freshwater habitat at fine spatial scales in different network configurations may be a means to better understand the potential effects of climate change on fish populations throughout river networks (Fullerton 2016). Scale of analysis can be important in differentiating between the role of temperature and stream geomorphology when distinguishing between cool- and coldwater fish assemblages, as temperature can be a strong driver at large spatial scales (Torgersen et al. 2006). Coho Salmon moved from natal habitats in tributaries to mainstem areas to find summer thermal refugia in the Klamath River, Oregon (Sutton and Soto 2012) — juvenile fishes reared in locations where cooler stream temperatures coincided with cover and low-velocity flows. In a watershed in Alaska, temperature is likely a determining habitat characteristic in daily use of freshwater habitats by juvenile Coho Salmon (Armstrong and Schindler 2013): juvenile fish fed in areas with high food availability, but then moved upstream to areas that were warmer to enhance digestion and food assimilation. Ultimately, thermal mosaics may influence juvenile Coho Salmon habitat use seasonally, resulting in varying movement strategies to exploit asynchronous thermal habitats and food sources (Baldock et al. 2016).

Estuary Environments

Anadromous fishes depend on estuary environments as they transition from freshwater to marine environments (Ray 2005). Estuary and tidal environments have been heavily altered by anthropogenic development. Tidal flood control structures on streams were associated with decreased abundance of five native fish species, including two salmonids, and increased diversity of non-native species in the Fraser River system in British Columbia, Canada (Scott et al. 2016). Estuary habitat availability for Pacific salmon and connection to freshwater environments may be constrained in future if predicted sea-level rise in Oregon estuaries floods existing highly productive salt marsh habitat (Flitcroft et al. 2013).

The importance of river/estuary connectivity for the expression of life-history diversity by Pacific salmon is an emerging topic with conservation implications (Koski 2009). Reimers (1971) described estuary life-history diversity in Chinook Salmon where the amount of time juvenile fish used the estuary led to different survival strategies at a population scale. Similarly, Jones et al. (2014) found that juvenile Coho Salmon whose habitat use spanned fresh and estuary environments expressed diverse movement life histories. Further, these juveniles had higher adult survival to spawning than the portion of the population that reared exclusively in freshwater. Estuary rearing by juveniles is also important to Sockeye Salmon that generally use lake environments (Simmons et al. 2013); the ability to exploit available estuary habitat when freshwater lacustrine habitat is limited can contribute to local population persistence.

The spatial location of estuary habitats for juvenile rearing was used in connectivity assessments between freshwater and estuaries in several recent studies. Bottom et al. (2005) found that restored salt marsh habitat facilitated the reemergence of estuary-rearing life histories in juvenile Chinook Salmon at Salmon River estuary in Oregon, USA. Juvenile Coho Salmon that use estuary environments can disproportionately contribute to the number of returning adult spawners in estuary-adjacent river reaches in Oregon (Weybright and Giannico 2018). Large estuary environments containing tidal marsh habitats are also important for Chinook Salmon rearing in the Columbia River Estuary (McNatt et al. 2016). But all estuary habitat is not the same for all salmonids: the five species of Pacific salmon present in the Columbia River estuary use shallow or deep estuary habitats at different times of the year in different ways (Roegner et al. 2016).

Marine Environments

Marine environments necessary for life stages of Pacific salmon include nearshore, continental shelf, and pelagic habitats. Connectivity between these environments is necessary for salmon to complete the portion of their life cycle that is dependent on marine environments. Few publications described the use of, patchiness in, or connectivity among marine habitats for Pacific salmon. McKinnell et al. (2014) suggested that nearshore coastal habitats are critical to explaining low Sockeye Salmon (*O. nerka*) returns to the Fraser River system in 2009. The authors explored the interaction between productivity and mixing in the water column along the migration route for smolts entering the ocean related to the bathymetry of the nearshore environment, and hypothesized about the effect of currents, temperature, mixing, and prey availability. This work points to the importance of nearshore environments and linkages to long-term ocean survival of salmonids.

Determining habitat distributions in marine environments is challenging. Bi et al. (2008) defined habitats using satellite-derived chlorophyll *a* and water depth to map patches of marine-rearing habitat in waters of the continental shelf off the coast of Washington and Oregon, USA. They used catch data to understand patterns of habitat usage by juvenile Chinook and Coho Salmon, and found the lowest habitat availability coincided with El Niño years.

Pan-Environments

The importance of habitat connectivity within and among freshwater, estuary, and marine environments, and the role of local adaptation to conditions in each of them is a critical frontier for fisheries science. Such research will be required for exploring potential population-scale response to climate change or other broad-scale disturbance processes. A few examples of research of this type can serve as models. Crozier et al. (2008) investigated the connection between freshwater habitat and marine survivorship when modeling the potential response to climate change in four populations of Chinook Salmon located in close proximity. They found that differential habitat and local adaptation to conditions resulted in variable potential responses of these populations to predicted changes in climate. Muir and Williams (2012) explored survival by outmigrating smolt and returning adult Chinook Salmon on the lower Snake and Columbia River systems as fishes traversed a series of hydroelectric dams. They showed that the physical alterations to dam passage that were currently in place would need to be supplemented with changes in flow management to allow better passage outcomes for outmigrants and returning adults.

GAPS IN WHAT WE KNOW

We found a strong focus in the literature on habitat connectivity for Coho Salmon, Sockeye Salmon, and Chinook Salmon, but limited information on other Pacific salmon species. Each species of Pacific salmon has a unique pattern of distribution and may use different combinations of habitats (Figures 1 and 3) (Groot and Margolis 2003). Therefore, investigations of habitat complementarity for Coho Salmon, for example, will not provide information relevant for Pink (*O. gorbuscha*) or Chum Salmon (*O. keta*). Both of these species tend to use larger mainstem habitats and estuaries in different ways for spawning and juvenile outmigration to the ocean compared with Coho Salmon (Figure 1). Research that addresses habitat needs for life stages of all species of Pacific salmon is not consistently available in the literature and poses a gap in species-specific and community-level restoration planning.

The paucity of marine habitat studies may reflect the challenge of assessments at the broad scale of the marine environment (Trudel et al. 2009). Additional challenges include the focus on population size inventories and stock assessment in marine settings as well as institutional separation and differences in jurisdiction among environments in management agencies, and disciplinary boundaries in academia (Bottom et al. 2009). Marine biologists tend not to focus on salmonids; likewise, salmon biologists tend to focus on freshwater. The resulting gap in understanding of important marine habitats necessary for salmonids makes holistic protection and restoration of habitats for these species problematic — particularly estuarine or marine habitats.

Limited pan-environment research for Pacific salmon is a significant gap in our understanding of habitat needs that may affect conservation actions aimed at population-scale restoration of these fishes. Most restoration and recovery planning for imperiled salmonids focuses exclusively on freshwater habitat. In work exploring the role of estuary habitats in recovery planning for salmon in the Columbia River Basin, Bottom et al. (2005) pointed to the gap in current restoration plans that tend to focus on freshwater areas to the exclusion of estuary habitats. Freshwater habitat that is the focus of restoration work is often not considered from the perspective of habitat connectivity, even for specific life stages. Rather, summaries of the amount of habitats for spawning or juvenile overwintering may be assessed and tallied at varying watershed scales. The ability of individual fish to move between habitats in a given season, or among habitats over time, which would help assess how much habitat can be used effectively by fishes, is rarely considered. This is ironic because connectivity among freshwater habitats has been demonstrated to explain patterns of adult spawning (Anlauf-Dunn et al. 2014), juvenile rearing (Flitcroft et al. 2012, 2014; Armstrong and Schindler 2013; Baldock et al. 2016), and overwinter survival (Ebersole et al. 2006). Additionally, freshwater habitat assessment generally focuses on shallow wadeable habitats rather than deeper mainstem areas that are more challenging to inventory or assess with traditional field survey methods. Yet these mainstem habitats provide both passage to upstream, tributary and headwater habitats, and may themselves pose barriers to in- and outmigration between marine, estuary, and upper freshwater habitats either through physical impediments, or temperature and flow conditions.

WHY CONNECTIVITY RESEARCH IS IMPORTANT

Research designed to understand habitat connectivity in aquatic environments for Pacific salmonids appears to be developing slowly. This contrasts with landscape ecology where research into habitat fragmentation that affects movement and migration is a fundamental perspective that drives the discipline and informs development of terrestrial reserves and conservation planning (Lindenmayer and Fischer 2006). The apparent delay in salmonid research may reflect, in part, the challenge of observing movement and habitat use by fishes that are concealed by high-flow or turbid water, deep water, or that travel vast distances. In this review, we found a variety of articles that addressed Pacific salmon within a particular type of environment (freshwater, estuary, or marine). In particular, we found that work on freshwater habitat connectivity is considerably more developed than work in other environments. Increasing numbers of publications in recent years may be a sign of increased interest in the topic of habitat connectivity (Appendix, Figure 1); however, this trend is confounded with increasing numbers of publications throughout the sciences in general (Fullerton et al. 2010).

Concern regarding the modifications that global climate change is predicted to make to aquatic habitats throughout freshwater and marine systems is a more recent topic of research, however, and may be one factor driving the increasing number of publications on habitat. Projected changes in streamflow and temperature due to climate change may result in differential effects on survival and reproductive success for salmonids (Mantua et al. 2010). These effects may be particularly detrimental in systems shifting from snow-dominated to rain-dominated hydrologies (Goode et al. 2013), making pan-environment or habitat connectivity research even more relevant for conservation planning. The warm "blob" in the eastern Pacific Ocean off

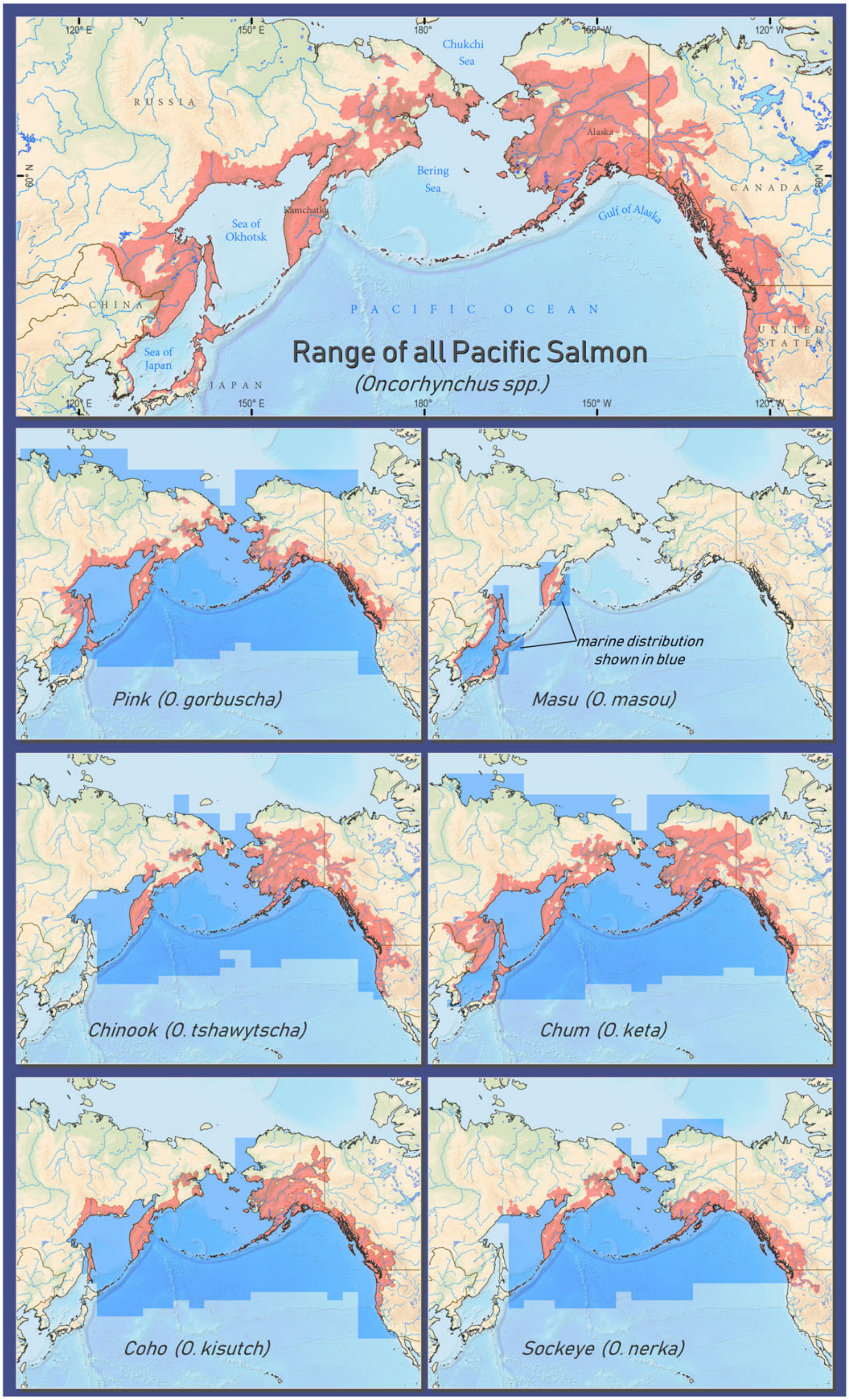

FIGURE 3. Geographic distributions of Pacific salmon. In many locations, distributions overlap, resulting in occupancy by multiple species of Pacific salmon that may or may not be seasonally synchronous. Species distribution data available from www.wildsalmoncenter.org/resources/state-salmon-database/.

the coasts of Oregon and Washington has been linked to lower survivorship and growth of salmonids, and is another emerging condition linked to environmental variability (Bond et al. 2015).

The multidisciplinary nature of management that seeks to support population-scale recovery of Pacific salmon requires incorporation of tools, techniques, and expertise from freshwater, estuary, and marine specialists. Methods relevant to inventories and assessment of habitat connectivity in small freshwater streams are different from those required to document deep-water river, estuary, or marine environments. Collaboration among disciplines would enhance the ability to knit together work completed using different techniques to better understand systems holistically.

Different spatial scales and resolution of information and technical understanding of habitat connectivity are relevant to restoration planning. Current understanding of adaptive resilience at population scales points to the importance of habitat connectivity that is linked to behavioral diversity of targeted species (Fausch et al. 2002; Bisson et al. 2009; Waples et al. 2009; Beechie et al. 2013; White et al. 2014). For example, by assessing patterns of spawning Sockeye Salmon in the Illiama Lake system, Alaska, Quinn et al. (2012) were able to describe the population structure as a small-scale metapopulation rather than panmictic, providing an important insight for management and conservation planning.

Effectiveness of restoration planning at broad spatial scales can be enhanced by using concepts of habitat connectivity in conservation designs. For example, Chelgren and Dunham (2015) found that systematic assessment at large spatial extents could enhance the targeting of barriers for replacement, thereby enhancing connectivity for stream fishes. Beechie et al. (2013) developed a decision support model that evaluated the effectiveness of restoration actions to ameliorate predicted future changes in streamflow and temperature in the Pacific Northwest of North America. They found that work that enhanced floodplain reconnection and restoration of natural processes was most effective at mitigating future climate effects. Roni et al. (2002) identified connectivity among habitats as the primary goal of instream restoration before a focus on restoration of natural processes could be effective. Schick and Lindley (2007) used directed network analysis to explore metapopulation connections to prioritize restoration planning for Chinook Salmon in California's Central Valley.

Logistical challenges and expense may be another challenge with pan-environment studies overall, and for marine studies in particular. Empirical studies that span environments would be costly to complete, requiring large numbers of people, time, and funding. Further, methods of fish capture, tracking, and monitoring vary by environment due, in part, to differences in environmental conditions (such as salinity) that require different technology and tools.

CONCLUSION

In order to design the most effective conservation plans for Pacific salmon or to identify the habitats or life stages most vulnerable to a changing climate, scientists, managers, and policy makers need to better understand habitat connectivity within and among environments. Many salmonid populations are listed as threatened or endangered in the southern extent of their range (e.g., California, Oregon, and Washington states, USA). Emerging research suggests that challenges to persistence of Pacific salmon may vary across species, cohort, life stages, and environments. Integrated science support, interdisciplinary research teams, and multidisciplinary communication among scientists, managers, and policy makers will help fill gaps in our collective understanding of salmonid requirements at individual life stages, and throughout their life cycle. This type of interdisciplinary research may require changes in the way agencies and academics conduct and report research findings to reflect the nature of connected systems from freshwater to the ocean that are critical for anadromous Pacific salmon.

APPENDIX REVIEW ARTICLE SEARCH AND SUMMARY INFORMATION

For this review, we sought articles that analyzed or reviewed connectivity among the same or different habitats, in freshwater, estuary, and marine environments. Because our focus was on habitat connectivity, we avoided papers on the topic of impairment of habitat connectivity, specifically, research related to migration or movement barriers. Instead, we searched for investigations into the importance of connectivity between specific habitat types for fish at various stages in their life cycle. Several avenues were pursued to identify articles for review. The need for multiple methods to identify articles of interest reflects inconsistency in the literature in the use of key terms to characterize publications focused on habitat connectivity. A Google Scholar search was completed using the terms: kisutch, tshawytscha, keta, nerka, gorbuscha, phenology, habitat connectivity, freshwater and estuary, and land use. This search resulted in 152

TABLE A1. Variables describing each article as part of this review of connectivity among habitats in freshwater, estuary, and marine environments for Pacific salmonids.

Review variables
id#
Title
First author
Publication year
Journal
DOI
Web link
Type of paper: empirical, model, review
Abstract
Country
State
River system
Environments: freshwater, estuary, marine
Salmon species
Life stage
Habitat connectivity between what types
Habitats discussed
Flow, temperature, other
Climate change implications
Finding

TABLE A2. Environments of interest in articles describing habitat connectivity for Pacific salmon.

Types of environments	
Freshwater	41
Estuary	7
Marine	2
Freshwater and estuary	3
Freshwater/estuary/marine	1

TABLE A3. Types of publications describing research on the topic of habitat connectivity for Pacific salmon.

Type of publication	
Empirical	20
Model	4
Review	11
Empirical/model	14
Theory	2
Thesis	3

articles of interest. We reviewed each article to ensure it focused on habitat connectivity. We also found additional articles by searching the literature cited sections of the articles from our initial selection. The final selection consisted of 54 articles (Supporting Information 1).

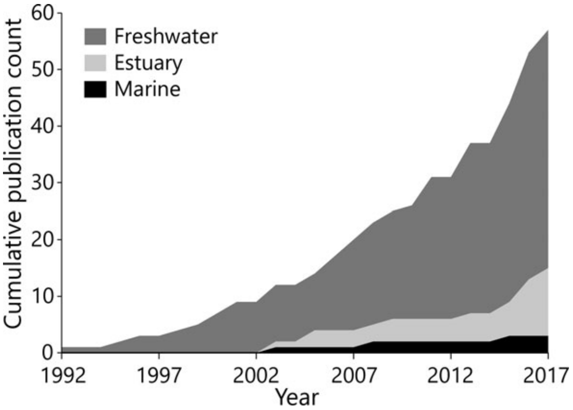

FIGURE A1. Cumulative counts of publications on the topic of Pacific salmon habitat connectivity between 1990 and 2018.

We read all articles identified for this review and developed a database that included assessments of information of interest. This included 20 variables encompassing source information-specific habitat types analyzed (Table A1). Summaries of different types of information included: location of work; types of publications; the number of articles that addressed habitat by environmental categories (freshwater, estuary, marine) or in combinations of categories (freshwater/estuary, freshwater/marine, estuary/marine, or freshwater/estuary/marine); and the number of habitat connectivity articles over time.

More articles were available that focused on connectivity of Pacific salmon in freshwater environments (*n* = 41) (Table A2). Most of the articles were empirical (*n* = 20), with empirically informed models also constituting a large number of articles (*n* = 14) (Table A3). Over time, the cumulative number of articles appeared to increase most sharply after 2012 (Figure A1).

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: The list of articles on the topic of connectivity within and among environments that was used as part of this review.

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