

Spatial linkages and stability of Pacific salmon

by

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Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

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SIMON FRASER UNIVERSITY

Spring 2022

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Abstract

Migratory animals cross the spatial boundaries of ecosystems and subsidize food web productivity through the input of externally derived resources. However, human activities have altered such spatial linkages through the spread of non-native species. Moreover, the conservation and management of migratory animals is complicated by the broad spatial scales over which they occur. In this thesis, I use field-based studies to examine the spatial linkages created by the Chinook salmon invasion of Patagonia, southern Chile, and apply a metacommunity framework to understand the spatial stability of Pacific salmon. First, I investigate whether Chinook salmon in Patagonia subsidize stream algae through the delivery of marine-derived nutrients. I show that marine-derived nutrients increase algal biomass, indicating that salmon have established a novel linkage between freshwater and marine ecosystems in Patagonia. Next, I use field-based observations and a literature review to examine the trophic interactions that have emerged following this invasion. I describe novel trophic interactions and present evidence that the pathways of salmon nutrient incorporation in North American food webs have functionally re-emerged in South America. Lastly, I use spatio-temporal reconstructions of annual Pacific salmon abundance across the North Pacific Ocean and within northern British Columbia (BC) to test the hypothesis that ecological properties temporally stabilize across larger areas. Across six decades of abundance estimates, I find that the temporal stability of annual salmon abundance is significantly greater in the North Pacific than in northern BC due to the stabilizing effect of spatial asynchrony. I also show that hatchery production of salmon has only a marginal effect on local stability in regions with viable salmon stocks, calling into question the efficacy of hatcheries in stabilizing salmon populations. Overall, this thesis enhances our understanding of the ecological impacts of Patagonian salmon and the effect of salmon management practices on stability while also addressing broader patterns in the trophic interactions that emerge following biological invasions and the emergent properties of ecological systems across spatial scales.

Keywords: invasive species; natural history; nutrient subsidy; Pacific salmon; Patagonia; portfolio effect

To my loving Grandy, Shirley Shore (1925 – 2021).

Every bird sings to me. Every flower blooms for me.

Acknowledgements

I'm incredibly grateful to have been able to work as a doctoral researcher for more than six years. It's a privilege to be able to explore ideas and have your work life guided by your interests, by what you feel in your heart. I have many people to thank for this.

Firstly, I thank John Reynolds and Bryan Neff for being excellent supervisors and consistent sources of support. John, thank you for taking a flyer on this guy that wanted to study Chilean salmon. It's been a pleasure working with you and within your research group; your passion for nature is infectious and has inspired the kind of work I'd like to do in my career. Bryan, thank you for supporting me and my work since day one in 2010. After my masters, I had doubts about my ability to go on in research, and I probably would not be writing a PhD thesis without the confidence you had in me.

I thank my two committee members – Wendy Palen and Jonathan Moore – for helping me navigate this work and helping me filter the good ideas from the not-so-good ones. The support and validation I received from you during our annual meetings was a major boost, especially in terms of my confidence and excitement for continuing this work.

I thank Cristián Correa and Brian Reid for being incredible collaborators and helping me lay the groundwork to create a new field research program in Patagonia. Beyond the logistical support, by welcoming me into your homes you helped me feel settled in a new place.

Además, agradezco el apoyo del personal del CIEP y la hospitalidad de varias personas en la región de Aysén. Esto incluye: Vicente Fuentes, Orelío Domingue, Silvia Vidal, Enrique Vidal, Catherin Fuentes, los Corrascos, Glauco Baez y su familia, Jonathan Poblete, Héléne Dubrasquet, Anna Astorga, Isai Madriz, Luis Uribe, y Sole Barahona. Muchísimas gracias.

I'm really grateful to have been part of the Reynolds lab and to have been colleagues and friends with so many wonderful people. Thank you Kirsten Wilcox, Marlene Wagner, Sean Godwin, Jane Pendray, Jess Walsh, Allison Dennert, Debora Obrist, Michael Price, Celeste Kieran, Eric Hertz, and Jess Edwards. Special thanks to Sandra Vishloff for putting up with my shenanigans. Similarly, E2O has been an incredible place to work for all these years, and I'll miss the many people that made this time a fun and fulfilling

one. Too many people to list, but a special thank you to Alex Sawyer for loving my avocados and Sarah Gravel for everything.

Thank you Eric Girard for being like a brother to me. Shoutout to squad.

Thank you Karen and Donna for welcoming me into your lives and making me feel at home. Thank you to my family out west for the much-needed family time, it meant a lot having you look out for me and being able to see you.

I couldn't have gotten through this without the love and support of my family. Thank you mom, dad, and Ti for always having my back and always making me feel grounded, even when times were tough. It meant the world to me that each of you came to visit while I was in Patagonia.

Last but not least, thank you Dawn. I could write an entire thesis about the joy you have added to my life and what it's meant to me. You've been a partner in every sense of the word, and I absolutely could not have done this without you.

I dedicated this thesis to my grandmother, Shirley Shore. When I first decided to do a PhD based out of Vancouver, she had a very Grandy-esque proposal: that we make a road trip out of it, driving from Ontario to BC. With Dawn, we made the trip, and celebrated her 90th birthday along the way. That encapsulates her in so many ways, her love, support, and sense of adventure. Thank you for a lifetime of love and inspiration, Grandy. I miss you.

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Chapter 1.

General Introduction

The natural world is one of connection. The movement of animals and nutrients across the spatial boundaries of ecosystems is ubiquitous and fundamental to the functioning of food webs (Polis et al. 1997). However, such resource linkages have been disrupted by human activities. Overexploitation of marine mammals has diminished the vertical and lateral movement of nutrients through the ocean by 95% from historical values, whereas the decline of anadromous fishes and seabirds has reduced the transfer of phosphorus from ocean to land by over 96% (Doughty et al. 2016). Indeed, migratory freshwater fishes have declined by an average of 76% globally (Deinet et al. 2020) and are disproportionately threatened relative to other fishes (Darwall and Freyhof 2016).

In addition to overexploitation, the spread of non-native species can also alter linkages among ecosystems. For example, non-native rats in the islands of the Chagos Archipelago reduce seabird densities and nitrogen deposition rates on land by 760 and 251 times, respectively, and subsequently reduce fish biomass in adjacent coral reef ecosystems due to the disruption of nutrient leaching from islands to the sea (Graham et al. 2018). Such severe impacts of invaders generally occur when non-native species are taxonomically and functionally unique in invaded food webs such that native species lack eco-evolutionary experience with the invader (Ricciardi and Atkinson 2004; Saul and Jeschke 2015; Schittko et al. 2020). Whereas a non-native predator can disrupt resource linkages due to the eco-evolutionary naivete of migratory prey (as occurs with the Chagos Archipelago rats), a non-native migratory species may establish a novel resource linkage between ecosystems.

The historical spread of non-native species is inextricably linked with colonialism. For example, as part of the “Columbian Exchange”, European colonizers introduced non-native pathogens to the Indigenous Peoples of the Americas to devastating effect, and also introduced a variety of Old World plant and animal species while converting habitat for non-native crop and livestock production (Nunn and Qian 2010). Contemporary invasions often occur incidentally as a by-product of human globalization

and commerce (Meyerson and Mooney 2007); however, the intentional introduction and propagation of non-native species is still widespread today (Ewel et al. 1999). Such propagation typically occurs when economic value can be derived from the ecosystem services provided by the non-native species, with some non-native species being considered desirable due to their socio-economic benefits and minimal or beneficial ecological impacts (Schlaepfer et al. 2011). However, the desirability of a given non-native species is subjective, and the ecological impacts of a novel introduction are difficult to predict (Vitule et al. 2012). Moreover, the economic benefits of non-native species can be concentrated within foreign-owned private enterprises, which risks continuing the ecological colonialism that has historically occurred in the Global South.

A fascinating study system for understanding the impacts of non-native species is the Patagonia region of southern Chile. Its mountainous terrain lined by coastal fjords has left this region free from large-scale industrial development and human settlement. These geographic barriers have also contributed to its biological diversity being relatively species-poor but highly endemic (Ormazabal 1993; Valdovinos 2006; Scherson et al. 2014; Cussac et al. 2016). Ecological theory predicts that such species-poor communities have low biotic resistance to invasions (Elton 1958) and, indeed, many non-native species have established in Patagonia. Several of the most impactful invaders were intentionally introduced from North America or Europe for commercial or recreational purposes, including rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), American mink (*Neovison vison*), pine trees (*Pinus contorta*), European hares (*Lepus europaeus*), North American beavers (*Castor canadensis*) and, most recently, Chinook salmon (*O. tshawytscha*).

Juvenile Chinook salmon were stocked in several streams in southern Chile from the mid-1970s to the early 80s by an American company and a Chilean economic development organization for “ocean ranching” aquaculture (Correa and Gross 2008). Adult returns were poor from these efforts, and ocean ranching was replaced by net-pen production, which proved exceptionally successful and led to Chile becoming one of the world’s largest producers of salmon (Correa and Gross 2008). However, the stocked fish seeded self-sustaining populations, and by the early 2000s annually spawning populations of Chinook had colonized all inhabitable watersheds in southern Chile (Correa and Gross 2008). This invasion has led to conflicting views among stakeholder groups regarding the desirability of wild Chinook, with some (such as environmentalists

and scientists) viewing the fish as a problematic invasive species and others (namely recreational fishers) viewing the fish as valuable and requiring protection (Cid-Aguayo et al. 2021). This conflict has been worsened by the legal invisibility of the species: the establishment of wild Chinook salmon has not been formally acknowledged by regulatory bodies, and any free-living salmon found in the waters of Chile is legally recognized to be the property of salmon aquaculture companies, with these companies having lobbied the government for the implementation of this law (Cid-Aguayo et al. 2021). There is now an artisanal fishery for Chinook salmon that is forced to operate illegally and under no formal management structure (although the first legal opening of a Chinook fishery occurred near the Toltén watershed in 2018) (Cid-Aguayo et al. 2021). Thus, there is a pressing need for some form of management action and for this action to be informed (in part) by the ecological impacts of Patagonian salmon.

Whereas the ecological effects of Chinook salmon in Patagonia have been seldom studied, such effects in the native range of Pacific salmon (*O. spp.*) have been thoroughly characterized. Indeed, Pacific salmon represent one of the best-studied examples of cross-boundary resource linkages, with their anadromous and semelparous life cycle connecting marine, freshwater, and terrestrial ecosystems (Gende et al. 2002; Naiman et al. 2002; Walsh et al. 2020). These species support ocean fisheries across Pacific North America and Asia, and their return to natal streams as adults supports place-based fisheries, the traditional use of salmon by hundreds of coastal First Nations (Gayeski et al. 2018), aquatic and riparian consumers (Walsh et al. 2020), and local ecotourism (e.g., PSF 2014). However, salmon populations have been declining in the southern portion of their native range for multiple decades, with many populations in the Pacific Northwest, USA and British Columbia (BC), Canada being threatened with extinction (Gustafson et al. 2007).

The conservation and management of migratory species is complicated by the broad spatial scales across which they occur, which can include multiple habitat types and span multiple jurisdictions. Such efforts can benefit from the emerging field of metacommunity and metaecosystem ecology, which recognizes the biotic and abiotic linkages among food webs and ecosystems and thus explicitly considers the spatial dynamics of species and ecological processes (Loreau et al. 2003; Leibold et al. 2004). Recently, a metacommunity framework has been developed that quantifies the drivers of the temporal stability (i.e., invariability through time) of aggregate ecological properties

(e.g., community biomass, metapopulation abundance), with stability at the metacommunity (i.e., regional) scale posited to be a product of stability at the local community (i.e., local) scale and asynchrony among local communities (Wang and Loreau 2014). The broad yet flexible spatial scales to which this framework can be applied make it a promising tool in the management of migratory species such as salmon. For example, if the artisanal fishery for Chinook salmon in Chile is eventually legalized, this tool could be used by managers to understand the inter-annual reliability of ecosystem services provided by Chinook salmon, both at the regional scale (e.g., catch and fisheries revenue in all of Chile) as well as those at local scales (e.g., delivery of marine-derived resources within individual watersheds, local ecotourism revenue).

In this thesis, I tested hypotheses concerning (1) the ecological impacts of Chinook salmon in Patagonia, and (2) the stability of ecological properties across spatial scales. Specifically, in Chapter 2 I investigate whether Chinook salmon stimulate the biomass of algae in Patagonian streams through the delivery of marine-derived nutrients. I present evidence that marine-derived nutrients from adult salmon increase algal biomass, indicating that salmon have established a novel resource linkage between stream and marine ecosystems in Patagonia. In Chapter 3, I examine the trophic interactions that have emerged following the Chinook salmon invasion of Patagonia using i) field-based observations of salmon carcass consumption and ii) a literature review of all documented interactions. I find that a multitude of native and non-native species in Patagonia consume the novel resources provided by post-reproductive salmon, and that these beneficiaries are phylogenetically similar to those in the native range of salmon. Lastly, in Chapter 4 I test a recent hypothesis in metacommunity ecology (Wang and Loreau 2014) that ecological properties temporally stabilize across increasingly large spatial scales. Using spatio-temporal reconstructions of Pacific salmon abundance across the North Pacific Ocean and within northern BC, I find that spatial asynchrony stabilizes annual salmon abundance to a greater degree in the North Pacific than in northern BC, supporting the hypothesis of Wang and Loreau (2014). Taken together, this work increases our understanding of the spatial linkages and stability of Pacific salmon and is relevant to the management of salmon in Patagonia as well as the management and study of ecosystem services across spatial scales.

Chapter 2.

Non-native Chinook salmon add nutrient subsidies and functional novelty to Patagonian streams¹

2.1. Abstract

The impacts of non-native species are hypothesized to be proportional to the functional distinctiveness of invaders in their invaded ecosystems. Throughout the Patagonia region of southern South America, Chinook salmon (*Oncorhynchus tshawytscha*) have recently established non-native populations, and their anadromous, semelparous life cycle could be functionally unique such that marine-derived nutrients are delivered to streams which have historically lacked such a resource linkage with the ocean. We tested the hypothesis that salmon subsidize biofilm-associated algae in streams throughout the Aysén province of southern Chile. Using spatial and temporal variation in the presence of salmon among multiple streams and across two spawning seasons, we found strong evidence of salmon-subsidized algae in three out of four streams examined that have spawning salmon populations. The biofilm of subsidized streams had enriched stable isotopic ratios of nitrogen and carbon, indicating that marine-derived nutrients were incorporated by biofilms. This nutrient uptake translated into increased algal biomass and percent of total biofilm biomass composed of algae, indicating that the incorporation of marine-derived nutrients stimulated autotrophic production of biomass. In one stream, the incorporation of marine-derived nutrients by biofilm occurred in only one of the two studied spawning seasons. Incorporation occurred in a year with low flows of water throughout salmon spawning (4.59 m³/sec) and did not occur in a year with much higher flows (41.6 m³/sec), suggesting that inter-annual variation in discharge can mediate the subsidizing effect of salmon. These results indicate that Chinook salmon have bridged the historical gap between productive marine ecosystems and nutrient-poor stream ecosystems in Patagonia. Anadromous salmon can be a significant source of nutrients in nutrient-limited catchments, and their ongoing expansion in

¹ A version of this chapter appears as Muñoz, N.J., Reid, B.L., Correa, C., Neff, B.D., Reynolds, J.D., 2021. Non-native Chinook salmon add nutrient subsidies and functional novelty to Patagonian streams. *Freshwater Biology* 66, 495–508.

southern South America is likely to entail ecological impacts in stream and riparian food webs.

2.2. Introduction

The movement of energy and nutrients among ecosystems is fundamental to the productivity and composition of biological communities (Polis et al. 1997). These resources are often transported into ecosystems through the movement of animals and they can increase the biomass within recipient food webs beyond that which can be supported by in situ productivity alone (e.g. Atlas et al. 2013; Graham et al. 2018). Such subsidies are recognized as having a vital ecological function. For example, seabirds and anadromous fish bring marine-derived nitrogen and phosphorus into terrestrial and freshwater ecosystems (e.g. Graham et al. 2018; Hood et al. 2019; Walsh et al. 2020), and the widespread collapse of seabird and anadromous fish populations has resulted in the global transfer of phosphorus from sea to land declining over 96% from historic levels (Doughty et al. 2016). Whereas the loss of historic connections among ecosystems disrupts nutrient cycles and recipient food web productivity (Gresh et al. 2000), the emergence of novel resource linkages among ecosystems that occur due to the establishment of non-native species could be equally disruptive.

One of the best described systems of resource subsidization concerns Pacific salmon (*Oncorhynchus* spp.) in freshwater and terrestrial ecosystems in Pacific North America. Pacific salmon are anadromous, gaining 99% of their biomass in the ocean before returning to their natal streams to spawn en masse and subsequently die of rapid senescence (Quinn 2018). Aquatic and terrestrial ecosystems are typically nutrient limited in that the biomass of primary producers is limited by the availability of nitrogen and phosphorus (Elser et al. 2007). As such, the annual pulse of marine-derived nitrogen and phosphorus from salmon carcasses can strongly subsidize autotrophic and heterotrophic production in both streams and the surrounding riparian habitat (Gende et al. 2002; Janetski et al. 2009; Walsh et al. 2020). Salmon-derived nutrients enter these food webs through a wide variety of pathways. Direct consumption of salmon carcasses increases the biomass of collector and shredder invertebrates (Chaloner and Wipfli 2002; Lessard and Merritt 2006), and consumption of salmon eggs increases the biomass of a variety of stream fishes (Scheuerell et al. 2007; Armstrong et al. 2010; Bentley et al. 2012; Swain et al. 2014; Bailey and Moore 2020; Hermann et al. 2020).

Carcasses that are deposited in the riparian zone are heavily consumed by terrestrial insects (Hocking and Reimchen 2002) and cause soils to accumulate nitrogen, affecting the composition of riparian plant assemblages (Hocking and Reynolds 2011; Morris and Stanford 2011) and enhancing the growth of spruce trees (Quinn et al. 2018). Some carcasses are flushed downstream into estuaries, where they are scavenged by gulls and subtidal invertebrates (Field and Reynolds 2013; Reimchen 2017). Alternatively, salmon-derived nutrients can enter stream food webs through the uptake of dissolved nutrients in the water column by the microbial communities comprising benthic biofilms.

Biofilms are a complex aggregation of algae, bacteria, protozoa, fungi, and archaea found on submerged rocks. They can be subsidized by salmon at multiple time scales, both during spawning (i.e., weeks; Schuldt and Hershey 1995; Chaloner et al. 2007) as well as months after spawning due to retention of salmon-derived nutrients within the ecosystem (O’Keefe and Edwards 2002; Harding et al. 2014). Conversely, salmon can have a negative effect on biofilm biomass during spawning due to the physical disturbance of the streambed caused by females digging nests (i.e., redds) (e.g., Moore and Schindler 2008; Holtgrieve and Schindler 2011), although streams that experience such disturbance during spawning can still retain salmon nutrients (Rex and Petticrew 2008) and can be subsidized by salmon months after spawning (Harding et al. 2014). Subsidized biofilm can propel salmon-derived nutrients up the food web. For example, biofilm biomass and macroinvertebrate density are 15 and 25 times higher, respectively, in a salmon subsidized stream in Alaska relative to a non-subsidized stream (Wipfli et al. 1998). In British Columbia, salmon spawner density among streams is positively associated with the abundance of biofilm-grazing mayflies (Verspoor et al. 2011) and insectivorous forest birds (Wagner and Reynolds 2019). Indeed, as the resource base for higher trophic levels, biofilms can have strong, bottom-up effects, as key sites of primary production and the transfer of carbon from autotrophic to heterotrophic organisms (Rosemond et al. 2000; Risse-Buhl et al. 2012).

One of the few instances of a Pacific salmon establishing self-sustaining populations outside of their native range has recently occurred in Patagonia, southern South America. Introduction attempts for commercial purposes in the 1970s and 80s seeded the establishment of Chinook salmon (*O. tshawytscha*) populations in a few streams in southern Chile (Correa and Gross 2008). Since these efforts, Chinook have colonized seemingly all inhabitable watersheds in southern Chile, from 39 to 55° S, and

have even crossed the Strait of Magellan and colonized Atlantic-draining watersheds in Argentine Patagonia (Di Prinzio and Pascual 2008). Most of the research to date on Patagonian Chinook has focused on genetic and life history diversity among populations (e.g., Araya et al. 2014; Correa and Moran 2017; Narum et al. 2017; Gomez-Uchida et al. 2018). Conversely, the food web and ecosystem impacts of these non-native populations have received little study (Soto et al. 2007; Ciancio et al. 2008; Arismendi and Soto 2012).

Chinook are the least abundant species of Pacific salmon in North America and require the largest streams and substrate sizes for spawning habitat (Kondolf and Wolman 1993; Gottesfeld et al. 2008). Larger substrates are harder to dislodge from the streambed and are therefore less prone to disturbance during salmon spawning (Janetski et al. 2009; Holtgrieve et al. 2010; Janetski et al. 2014). The larger substrates and lower densities in which Chinook spawn (relative to other salmon species) could mean that, in general, their disturbance (i.e., negative) effects are smaller than their subsidy (i.e., positive) effects on stream biofilms. For example, low densities of spawning Chinook salmon (<0.001 spawners/m²) caused a 46% increase in the gross primary production of three streams in Washington, USA (Benjamin et al. 2016), whereas moderate densities of spawning sockeye (*O. nerka*) salmon (>0.6 spawners/m²) caused a 72% reduction in gross primary production in three streams in Alaska (Holtgrieve and Schindler 2011). Although Chinook can have dramatic disturbance effects through the creation of spawning 'dunes' in the streambed (Gottesfeld et al. 2008), this behaviour is observed only in the largest rivers in which they spawn and has not been reported in Patagonia, suggesting that they could be more likely to have a subsidy effect in their South American range.

If Chinook salmon subsidize stream biofilms in Patagonia, these subsidies would represent a novel resource linkage between marine and freshwater ecosystems. The delivery of marine-derived nutrients to these ecosystems has historically not occurred due to the apparent absence of any native anadromous fish that spawn in the upper reaches of Andean watersheds (Alò et al. 2019). As such, Chinook are functionally unique in Patagonia. The ecological impacts of invasive species are hypothesized to be proportional to the functional distinctiveness of the invader in the recipient community (Vitousek 1990; Ricciardi and Atkinson 2004; Ricciardi et al. 2013; Schittko et al. 2020), meaning the novel function performed by Chinook would be predicted to have large

impacts. Moreover, southern Chile has one of the lowest rates of atmospheric nitrogen deposition in the world (Dentener et al. 2006). An annual pulse of marine-derived nutrients in these otherwise nutrient-poor systems (Perakis and Hedin 2002; Diaz et al. 2007) could therefore have a disproportionately strong ecological effect (Flecker et al. 2010).

The aim of this study was to test the hypothesis that nutrients from non-native Chinook salmon subsidize biofilm-associated algae in Patagonian streams. We sampled biofilm in the presence and absence of senescent salmon across two years and multiple streams. We used stable isotope analysis to assess the incorporation of marine-derived carbon and nitrogen by biofilms. Stable isotope analysis is a powerful, time-integrated technique for assessing sources of nutrients in food webs (Peterson and Fry 1987). Salmon tissue is highly enriched in ^{13}C and ^{15}N due to their trophic interactions in the marine food web, allowing the use of carbon and nitrogen isotopic ratios to test for the incorporation of marine-derived nutrients in consumer tissue (Gende et al. 2002; Naiman et al. 2002). To infer the presence or absence of a subsidy effect (i.e., an increase in biomass due to incorporation of an externally-produced, donor-controlled resource), we also tested whether marine-derived nutrients increase the biomass of algae by measuring biofilm chlorophyll *a* (a measure of algal biomass) and ash-free dry mass (a measure of total organic matter). We tested our hypothesis using two experimental designs that utilized spatial and temporal differences in the presence of senescent salmon.

2.3. Methods

2.3.1. Study sites

Field surveys were conducted in streams throughout the Aysén province of southern Chile (Figure 2.1). This area is in the Valdivian temperate rainforest ecoregion and is characterized by relatively low levels of human-modified land cover, forests dominated by southern beech trees (*Nothofagus* spp.), a seasonal climate, and strong longitudinal gradients in rainfall. Chinook salmon were first reported in this province in the early 2000s (Correa and Gross 2008) and now have annual spawning runs in many tributaries of its Andean watersheds. The main point sources for the Chinook invasion of Chile were stocking efforts between 1976 and 1987 in a few streams to the north (42° S)

and south (51° S) of the Aysén province, suggesting that watersheds here were colonized by straying salmon from established populations (Correa and Gross 2008; Correa and Moran 2017).

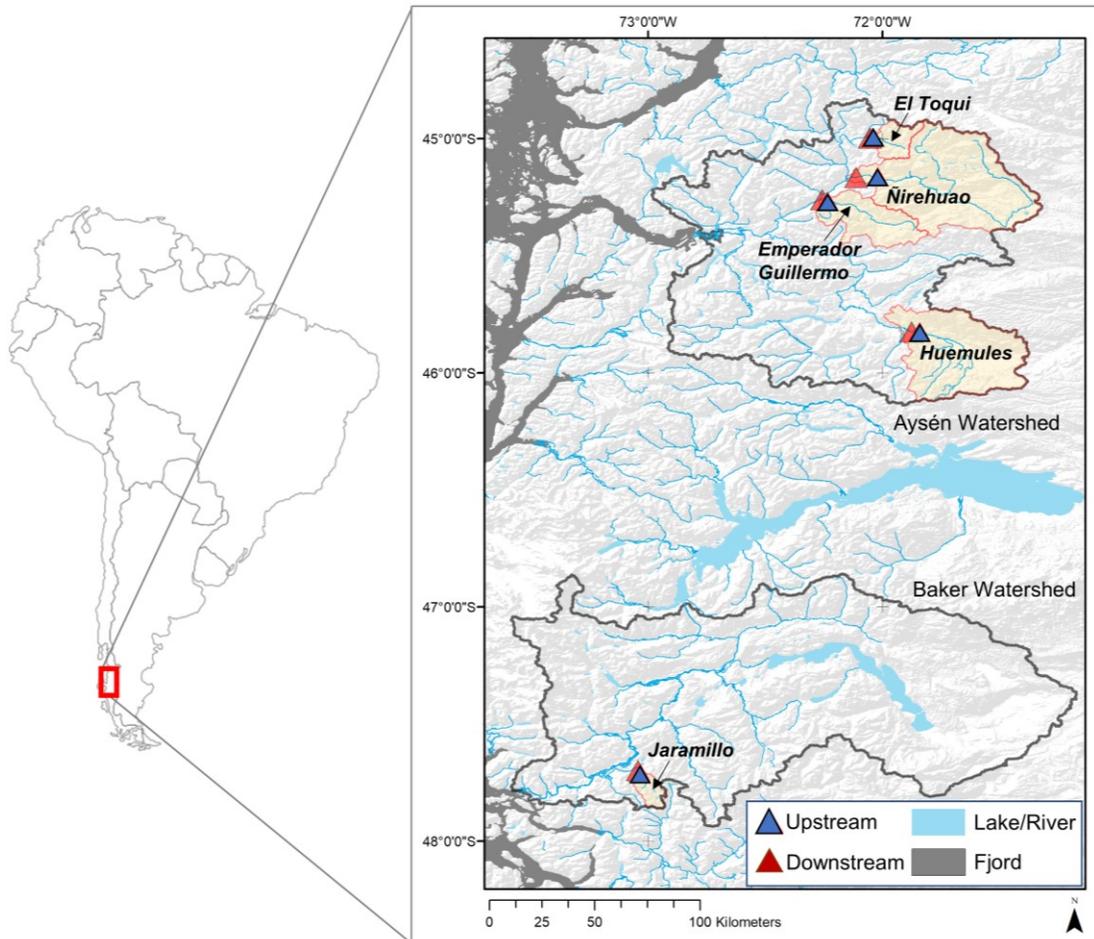


Figure 2.1 Map of study streams located throughout the Aysén province of southern Chile.

Shown are the upstream and downstream sites that were sampled in this study, as well as the drainage areas of each study stream (outlined in red) and of the two watersheds in which study streams were located (outlined in grey).

Five streams were used in this study: four in the Río Aysén watershed (El Toqui, Ñirehuao, Emperador Guillermo, and Huemules) and one in the Río Baker watershed (Jaramillo; Figure 2.1). These streams are dominated by non-native rainbow trout (*O. mykiss*) and brown trout (*Salmo trutta*), with native fishes being rare (Muñoz NJ, unpublished data) likely because of predation and competition imposed by trout (Correa and Hendry 2012). The streams range from third to fifth order and from 6 to 65 km in total length, the largest being Ñirehuao, which drains nearly 2,000 km² (Table 2.1).

Flows in these streams generally follow a rainfall-snowmelt transitional hydrologic regime and are typically high during the salmon spawning season due to heavy autumn rains. In Jaramillo, flows are regulated by a small, nearby lake. These streams were selected for the study due to the presence of a barrier to salmon migration in each one, which was key to the study design (described below). Additional criteria included accessibility, evidence of salmon runs, and similar land use upstream vs. downstream of the barrier.

Table 2.1 Stream and survey characteristics for study systems in Patagonia, southern Chile.

Stream name	Drainage area (km ²)	Order	Mean discharge (m ³ /s) †	Total length (km)	Length of surveys for salmon	No. fish observed §	Mean NO ₃ ²⁻ (µg/l) ¶
El Toqui	207	4	4.6	31	1.5	25	0.081 (0.077)
Ñirehuao	1971	5	31.4	65	2.3	26	0.048 (0.055)
Emperador	566	5	13.4	29	2.1	0	0.048 (0.049)
Huemules	1423	5	15.8	34	1.8	34	N/A
Jaramillo	117	3	2.8	6	1.0	63	0.032 (0.017)

†Mean discharge represents the annual mean discharge and was calculated using long-term mean precipitation and drainage area.

§No. fish observed is the maximum number of live and dead salmon observed on an individual survey date.

¶Mean (and standard deviation) nitrate (NO₃²⁻) concentration in each stream was obtained from the Government of Chile's water quality monitoring program. These values were calculated using measurements taken across seasons and in multiple years. No nutrient data were available for Huemules

2.3.2. Control-Impact study design

In February–May 2016, we conducted a “Control-Impact” (CI) study in four streams (El Toqui, Ñirehuao, Emperador Guillermo, and Jaramillo, with Huemules omitted due to logistical constraints). “Control” and “Impact” refer to paired sites within a stream that differ in the presence of salmon. In El Toqui, Ñirehuao, Huemules and Jaramillo, adult Chinook salmon arrive throughout February and March and, over the course of several weeks, aggregate at distinct spawning sites and eventually die of senescence. Upstream of these spawning sites in each stream is habitat that is not occupied by salmon due to a natural barrier to salmon migration in the form of a waterfall (except for El Toqui, see below). Thus, upstream sites were paired with downstream sites such that they differ in the presence of salmon. This upstream-downstream

approach has been used by several other studies (e.g., Hocking and Reimchen 2002; Mitchell and Lamberti 2005; Lessard and Merritt 2006; Chaloner et al. 2007; Christie and Reimchen 2008; Harding et al. 2014) and is powerful in that it controls for the physical and chemical attributes of the streams (see below for relevance of variables that affect biofilm).

In El Toqui, a small, run-of-the-river hydroelectric facility diverts water at a small dam located directly upstream of a steep gradient in the stream. It releases the water back into the stream at the bottom of the gradient, upstream of the observed spawning habitat. The habitat between the release site and the dam consists of pool-riffle habitat caused by the steep elevation gain. Such habitat is unsuitable for Chinook spawning, and visual surveys found no evidence of spawning throughout this section. This allowed us to place the Control site below the gradient and shortly downstream of the release site, thereby maintaining the key feature of the CI design of having only the presence of salmon being different between the sites.

Emperador Guillermo (Emperador hereafter) was used as a reference stream in the CI study because it has a waterfall shortly upstream (~2 km) of its confluence with the main stem and seemingly no salmon that spawn in the available habitat below this waterfall. Discussions with several local people yielded mixed responses as to whether adult salmon enter the reach below the waterfall. In a snorkel survey in 2018 we identified juvenile Chinook in the reach below the waterfall (Muñoz NJ, unpublished data). However, multiple foot surveys were conducted at each stream during the CI study and Emperador was the only one in which there were no live or dead adult salmon observed at any point. Although it is possible that salmon spawn in the downstream portion of Emperador, we concluded that it would have to be limited to far fewer individuals than at the other streams, thereby allowing us to use it as a reference system for the upstream vs. downstream comparisons.

We deployed unglazed ceramic tiles (30 × 20 cm) to measure biofilm biomass and stable isotope composition at each Control and Impact site. Ceramic tiles reduce the sampling variability inherent in sampling biofilm from natural rock surfaces while accurately representing the algal, bacterial, and macroinvertebrate densities and species compositions of rocks after only a few weeks of incubation (Lamberti and Resh 1985). The timing of tile deployment was based on the salmon spawn timing observed in each

stream. Spawn timing was assessed using repeated visual surveys on foot, beginning in early February. The number of live and dead salmon observed during each survey was recorded (Table 2.1); while not exhaustive, these surveys were sufficient to reveal temporal patterns of spawner presence and behaviour. In general, fish occupied pool habitats in February and early March, then occupied riffle-run transition zones in mid-March through April and displayed mating behaviours such as redd construction and maintenance. Impact sites were chosen at locations downstream of the majority of observed spawning (0.13 to 0.2 km downstream of closest spawning location across streams). Tile deployment occurred part way through the spawning season, shortly after the first observation of mating behaviours (mid-March to mid-April across all four streams). Tiles were deployed in the corresponding Control sites within 24 h of Impact site deployment. At each site, tiles were arrayed across the width of the stream in multiple rows, directly upstream of riffle habitat. In more narrow streams, tiles were deployed as such in front of two adjacent riffle habitats. Each tile was glued to a heavy brick, anchoring them to the streambed. Nine to 12 tiles were deployed at each site.

We selected the location of each Impact and Control site with the intention of minimizing any longitudinal (i.e., upstream to downstream) variation in physical characteristics among sites. An important longitudinal effect in rivers is that water generally increases in temperature as it moves from headwaters to the terminal mouth (Vannote et al 1980). To minimize any temperature differences, paired sites were placed as closely together as possible, with no significant tributaries entering streams between sites (as confirmed through stream surveys and satellite imagery). Sites were 1.5 to 2.2 km apart in El Toqui, Emperador, and Jaramillo (Appendix Table A1; Figure 2.1). Long, inaccessible reaches throughout Ñirehuao necessitated that sites there were 9.2 km apart. To evaluate if temperatures differed among sites, we recorded hourly temperatures at each site in Ñirehuao and Jaramillo using HOBO temperature loggers (Onset, Bourne, MA) from March through May. Problems with logger and data retrieval prevented temperatures in the other two streams from being recorded. Also, to account for variation in light availability, we measured percent open canopy at each tile using a spherical densiometer as well as the depth of each tile in the water column on the day of sampling (Table A1).

Biofilm samples were collected 10 weeks after deployment and more than 4 weeks after all spawning had occurred (i.e., no live salmon in the streams, only

carcasses). Control sites were sampled either on the same day or within 24 h of their corresponding Impact site. Any invertebrates present on the tiles at the time of collection were removed. A portion of tiles were lost in all but two sites, often due to water levels decreasing over the study period such that tiles placed in shallower locations (e.g., near banks) were out of water at some point (tiles sampled at each site: $n = 5-12$, Table A1).

Samples for stable isotope analysis were taken from approximately 576 cm² of tile surface area. Stream water and a brush were used to transfer the biofilm in this area into a plastic container. Containers were kept in the dark and on ice for 2-8 hours, during which they were transported to laboratory facilities at the Centro de Investigación en Ecosistemas de la Patagonia (CIEP) in Coyhaique. Upon arrival at CIEP, samples were dried at 70°C, coarsely ground, and stored until further processing. Later, samples were ground into a fine powder and a subsample (2-3 mg dried weight) was analyzed for nitrogen and carbon isotope abundance at the UC Davis Stable Isotope laboratory (<http://stableisotopefacility.ucdavis.edu/>). Analysis employed a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotopes are expressed in delta notation (δ) as ratios of isotopes in the sample relative to that in a standard (atmospheric N₂ for nitrogen, Vienna PeeDee Belemnite for carbon). This ratio is expressed in parts per thousand following:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where R is the ratio of the heavy isotope (¹⁵N or ¹³C) to light isotope (¹⁴N or ¹²C). One value of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was obtained for each sampled tile. Tiles at the Jaramillo Control site had low levels of biofilm biomass and only four tiles were able to be sampled for isotope analysis. Of these four samples, three contained insufficient nitrogen content for $\delta^{15}\text{N}$ determination (but enough carbon for $\delta^{13}\text{C}$ determination).

Chlorophyll *a* (chl *a*) is the most abundant photosynthetic pigment in plants and provides an estimate of algal (i.e., autotrophic) biomass (Steinman et al. 2017). Ash-free dry mass (AFDM) is a measurement of the loss of mass upon oxidation and estimates the biomass of all organic matter in biofilm including algae, bacteria, detritus, etc. Samples for chl *a* and AFDM were taken from a circular area (23.8 cm²) in the centre of each tile. Samples were collected and transported to CIEP as described above. At CIEP,

samples were filtered onto glass fibre filters (Whatman, 47 mm, 0.7 µm) and stored in the dark at -20°C. Pigments were extracted into 10 ml of 90% acetone for 24 h and measured using the spectrophotometry method described in Steinman et al. (2017) whereby absorbance measurements are taken before and after acidification to account for chlorophyll degradation products. Using the remaining material (i.e., after pigment extraction), filters were dried, weighed, oxidized at 500°C for 1 h, cooled to room temperature, and then weighed again to estimate AFDM (following Steinman et al., 2017). One value of chl *a* (µg cm⁻²) and AFDM (mg cm⁻²) was obtained for each sampled tile. Because the samples that we used to estimate AFDM were washed with acetone beforehand, our measure of AFDM estimates the total organic material in the sample apart from non-polar organic matter such as chlorophylls and accessory pigments (e.g., Mitchell and Lamberti 2005; Chaloner et al. 2007). To assess the relative amount of chl *a* to total (non-polar) organic matter, the percent of total biofilm biomass composed of chl *a* (chl *a* %) was calculated by converting AFDM to µg cm⁻² and using the following formula:

$$\text{chl } a \% = \frac{\text{chl } a}{\text{chl } a + \text{AFDM}} \times 100$$

Higher chl *a* % values indicate that algae (and cyanobacteria, which are photosynthetic bacteria containing chlorophyll *a*) make up a greater proportion of total biofilm biomass relative to heterotrophic or detrital components of biofilm. Because we hypothesized that salmon-derived nutrients would increase autotrophic biomass, we predicted that chl *a* % would be higher in Impact sites relative to Control sites.

2.3.3. Before-After-Control-Impact study design

In addition to the CI study, we conducted a Before-After-Control-Impact (BACI) study in January–May 2018 to further assess the effect of salmon on stream biofilms. BACI designs are broadly used in environmental monitoring programs because they provide rigorous tests of the impacts of specific activities (Downes et al. 2002). Here, this design included the Control-Impact comparison of the CI study as well as a Before-After comparison at each site to account for any confounding differences between upstream and downstream sites (e.g., temperature differences).

The BACI study was conducted in Ríos Ñirehuao and Huemules. El Toqui was originally included in this design, however all tiles were lost in this stream after a storm during the study. Indeed, the summer and fall of 2018 had much more precipitation than in 2016, resulting in substantially higher levels of discharge during the BACI study (e.g., monthly mean discharge in April 2016 and April 2018 was 4.59 and 41.6 m³/sec, respectively, in Ñirehuao). In the Before period, fifteen tiles were deployed at each site in early January and sampled after 5 weeks, before salmon had returned to spawn. Tiles were returned to the stream after sampling. Visual surveys downstream of the migration barriers were again used to monitor the progression of spawning in February through April. Initiation of the After period occurred in the second week of April, when carcasses had begun accumulating in both streams (in a ratio of dead to live fish of about 1:2). At this time, all tiles were thoroughly cleaned using a large brush, removing the biofilm that had accumulated since the end of the Before period. Control and Impact sites were cleaned within 24 h of each other. Tiles were then incubated in the streams for 5 weeks, after which they were sampled, processed, and analyzed for biomass and isotopic composition as described above. Site and sampling characteristics of the BACI study are described in Table A2. Hydrographs of Ñirehuao and Huemules during the study period are shown in Appendix Figure A1, with reference to the timing of tile deployment.

2.3.4. Data analysis

Within each stream in the CI study, we assessed whether tile depth or percent open canopy were to be included as covariates in the full models by testing for differences in these variables between upstream and downstream sites and by regressing the five response variables ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, chl *a*, AFDM and chl *a* %) onto depth and canopy cover. Tile depth and percent open canopy were not significantly different between upstream and downstream sites (Table A1) and were not significantly associated with response variables ($0.001 > r^2 > 0.22$) except for a negative relationship between percent open canopy and AFDM in Emperador ($r^2 = 0.31$, $P = 0.024$). Because this relationship was found in only one stream and was in the opposite direction as expected and thus likely spurious, we did not include canopy cover (or depth) as a covariate in the full models.

For the CI study, we used linear models with stream (four levels) and site (two levels) as fixed effects to analyze the variation in the response variables. We also

included the site \times stream interaction because we predicted that the reference stream (Emperador) would not differ between sites. Tukey's post hoc tests were used to evaluate stream-specific differences between Control and Impact sites. Because only one $\delta^{15}\text{N}$ value was obtained from the Jaramillo Control site, Jaramillo was not included in the $\delta^{15}\text{N}$ analysis. The assumptions of normality were inspected, and Box Cox transformations were used for $\delta^{13}\text{C}$, chl *a*, AFDM, and chl *a* % to improve normality ($\lambda = 0.75, 0.26, 0.06, \text{ and } 0.63$, respectively). The relationship between chl *a* and $\delta^{15}\text{N}$ within streams was assessed using linear regression. These relationships were used as an additional line of evidence as to whether differences in algal biomass between Control and Impact sites were driven by salmon. Specifically, if the relationship between chl *a* and $\delta^{15}\text{N}$ within streams was positive, and if this relationship was stronger in salmon-bearing streams compared to the reference stream, this would suggest that the incorporation of salmon-derived nitrogen increased algal biomass.

In the BACI study, there were no significant relationships (within streams and periods) between any of the response variables and percent open canopy or tile depth ($0.001 > r^2 > 0.12$). In Ñirehuao during the After period, tile depth was significantly lower in the downstream site than in the upstream site (Table A2); however, because this difference was not associated with variation in any of the response variables, we did not include depth (or canopy cover) as a covariate in the full models. We used linear models with site, period, and stream as fixed factors (all with two levels) to analyze the variation in the five response variables. Given the stream-specific effects observed in the CI study (described below), we included all interaction terms. In this BACI design, an impact of salmon would be indicated by a significant site \times period effect (Downes et al. 2002). If the two streams were differentially impacted by salmon (e.g., an impact in only one of the streams), this would be indicated by a significant site \times period \times stream effect. The other interaction effects (i.e., site \times stream and period \times stream) were not of direct interest but were included in the models because stream-specific effects were expected. The assumptions of models were inspected, and Box Cox transformations were used for chl *a*, AFDM, and chl *a* % to improve normality ($\lambda = 0.14, 0.42 \text{ and } 0.63$, respectively). Tukey's post hoc tests were used to evaluate differences between Control and Impact sites within streams and periods. The relationship between chl *a* and $\delta^{15}\text{N}$ within streams and periods was assessed using linear regression. All linear models were analyzed using the 'lm()' function in R (R Core Team, 2020).

2.4. Results

2.4.1. Control-Impact study

The results of the CI study support a nutrient subsidy effect of salmon in El Toqui and Jaramillo but not in Ñirehuao. In general, biofilm isotopic composition and biomass differed between upstream and downstream sites, and this difference depended on the stream (Table 2.2). As predicted, biofilm $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significantly enriched in the downstream (Impact) sites of each salmon-bearing stream relative to upstream (Control) sites, and they were not different between sites in the salmon-free reference stream (i.e., Emperador; Figure 2.2a, b). The salmon-impacted sites of Jaramillo and El Toqui had significantly higher chl *a* than upstream sites, whereas there was no difference in chl *a* between sites at both Ñirehuao and the reference stream (Figure 2.2c). AFDM was significantly higher at the salmon-impacted site of Jaramillo relative to the upstream site (Figure 2.2d). Chl *a* and AFDM were strongly and positively associated in El Toqui ($r^2 = 0.83$, $P < 0.001$), Ñirehuao ($r^2 = 0.89$, $P < 0.001$), Jaramillo ($r^2 = 0.90$; $P < 0.001$), and, to a lesser extent, the reference stream ($r^2 = 0.23$, $P = 0.058$; Figure A2). Chl *a* % was significantly higher in the salmon-impacted sites of El Toqui and Jaramillo relative to upstream sites, increasing by an average of 25% and 74%, respectively (Figure 2.2e).

Chl *a* and $\delta^{15}\text{N}$ were strongly and positively associated in El Toqui ($r^2 = 0.78$, $P < 0.001$), whereas they were not associated in Ñirehuao ($r^2 = 0.02$) or the reference stream ($r^2 = 0.01$; Figure 2.3a). While being limited by having only one $\delta^{15}\text{N}$ value from the Control site, this relationship was also positive in Jaramillo ($r^2 = 0.22$).

The mean (\pm SD) temperature at the downstream site in Ñirehuao was $0.25 \pm 0.30^\circ\text{C}$ warmer than at the upstream site, whereas temperatures at the downstream site in Jaramillo were very similar to those at the upstream site ($0.03 \pm 0.22^\circ\text{C}$ warmer; Table A1). Because they are similar distances apart, the sites in Emperador and El Toqui are likely to have negligible temperature differences, as with those in Jaramillo.

Table 2.2 Effects of site (upstream or downstream) and stream on biofilm biomass and isotopic traits in the Control-Impact study of Chinook salmon in Patagonia, southern Chile.

Trait	df	SS	F	<i>P</i>	η^2
$\delta^{13}\text{C}$					
<i>site</i>	1	34.5	59.3	< 0.001	0.59
<i>stream</i>	3	61.2	35.0	< 0.001	0.72
<i>site</i> × <i>stream</i>	3	7.88	4.51	0.008	0.25
<i>residual</i>	41	23.9			
$\delta^{15}\text{N}$					
<i>site</i>	1	14.4	87.4	< 0.001	0.73
<i>stream</i>	2	7.23	22.0	< 0.001	0.57
<i>site</i> × <i>stream</i>	2	15.7	47.8	< 0.001	0.74
<i>residual</i>	33	5.43			
chl <i>a</i>					
<i>site</i>	1	0.18	21.6	< 0.001	0.29
<i>stream</i>	3	4.34	179	< 0.001	0.91
<i>site</i> × <i>stream</i>	3	0.11	4.55	0.006	0.20
<i>residual</i>	54	0.44			
AFDM					
<i>site</i>	1	0.001	5.64	0.021	0.09
<i>stream</i>	3	0.17	261	< 0.001	0.94
<i>site</i> × <i>stream</i>	3	0.001	2.21	0.097	0.11
<i>residual</i>	54	0.01			
chl <i>a</i> %					
<i>site</i>	1	0.07	36.6	< 0.001	0.40
<i>stream</i>	3	0.76	126	< 0.001	0.88
<i>site</i> × <i>stream</i>	3	0.06	10.6	< 0.001	0.37
<i>residual</i>	54	0.11			

The results of linear models are summarized for effects on biofilm isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) as well as algal biomass (chl *a*), total biofilm biomass (AFDM), and percent of total biomass composed of chl *a* (chl *a* %). Significant effects are bolded ($P < 0.05$). Effect size (partial eta squared η^2) is also shown for each effect.

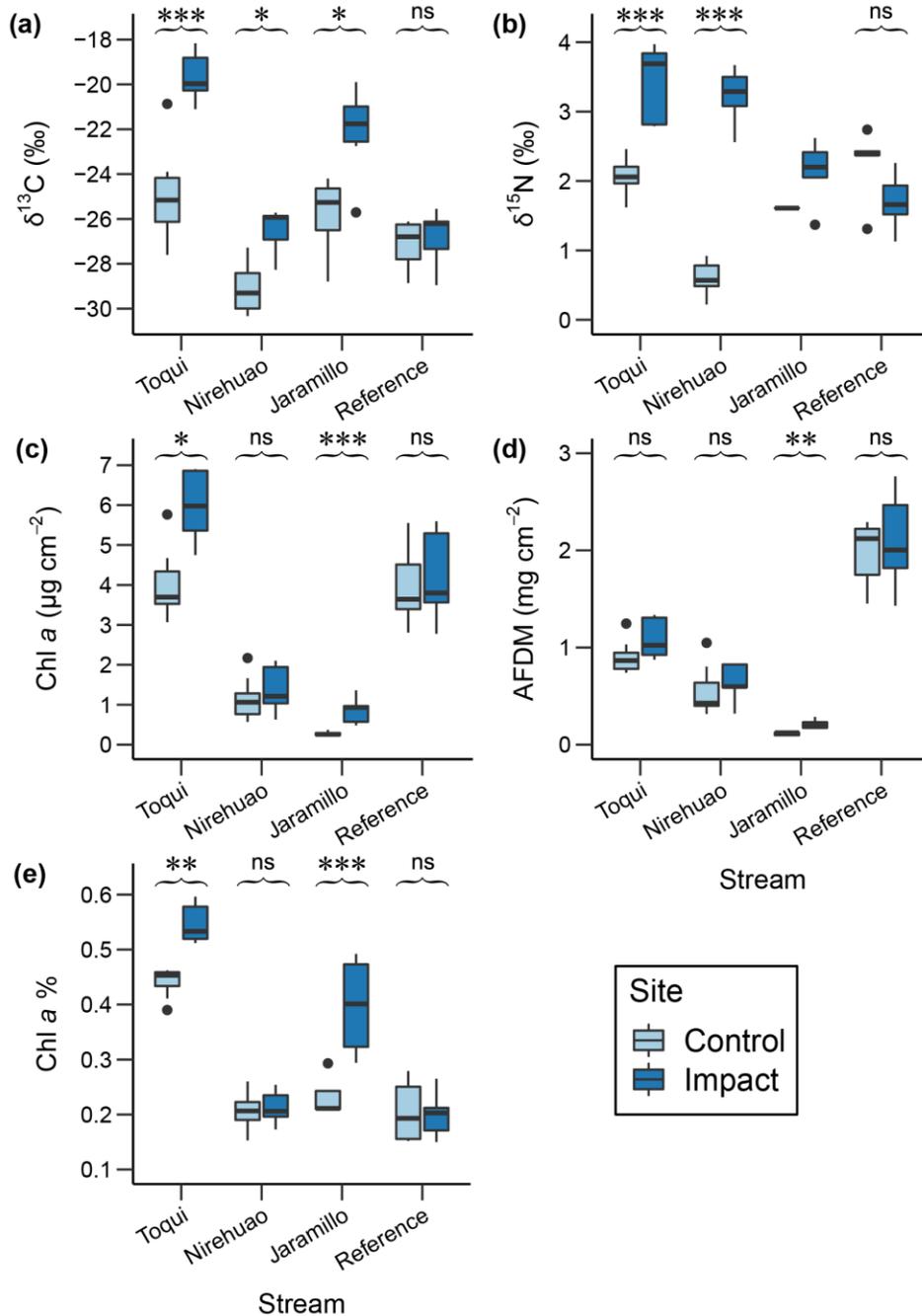


Figure 2.2 Effect of Chinook salmon on (a) biofilm isotopic ratio of carbon ($\delta^{13}\text{C}$), (b) biofilm isotopic ratio of nitrogen ($\delta^{15}\text{N}$), (c) algal biomass (chl a), (d) total biofilm biomass (AFDM), and (e) percent of biofilm biomass composed of chlorophyll a (chl a %) among streams in the Control-Impact study.

Biofilm was sampled in Control (upstream, salmon-free) and Impact (downstream, salmon-impacted) sites of four streams, one of which (the reference stream) had no salmon in the downstream site. Only one $\delta^{15}\text{N}$ value was collected from the Jaramillo Control site, preventing comparison of $\delta^{15}\text{N}$ for this stream. The results of Tukey's post hoc comparisons of Control and Impact sites are displayed (***) $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$).

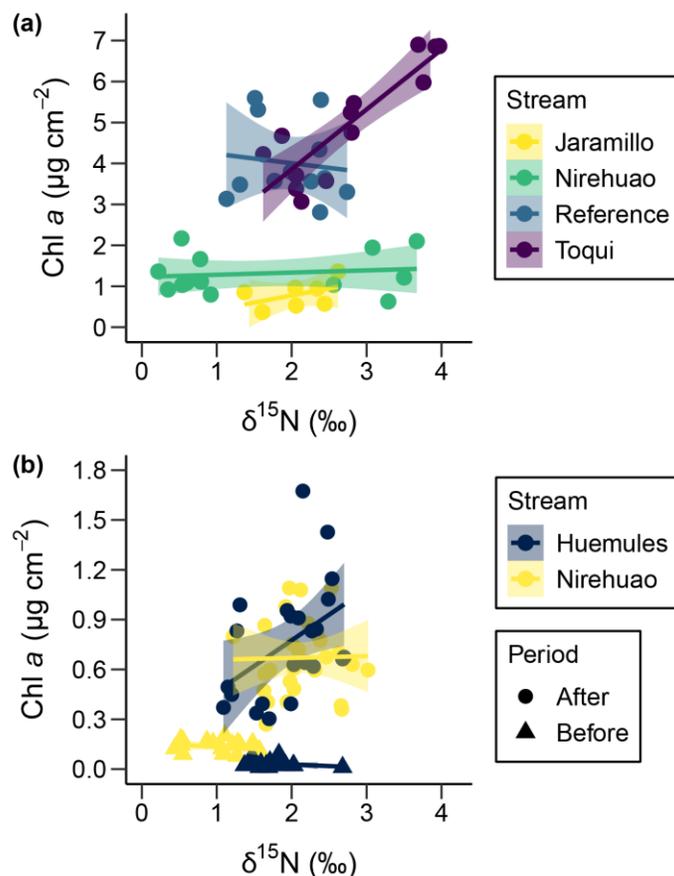


Figure 2.3 Relationship between biofilm isotopic ratio of nitrogen ($\delta^{15}\text{N}$) and algal biomass (chl a) (a) among streams in the Control-Impact study, and (b) among streams and periods in the Before-After-Control-Impact study.

Shading represents 95% confidence intervals for predictions from a linear model.

2.4.2. Before-After-Control-Impact study

The results of the BACI study support a nutrient subsidy effect of salmon in Huemules but not in Ñirehuao. The effect of salmon on biofilm stable isotopic composition differed between streams, with significant site \times period \times stream effects on biofilm $\delta^{13}\text{C}$ ($F_{1,83} = 55.6$, $P < 0.001$) and $\delta^{15}\text{N}$ ($F_{1,83} = 22.1$, $P < 0.001$; Table A3). In Huemules, after the senescence of salmon, biofilm $\delta^{13}\text{C}$ was more enriched in the downstream (Impact) site than in the upstream (Control) site, whereas the opposite was true before the arrival of salmon (Figure 2.4a). $\delta^{15}\text{N}$ did not differ between sites at Huemules before the arrival of salmon, but after salmon senescence the downstream site was significantly enriched in $\delta^{15}\text{N}$ relative to the upstream site (Figure 2.4b). These data indicate that salmon-derived carbon and nitrogen were incorporated into biofilm in

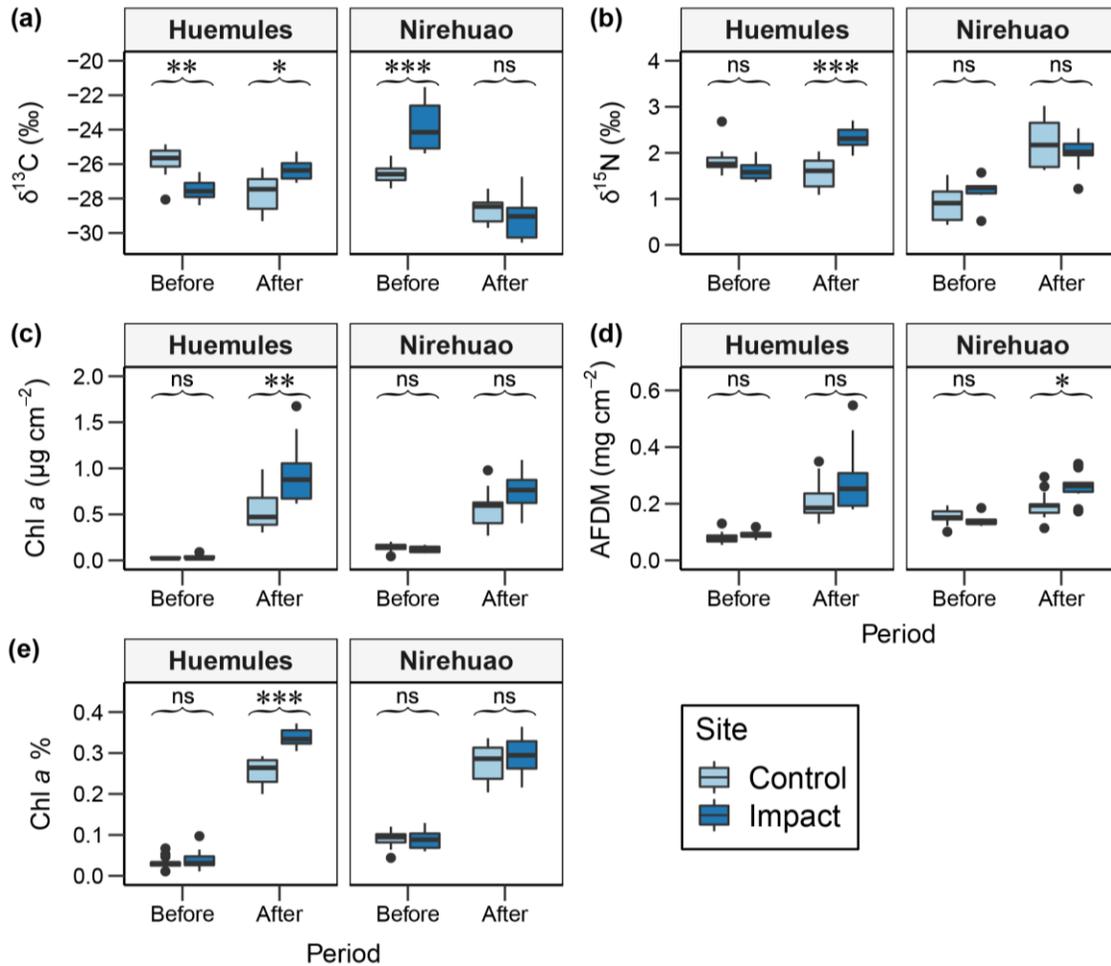


Figure 2.4 Effect of Chinook salmon on (a) biofilm isotopic ratio of carbon ($\delta^{13}\text{C}$), (b) biofilm isotopic ratio of nitrogen ($\delta^{15}\text{N}$), (c) algal biomass (chl a), (d) total biofilm biomass (AFDM), and (e) percent of biofilm biomass composed of chlorophyll a (chl a %) among streams in the Before-After-Control-Impact study.

Biofilm was sampled in Control (upstream, salmon-free) and Impact (downstream, salmon-impacted) sites of two streams (Huemules and Nirehuao), before and after salmon spawning. The results of Tukey's post hoc comparisons of Control and Impact sites within periods are displayed (** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$).

Huemules. Conversely, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were not different between sites at Nirehuao after salmon senescence (Figure 2.4a, b), indicating that salmon-derived carbon and nitrogen were not incorporated into biofilm in this stream. Instead, there was a depletion in $\delta^{13}\text{C}$ and an enrichment in $\delta^{15}\text{N}$ from the Before to the After period, irrespective of site.

There was an effect of salmon on algal and biofilm biomass that was similar in the two streams, with significant site \times period effects on biofilm chl a ($F_{1,87} = 10.5$, $P = 0.002$), AFDM ($F_{1,87} = 9.69$, $P = 0.003$), and chl a % ($F_{1,87} = 8.42$, $P = 0.005$) and non-

significant site \times period \times stream effects on these traits (Table A3). Indeed, the median value of each of these three traits was consistently higher in the downstream sites than in the upstream sites following salmon senescence (Figure 2.4c-e). However, post hoc tests found that, after salmon senescence, chl *a* and chl *a* % were significantly higher in the downstream site of Huemules only, whereas AFDM was significantly higher in Ñirehuao only (Figure 2.4c-e). Before the arrival of salmon, there were no differences in chl *a*, AFDM, or chl *a* % between sites in both streams. There was also a strong temporal (i.e., period) effect on these three traits, with each one being significantly higher in the fall (after salmon senescence) relative to the summer (before salmon senescence) (Table A3, Figure 2.4c-e). Chl *a* and AFDM were strongly and positively associated within both time periods in both streams (Figure A3).

$\delta^{15}\text{N}$ and chl *a* were positively and significantly associated in Huemules after salmon senescence ($r^2 = 0.20$, $P = 0.032$) but were not associated beforehand in Huemules ($r^2 = 0.08$) or in Ñirehuao during either period ($r^2 \leq 0.06$; Figure 2.3b).

2.5. Discussion

The results of the two studies presented here provide evidence of salmon-mediated nutrient subsidies in three out of the four streams examined that have spawning Chinook salmon populations. These subsidies represent a novel resource linkage between marine and freshwater ecosystems in Patagonia, with non-native salmon contributing marine-derived nutrients to systems in which nutrients have historically only flowed downstream, from stream to sea. By performing a novel function in these invaded systems, salmon in Patagonia are likely to have ecological impacts (Vitousek 1990; Ricciardi and Atkinson 2004; Ricciardi et al. 2013).

The effects of salmon-mediated nutrient additions can be limited by the environmental context in which salmon spawning occurs, such as the temperature, light, discharge, and nutrient limitation status of streams (Chaloner et al., 2007; Armstrong et al., 2010; Bentley et al., 2012). If this context is poorly suited for additional growth of algae (e.g., nutrient-rich streams), salmon nutrients can have little effect on algal biomass (e.g., Rand et al., 1992; Janetski et al., 2014) and, subsequently, fail to support higher trophic levels (e.g., Lessard and Merritt 2006). In three streams (El Toqui, Jaramillo, and Huemules), we found evidence that marine-derived nutrients were

incorporated by biofilms and increased the biomass of algae (chl *a*; including cyanobacteria) as well as the proportion of biofilm biomass that is composed of algae (chl *a* %). We also found that total biofilm biomass (AFDM) and chl *a* were strongly and positively associated in all salmon-bearing streams and, in the BACI study, streams had higher chl *a*, AFDM, and chl *a* % in the fall (after spawning) relative to the summer. These results suggest that: (1) algae are major components of biofilm in these streams; (2) marine-derived nutrients enter these streams at a time of year when algae are relatively abundant and comprise a greater proportion of total biofilm biomass, indicating that stream conditions are well-suited for algal growth; and (3) marine-derived nutrients significantly increase algal biomass after spawning in the fall (except for in Ñirehuao, discussed below). The positive response of algae to salmon in El Toqui, Jaramillo, and Huemules is likely underlain by the strong nutrient limitation that is found in southern Chile (Perakis and Hedin 2002) and represents the first described ecological impact of Patagonian salmon.

One of the environmental variables that modulates the effects of nutrient additions in streams is discharge. Temporary bouts of high stream flows (i.e., spates) or sustained high flows can scour the streambed and flush carcasses and dissolved nutrients downstream, thereby preventing salmon nutrients from being incorporated by biofilms (Richey et al. 1975; Chaloner et al. 2007). Inter-annual variation in discharge could explain the differences in biofilm incorporation of marine-derived nutrients observed in Ñirehuao during the CI and BACI studies here. During the BACI study in 2018, flows were high in Ñirehuao throughout the autumn spawning season (41.6 m³/sec for all of April, compared to 4.89 m³/sec in Huemules) and marine-derived nutrients were not incorporated by biofilm in this stream. Conversely, flows were exceptionally low during the CI study in 2016 (April discharge of 4.59 m³/sec in Ñirehuao) and, unlike in 2018, the salmon-impacted site at Ñirehuao was enriched in biofilm $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to the upstream site. These results suggest that the low flows of 2016 could have facilitated the incorporation of marine-derived carbon and nitrogen by biofilm. However, the incorporation of marine-derived nutrients in 2016 did not cause an increase in algal biomass in Ñirehuao, indicating that algal biomass in this stream is limited by some environmental variable other than nutrients. The lack of a subsidy effect in Ñirehuao and the difference in salmon nutrient incorporation among years are in line with other studies demonstrating that the effect of spawning salmon differs among

streams and among years in individual streams (e.g., Mitchell and Lamberti 2005; Chaloner et al. 2007). As such, the vulnerability of individual streams in Patagonia to the subsidizing effect of salmon is likely set by an inter-annual interplay between discharge and other environmental variables such as baseline nutrient regime, geomorphology, and temperature.

The abiotic and biotic characteristics of lotic ecosystems change predictably from headwaters to terminal mouths (Vannote et al. 1980) and can potentially confound upstream-downstream comparisons. During the CI study here, the stream with the largest distance between study sites (Ñirehuao, 9.2 km apart) was $0.25 \pm 0.30^{\circ}\text{C}$ warmer at the downstream site relative to the upstream site. This small difference in temperature could slightly confound our between-site comparisons of biofilm biomass and isotopic signatures in this stream. Nevertheless, there were no significant differences in chl *a* or AFDM between sites in Ñirehuao during the CI study, and the magnitude of difference in $\delta^{15}\text{N}$ between sites was large, so this small difference in temperature does not change our interpretation of these results. Another factor that could confound these comparisons is differences in grazing intensity. Grazers directly remove an average of 55% of total algal biomass (Hillebrand 2009) but also indirectly increase algal biomass by increasing light penetration and nutrient availability to underlying algae (Power 1990; Andre et al. 2003). Grazing intensity was not quantified at our study sites and could confound the comparisons of biofilm biomass in the CI study. However, because all paired study sites were of the same stream size (i.e., order), and because longitudinal changes in grazer abundance occur at the level of stream order (Vannote et al. 1980), we assume that differences in grazing intensity were negligible.

Many studies have reported that the principal effect of spawning salmon on biofilm is a positive, nutrient subsidy effect (e.g., Wipfli et al. 1998; Mitchell and Lamberti 2005; Chaloner et al. 2007), whereas many others have reported a negative, disturbance effect (e.g., Moore and Schindler 2008; Holtgrieve and Schindler 2011; Rüegg et al. 2020). Whether a given salmon population has a net positive or negative effect on stream biofilm biomass is likely mediated by substrate size, spawner density, and background nutrient levels (Janetski et al. 2009; Holtgrieve et al. 2010; Janetski et al. 2014). Such influence of environmental conditions on responses to spawning salmon has been observed in the watersheds of the Laurentian Great Lakes, where Chinook salmon have similarly established non-native populations. There, some streams are

nutrient-limited and have increased algal biomass in reaches downstream of Chinook spawning relative to upstream (Schuldt and Hershey 1995), whereas other streams have negligible subsidy effects and strong disturbance effects in salmon-impacted reaches, likely due to high background nutrient levels and small substrate sizes (Janetski et al. 2014). Although we found a nutrient subsidy effect, our methods likely would not have captured a disturbance effect; we generally did not observe Chinook spawning in the immediate vicinity of the tiles that we used to measure biofilm, and if a tile had been turned over by a spawning salmon it would not have been sampled for biofilm. As such, our study does not rule out disturbance effects of salmon in these streams. Disturbance of the streambed likely happens to some degree in these streams, and at the whole-stream scale, this would reduce the net benefit of salmon to algal biomass (e.g., Holtgrieve et al. 2010). However, because Chinook build redds in specific microhabitats that comprise a small proportion of total stream habitat, and because their spawning densities seem generally low in Patagonia, we suspect that subsidy effects are stronger than disturbance effects in these streams.

In resource-limited ecosystems that receive a pulsed subsidy, organisms optimize resource use when resources become available (Sears et al. 2004). Because the streams in southern Chile are highly nutrient-limited, salmon subsidies that increase algal biomass likely have bottom-up effects such that some heterotrophic species also increase in biomass (Wipfli et al. 1998; Rosemond et al. 2000; Risse-Buhl et al. 2012). Increased algal biomass could benefit consumers such as biofilm-grazing invertebrates (e.g., Verspoor et al. 2011), stream fishes (e.g., Kohler et al. 2012), and insectivorous forest birds (e.g., Wagner and Reynolds 2019). Benefits to heterotrophic species can extend beyond the autumn spawning season due to the variety of mechanisms that retain salmon-derived nutrients in stream and riparian food webs year-round (Gende et al. 2002; O'Keefe and Edwards 2002). Indeed, six months after salmon spawning in British Columbia, algal biomass is higher in salmon-impacted stream reaches (Harding et al. 2014). The subsidization of algae can represent a positive feedback link between adult salmon and their progeny such that nutrients from adult salmon carcasses increase in situ primary productivity, causing increased productivity among the invertebrate prey of juvenile salmon in the spring and, ultimately, resulting in enhanced recruitment of juvenile salmon (Benjamin et al. 2020; Kaylor et al. 2020). As such, the subsidy effect described here could help sustain Chinook salmon populations in Patagonia.

The functional novelty described here should increase the degree of ecological change in Patagonia (Schittko et al. 2020). This change will likely involve some native species benefitting from the novel availability of marine-derived nutrients. It will likely also involve benefits to non-native species. Rainbow trout (*O. mykiss*) and American mink (*Neovison vison*) are invasive in Patagonia and coevolved with and strongly benefit from Pacific salmon subsidies in their native ranges (Ben-David et al. 1997; Scheuerell et al. 2007). Both of these invaders have negative effects on the abundance and distribution of their native prey in Patagonian streams and forests (e.g., Schüttler et al. 2009; Habit et al. 2010; Correa and Hendry 2012; Valenzuela et al. 2013), and salmon subsidies could strengthen these negative effects through apparent competition (Sears et al. 2004). The native aquatic fauna in Patagonia is characterized by low species richness but high levels of endemism (Valdovinos 2006; Cussac et al. 2016), making the increasing abundance of non-native species a threat to local biodiversity (Habit and Cussac 2016). At the same time, recreational fisheries in Patagonia are a key contributor to the regional tourism industry, and Chinook have added value to these fisheries. Nevertheless, it is clear that non-native salmonids are contributing to ecological change in Patagonia. Conservation planning that uses hydrologic isolation and barriers to salmonid migration to identify priority water bodies for protection could be an effective way of ensuring the persistence of salmonid-free ecosystems and the many unique species that inhabit them.

Chapter 3.

Emergent trophic interactions following the Chinook salmon invasion of Patagonia²

3.1. Abstract

In their native range, Pacific salmon (*Oncorhynchus* spp.) have strong interactions with a multitude of species due to the annual pulse of marine-derived nutrients that they deliver to streams and forests when they spawn and die. Over the past few decades, Chinook salmon (*O. tshawytscha*) have established non-native populations throughout the Patagonia region of southern South America. Here, we provide the first assessment of the pathways through which salmon-derived nutrients enter stream and forest food webs in Patagonia by surveying multiple streams in southern Chile to identify invertebrate and vertebrate consumers of salmon carcasses and summarizing all documented trophic interactions of Chinook salmon in Patagonia. Blowflies (Calliphoridae) were the dominant colonizer of carcasses in the riparian zone, and midge flies (Chironomidae) were the most common invertebrate on submerged carcasses. Camera trap monitoring in the riparian zone revealed consumption of carcasses or carcass-associated invertebrates by the insectivorous passerine bird 'chucaco' (*Scelorchilis rubecula*), small rodents (black rat *Rattus rattus*, house mouse *Mus musculus*, and/or colilargo *Oligoryzomys longicaudatus*), the South American fox 'culpeo' (*Lycalopex culpaeus*), and the invasive American mink (*Neovison vison*). A mink was filmed transferring a carcass from stream to streambank, indicating that vertebrate scavenging likely increases the degree to which marine-derived nutrients enter terrestrial food webs. The native taxa that consume salmon are closely related to species that benefit from salmon consumption in North America, suggesting that the pathways of salmon nutrient incorporation in North American food webs have functionally re-emerged in South America. Similarly, non-native trout (*O. mykiss* and *Salmo trutta*) and mink consume salmon in Patagonia, and their eco-evolutionary history of coexistence with salmon could mean that they are pre-adapted for salmon consumption and could thus be key

² A version of this chapter appears as Muñoz, N.J., Reid, B.L., Correa, C., Madriz, R.I., Neff, B.D., Reynolds, J.D., 2021. Emergent trophic interactions following the Chinook salmon invasion of Patagonia. *Ecosphere* 13, e3910.

beneficiaries of this invasion. Expanded monitoring of the abundance and impacts of salmon will be vital for understanding how these novel inputs of marine-derived nutrients alter Patagonian food webs.

3.2. Introduction

Among the main drivers of global biodiversity loss, invasive species are unique in that their impacts are integrated within biological communities through the creation of novel trophic interactions and the disruption of existing interactions (Jackson et al. 2017). The most severe impacts of invaders are typically due to direct, top-down effects of predation (Salo et al. 2007; David et al. 2017; Mollot et al. 2017). Conversely, non-native species can have positive, bottom-up effects on the species that directly consume them, although any positive effects on the biomass of resident species can be offset by the many indirect effects that can ripple through food webs (e.g., trophic cascades, apparent competition; White et al. 2006; David et al. 2017). The novel interactions that emerge in invaded food webs are influenced by the familiarity of resident species with the invader; that is, their eco-evolutionary experience interacting with the non-native species or with species that are functionally and behaviourally similar to the non-native species (Pearse and Altermatt 2013; Carthey and Banks 2014; Saul and Jeschke 2015). Thus, interactions that an invader has in its native range may re-emerge in invaded food webs if there are resident species that occur in the invader's native range or that are phylogenetically similar to interactors in the invader's native range.

A recent invasion that has been subject to little ecological study despite potentially having significant ecological consequences is that of Chinook salmon (*Oncorhynchus tshawytscha*) in the Patagonia region of southern South America. Chinook salmon were introduced to a few streams in southern Chile in the 1970s and 80s and have since colonized all of the inhabitable watersheds in southern Chile (39–55°S) as well as Atlantic-draining watersheds in southern Argentina (Figure 3.1a; Correa and Gross 2008; Ciancio et al. 2015). Initial research on Patagonian Chinook salmon has largely focused on the origin and life history characteristics of populations (e.g., Araya et al. 2014; Di Prinzio et al. 2015; Correa and Moran 2017; Musleh et al. 2020). However, little is known about the trophic interactions that have emerged within the food webs invaded by salmon or the consequences of these interactions.

In their native range of Pacific North America and Asia, Pacific salmon (*Oncorhynchus* spp.) have strong interactions with many co-occurring species, largely due to the marine-derived nutrients that they deliver to streams and forests when they spawn and subsequently die. Pacific salmon are anadromous and amass 99% of their body size in the ocean (Quinn 2005). Their annual return to fresh water to spawn en masse represents a pulse of food for animal consumers as well as a pulse of nutrients for nutrient-limited primary producers (i.e., positive, bottom-up effects). These resources are vital for many consumer taxa. Stream-resident brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*) feed principally on salmon eggs and carcasses upon the return of adult salmon, with their growth trajectories largely dependent on this consumption (Scheuerell et al. 2007; Ivan et al. 2011; Hermann et al. 2020). Mobile terrestrial consumers such as brown bears (*Ursus arctos*) and glaucous-winged gulls (*Larus glaucescens*) track temporal variation in salmon spawning among watersheds (Field and Reynolds 2013; Schindler et al. 2013). Adult and juvenile salmon comprise the majority of the diet of riverine American mink (*Neovison vison*) throughout the year (Ben-David et al. 1997), benefitting mink to the extent that the timing of mink lactation has seemingly synchronized with the spawn timing of salmon (Ben-David 1997).

Such direct effects of salmon on consumer taxa can cause cascading effects through food webs. For example, the abundance of insectivorous birds is positively associated with the abundance of adult salmon among streams (Field and Reynolds 2011; Wagner and Reynolds 2019), a relationship explained by aquatic and terrestrial insects being more abundant in salmon-bearing streams (e.g., Verspoor et al. 2011). With such diverse and consequential pathways through which they interact with co-occurring species, Pacific salmon can play a role in the ecological integrity of their native food webs (Willson and Halupka 1995; Darimont et al. 2010). As such, the potential for Chinook salmon to affect co-occurring species in their non-native range is large.

The aim of this study was to identify species in southern Chile that consume the novel marine-derived resources that adult Chinook salmon deliver to streams and forests, and to conceptualize the potential food web impacts of salmon in Patagonia. Consumption of salmon carcasses in freshwater and riparian habitats was qualitatively monitored using (1) sampling of invertebrate consumers found on submerged and out-of-water carcasses, and (2) motion-activated cameras baited with carcasses to identify vertebrate consumers in the riparian zone. The trophic interactions of Chinook salmon in

Patagonia were then summarized using all documented interactions, including those presented here for the first time as well as previously-reported observations.

3.3. Methods

3.3.1. Study sites

Stream surveys were conducted in the Aysén province of southern Chile (Figure 3.1). This region is sparsely populated, contains large tracts of temperate rainforest dominated by southern beech trees (*Nothofagus* spp.) intermixed with low-intensity silvopastoral lands, and is characterized by a strong longitudinal gradient in rainfall that becomes drier towards headwaters in the east. Chinook salmon were first observed in this region in the early 2000s (Correa and Gross 2008) and have since established annual spawning runs in watersheds throughout the region.

Stream surveys were conducted during the late summer/autumn spawning season (February through June) in 2016 and 2018. In 2016, four streams were surveyed, including three streams in the Río Aysén watershed (El Toqui, Ñirehuao, and Huemules) and one stream in the Río Baker watershed (Jaramillo; Figure 3.1b). In 2018, the three streams in the Aysén watershed were again surveyed, but Jaramillo was excluded due to logistical constraints. These study systems are third to fifth order streams with mean discharges that range from 2.8 to 31.4 m³/s (Table 3.1). During the two studied spawning seasons, each stream was visually surveyed multiple times throughout 1.0 to 2.3 km of stream reaches. The number of live and dead salmon were opportunistically counted during each survey, and the location of carcasses (in or out of the stream) was also recorded. These counts were not exhaustive given that they were typically conducted from one side of the stream only and spawning salmon and carcasses were observed downstream of the surveyed reaches in every stream. While not representing the total number of salmon in each stream, these counts characterized temporal patterns in spawning behaviour and carcass availability.

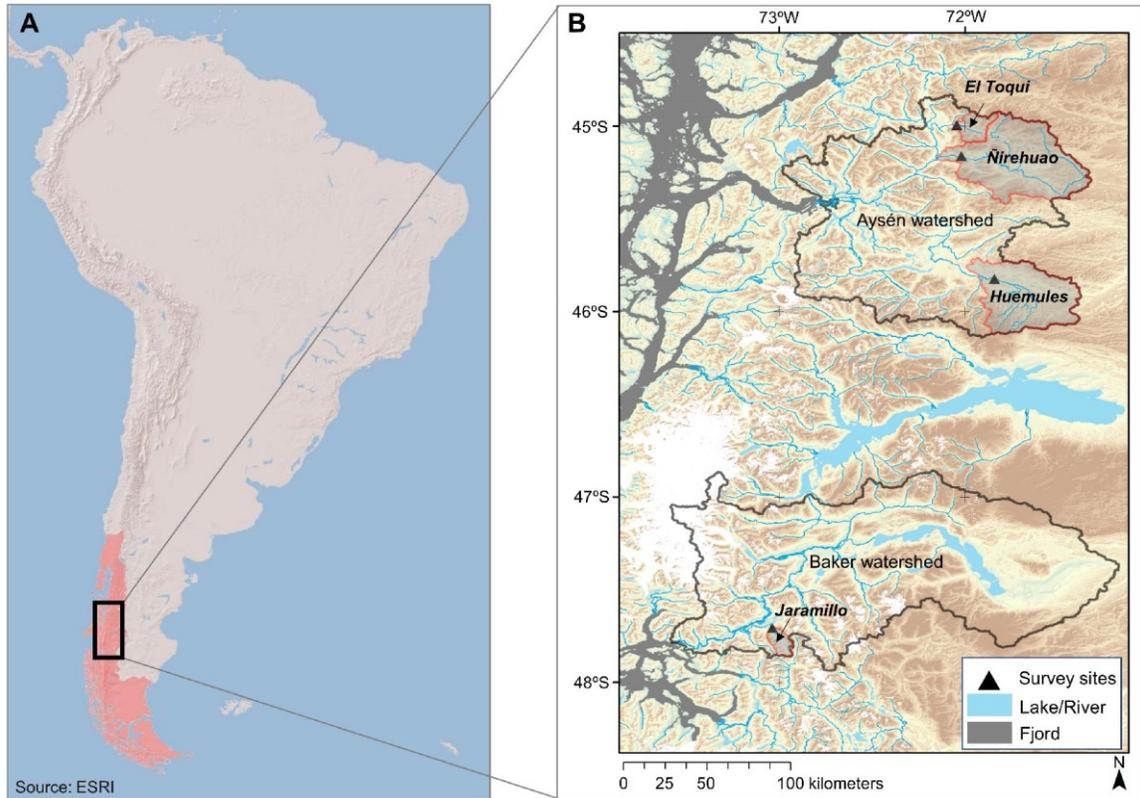


Figure 3.1 (a) Map of South America showing the regional distribution of Chinook salmon in southern Chile and Argentina (highlighted in red); (b) study streams located throughout the Chilean province of Aysén

Table 3.1 Stream and survey characteristics for study systems in Patagonia, southern Chile.

Stream	Drainage area (km ²)	Order	Mean discharge (m ³ /s)	Length of surveys for salmon (km)	Live fish observed †	Carcasses observed ‡	Carcasses out of water §
El Toqui	207	4	4.6	1.5	25	17	29%
Ñirehuao	1971	5	31.4	2.3	26	5	40%
Huemules	1423	5	15.8	1.8	30	22	32%
Jaramillo	117	3	2.8	1.0	44	39	36%

† The maximum number of live adult salmon observed on an individual survey date.

‡ The maximum number of dead adult salmon observed on an individual survey date.

§ The percent of carcasses found partially or fully out of water on the date that the maximum number of dead salmon was observed.

3.3.2. Invertebrate consumption

In 2016, invertebrate abundance on Chinook carcasses was quantified during one or two survey dates at all four streams. This survey occurred midway through the spawning season and used naturally-occurring carcasses that were encountered while surveying the streams. In total, 39 out-of-water carcasses and 50 underwater carcasses were sampled. Following Chaloner et al. (2002), the relative abundance of invertebrate taxa found on each carcass was estimated as 1-9, 10-99, 100-1000 or >1000 individuals. Larval flies (order: Diptera) on terrestrial carcasses were not identified beyond the order level. Instead, fly larvae were assumed to belong to the adult families that were observed on carcasses throughout the study period in 2016. Submerged carcasses were scanned visually, and invertebrates found on them were removed and stored for later identification (at the order or family level). This aquatic sampling procedure was likely biased against capturing highly mobile consumers such as decapods and did not account for any invertebrates that were inside carcasses. At each stream, taxa were categorized as absent, rare (1-9 individuals), present (10-99), or common (>100) based on their median relative abundance on carcasses.

Given the abundance of terrestrial flies found on carcasses in 2016 (described below), we deployed plastic funnel fly traps baited with salmon carcass flesh midway through the spawning season in 2018 to identify fly consumers at a higher taxonomic level. At El Toqui, Ñirehuao, and Huemules, five traps were left in riparian habitat for 24 h. Trapped adult flies were identified to the family level, and those belonging to family Calliphoridae (blowflies) were identified to species using Gonzalez et al. (2017).

In addition to the more formal sampling described above, opportunistic observations of invertebrate interactions with out-of-water carcasses were made throughout both spawning seasons. This included watching individual carcasses to observe invertebrate behaviour and photographing individual carcasses on different survey dates to visualize the loss of carcass mass due to invertebrate consumption.

3.3.3. Vertebrate consumption

Camera traps were used to monitor carcass consumption by terrestrial vertebrates. This monitoring took place at El Toqui, Ñirehuao, and Huemules in 2016

and again in El Toqui and Huemules in 2018. At the onset of carcass availability, one motion-activated camera per stream (Stealth Cam, Grand Prairie, TX, USA) was placed within 10 m of the stream edge and baited with a staked carcass that was found in or along the stream. The carcasses used were spawned-out albeit fresh, being fully intact with few signs of decomposition. Cameras were programmed to take three pictures per trigger, with a 30 second delay between triggers. In 2016, carcasses were monitored for 50, 13, and 45 days at El Toqui, Ñirehuao, and Huemules, respectively. In 2018, they were monitored for 16 and 20 days at El Toqui and Huemules, respectively. At the end of these sampling periods, baited carcasses had either been fully consumed or had only pieces of head, skin, and cartilage remaining. Encounter rates were quantified by counting the total number of camera triggers among consumer taxa at each site and then dividing by the total number of camera-days (i.e., encounters per camera-day). To avoid overestimating encounter rates by including consecutive triggers by the same individual, pictures of the same consumer taxon that were taken consecutively (i.e. one minute apart or less) were counted as a single encounter. These data were not analyzed statistically.

During consecutive days of work at El Toqui in March 2018, we observed carcasses that appeared to have been moved from the stream to nearby banks overnight, despite no significant change in water levels. Accordingly, we placed a camera in a cut-bank directly beside the stream edge and placed a carcass in the water in front of the camera. The carcass was wedged underneath a log to keep it submerged and in place. The camera was set to record video and was left overnight.

3.3.4. Community interactions

We summarized the community interactions involving Chinook salmon in Patagonia by categorizing all documented interactions in freshwater and terrestrial habitats using the framework presented in Simberloff and Von Holle (1999). This framework is used to describe potential food web impacts of invasive species (e.g., Crego et al. 2016) and identifies four types of pairwise species interactions: '+/+' denotes interactions in which individuals of two species directly benefit from the presence of the other species; '+/0' denotes those in which individuals of one species benefit from the presence of the other species, whereas individuals of the second species are not affected by the first (e.g., a donor-controlled subsidy); '+/-' denotes interactions in which

individuals of one species benefit from the presence of the other, however individuals of the other species are negatively affected by the first species (e.g., predator-prey interactions); and ‘-/-’ denotes interactions that are detrimental to individuals from both species. We added ‘0/+/+’ to describe tri-trophic interactions in which individuals from a third species benefit from the presence of the benefitting species in a ‘0/+’ interaction. These categories describe individual-level interactions. These interactions could have population-level consequences for one or both species and therefore conceptualize potential food web impacts of invaders. The salmon interactions used here include those described in this study as well as those previously reported in the literature. Published observations were obtained by searching Web of Science using the search term “(Chinook salmon AND ("Chile" OR "Argentina" OR "Patagonia"))”.

If Chinook and an interacting taxon have multiple interaction types in another location (e.g., the native range of salmon), all of these interaction types were inferred to be present in Patagonia if at least one of the interactions was documented in Patagonia. Indirect interactions involving Chinook (e.g., tri-trophic interactions 0/+/) were only included if they were directly observed. Likewise, negative interactions resulting from exploitative competition (-/-) were only included if shared prey items have been shown to be limiting. Aquatic macroinvertebrates and terrestrial insects were considered two groups of interacting organisms, with interactions with individual taxa beyond the scope of this analysis. Interactions among the interacting taxa (i.e., not involving Chinook salmon) were not assessed.

3.4. Results

3.4.1. Carcass availability

Across streams in both 2016 and 2018, adult Chinook salmon occupied pool habitats in mid-February and then occupied riffle-run transition habitats throughout March and April and displayed breeding behaviours such as redd construction and maintenance. Carcasses appeared between early March and early April (depending on the stream) and were observed on final survey dates in early June, weeks after spawning had completed. Few carcasses were observed at Ñirehuao relative to the other streams (Table 3.1). On the day that the maximum number of carcasses was

observed at each stream, 29-40% of carcasses were found partially or fully out of water (Table 3.1).

3.4.2. Invertebrate consumers

In 2016, the adult flies found eating or laying eggs on out-of-water carcasses were primarily blowflies (family: Calliphoridae) (Figure 3.2a) but also included flesh flies (Sarcophagidae) and March flies (Bibionidae) (Appendix Figure B1). Terrestrial flies were abundant on carcasses, averaging over 1000 larvae per carcass across all streams (Table 3.2). Larvae were typically found on the underside of carcasses (Figure 3.2b), on gills, in the mouth, and under fins (Figure 3.2c). Heavy colonization of carcasses by fly larvae caused rapid depletion of carcass mass, with individual carcasses changing from nearly whole to only skin, cartilage, and bones within a few days (Figure 3.2c, d). Fly traps (baited with carcass flesh) were successful in attracting flies, with each trap typically containing well over 100 individuals. Blowflies comprised over 95% of the trapped flies at each stream. Of the blowflies, 99% of individuals were the cosmopolitan species *Calliphora vicina*. Flesh flies were also found in the traps (< 5% of trapped flies).

Table 3.2 Median abundance of terrestrial and aquatic invertebrate taxa found on naturally occurring Chinook salmon carcasses at four streams in southern Chile.

Taxon	Stream			
	Ñirehuao	El Toqui	Huemules	Jaramillo
Terrestrial				
Diptera†	+++	+++	+++	+++
Hymenoptera				
Vespidae	+	NA	NA	+
Aquatic				
Diptera				
Chironomidae	++	++	++	++
Simuliidae	+	+	NA	++
Plecoptera	+	+	+	+
Trichoptera	+	+	NA	NA

Terrestrial taxa colonized carcasses that were out of water, whereas aquatic taxa colonized submerged carcasses. Abundance categories are NA (absent), + (rare; 1-9 individuals), ++ (present; 10-99 individuals) and +++ (common; >100 individuals).

† Calliphoridae, Sarcophagidae, Bibionidae.



Figure 3.2 Colonization and consumption of out-of-water salmon carcasses by terrestrial flies in southern Chile.

Pictured are (a) adult blowflies (Calliphoridae) on a fresh carcass, (b) hundreds of fly larvae on the underside of a carcass, (c) fly larvae under a carcass fin, and (d) a carcass left with only skin, cartilage, and bone after fly consumption. Photos (c) and (d) show the same carcass six days apart, illustrating rapid loss of carcass mass due to fly consumption.

Non-native yellow jacket wasps (genus *Vespula*) were found on several out-of-water carcasses at Ñirehuao and Jaramillo (Table 3.2; Figure B1d). There were also several opportunistic observations made in 2018: dozens of carrion beetles from the family Silphidae (genera *Oxelytrum* and *Nicrophorus*) were observed feeding on multiple carcasses (Figure B2); predatory beetles (Staphylinidae and Carabidae: *Ceroglossus*) fed on insects that were feeding on a carcass; predatory balloon flies (Empididae: Hemerodromiinae) hunted small Acaliptratae flies that were feeding on a carcass; and, lastly, a male Darwin's beetle (*Chiasognathus grantii*) was observed feeding on carcass liquids and fending off other males from a carcass.

Carcasses submerged underwater had lower levels of invertebrate abundance relative to riparian carcasses (Table 3.2). Chironomid midge (Chironomidae) larvae averaged 10–99 individuals per carcass at all four streams. Blackfly (Simuliidae) larvae were the second most abundant taxon, although they were likely not feeding directly on

carcasses because they attach themselves to substrate and feed on floating organic debris. Stoneflies (Plecoptera) and caddisflies (Trichoptera) were rare (i.e., 1-9 individuals per carcass on average), while mayflies (Ephemeroptera) were found on several carcasses but were absent from carcasses on average. Weeks after the appearance of carcasses (late April and May), underwater carcasses were covered with a thick, mould-like biofilm (Figure B3).

3.4.3. Vertebrate consumers



Figure 3.3 Evidence of vertebrate consumption of (a) a partially submerged carcass in Río El Toqui, and (b) a carcass in riparian habitat at Río Huemules.

Such carcasses were found largely consumed with mostly bones remaining, indicating consumption by animal scavengers.

Evidence of vertebrate consumption of naturally occurring carcasses was commonly observed during surveys (Figure 3.3). Camera trap monitoring in 2016 found four vertebrate taxa that consumed riparian carcasses: small rodents (black rats *Rattus rattus*, house mice *Mus musculus*, and/or colilargos *Oligoryzomys longicaudatus*), the ground-foraging passerine bird ‘chucaco’ (*Scelorchilis rubecula*), the South American fox ‘culpeo’ (*Lycalopex culpaeus*), and the invasive American mink (Figure 3.4). Encounter rates varied among species and streams (Figure 3.5a). At Ñirehuao and El Toqui, rodents and chucaos averaged multiple encounters per camera-day whereas foxes were less common; conversely, only foxes and mink were encountered at Huemules (Figure 3.5a). Foraging behaviour was not directly evident in some encounters, however foraging on carcasses was frequently observed for each consumer taxa. Rodents foraged extensively adjacent to and directly on carcasses, and only at night. Species identification for these rodent encounters was challenging due to their nocturnal activity

and their morphological similarity. Although definitively identifying species was not possible, there were visual indications for the native cricetid 'colilargo' as well as the non-native black rat and house mouse, suggesting that the encounters consisted of a combination of these three species. Chucaos visited carcasses during daylight and demonstrated gleaning behaviour, feeding on invertebrates that had colonized the carcasses. Foxes visited carcasses both day and night, often urinated on carcasses seemingly without feeding on them, and occasionally ripped off large portions of the carcass when feeding. Mink were only encountered at nighttime and were observed biting at the carcass and attempting to remove it. Mink encounters occurred within a week of the camera trap being set, likely indicative of a preference for fresh prey.



Figure 3.4 Chinook salmon carcass visits by (a) a small rodent, (b) a chucao, (c) an American mink, and (d) a culpeo fox.

Carcasses were staked in riparian habitat adjacent to streams in southern Chile.

During camera trap monitoring in 2018, culpeo foxes averaged over one carcass encounter per day at Huemules and were again present at El Toqui (Figure 3.5b). Mink were not encountered at Huemules but were encountered at El Toqui and, again, these

encounters only occurred within one week of the camera trap being set. Rodents and chucaos were encountered less frequently at El Toqui in 2018 compared to 2016 (Figure 3.5). Additionally, the passerine bird ‘thorn-tailed rayadito’ (*Aphrastura spinicauda*) visited the carcass at El Toqui and seemingly fed on invertebrates off the carcass. Across streams and years ($n = 5$), lower rates of fox and mink encounters (combined) were associated with increased rates of rodent and passerine encounters (Figure B4).

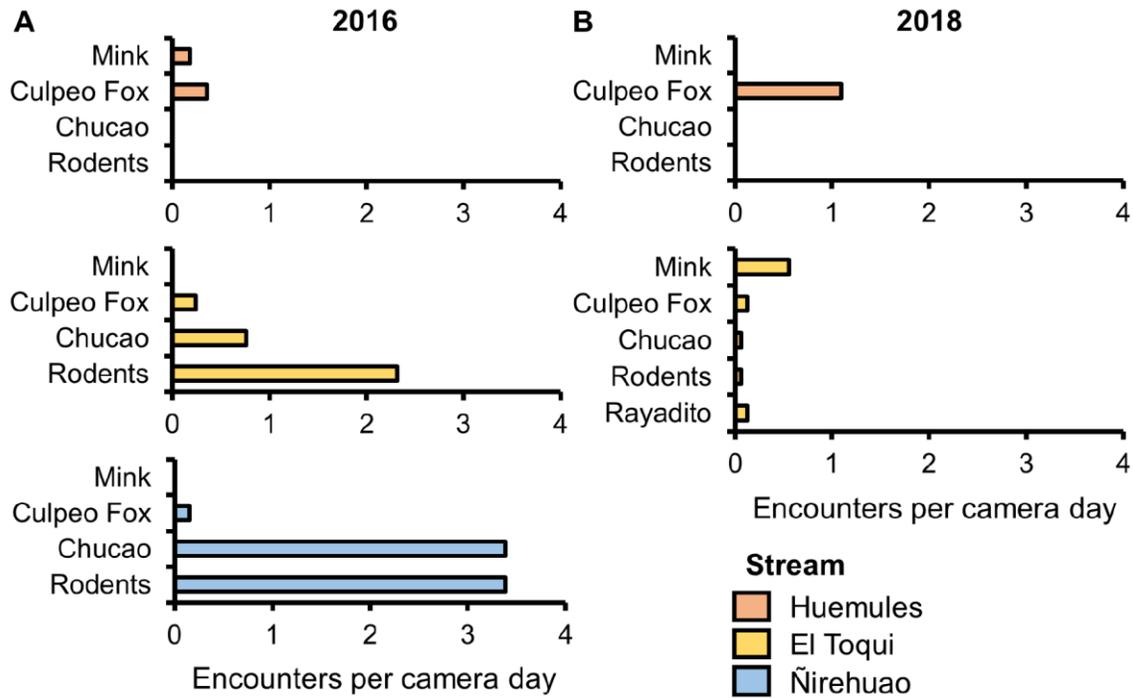


Figure 3.5 Vertebrate consumers of out-of-water salmon carcasses in southern Chile.

Camera traps were baited with salmon carcasses adjacent to streams. Consumer encounter rates per camera day were calculated (a) for three streams in 2016, and (b) for two streams in 2018. Consumer taxa were American mink, culpeo fox, a passerine bird ‘chucao’, rodents (black rats, house mice, and/or colilargos), and a passerine bird ‘thorn-tailed rayadito’.

Video monitoring of a submerged carcass in El Toqui showed an individual mink walking along the streambank, submerging its head repeatedly to feed on the carcass, making repeated attempts to dislodge the carcass, and, finally, feeding on the carcass along the streambank after having removed it from the water (Figure B5). This footage demonstrates carcass transfer from stream to streambank by a vertebrate scavenger.

3.4.4. Community interactions

The literature search yielded 65 returns, of which six contained observations of trophic interactions between Chinook salmon and freshwater or riparian taxa (Table B1). Including those presented here, the documented interactions in Patagonia consist of scavenging salmon carcasses or spilt eggs (0/+, $n = 7$), predator-prey interactions (-/+ or +/-, $n = 4$), nutrient subsidies (0/+, $n = 1$), terrestrial prey subsidies (+/0, $n = 1$), and tri-trophic interactions (0/+/, $n = 1$; Table A1). Other than a nutrient subsidy effect on stream algae (Muñoz et al. 2021), none of these interactions have been studied at the population level (i.e., impacts on abundance or biomass).

Our proposed framework of the role of Chinook salmon in Patagonian food webs reveals numerous interactions involving a diverse group of taxa and trophic levels (Figure 3.6). In streams, nutrients from adult salmon carcasses benefit stream algae (Muñoz et al. 2021), and salmon carcasses or spilt eggs are scavenged by trout and macroinvertebrates such as chironomid midges and freshwater crabs (*Aegla* sp.; Soto et al. 2007; Arismendi and Soto 2012). As predators, juvenile or sub-adult salmon negatively affect native galaxiid fishes (family: Galaxiidae) and macroinvertebrates such as mayfly and stonefly nymphs (Ibarra et al. 2011; Chalde and Fernandez 2017; Di Prinzio and Arismendi 2018; Bravo et al. 2019). As prey, juvenile salmon likely benefit adult trout and riverine mink (Ben-David et al. 1997; Tabor et al. 2004). Terrestrial insects that fall into streams benefit juvenile salmon as a donor-controlled prey resource (Chalde and Fernandez 2017; Di Prinzio and Arismendi 2018). Adult salmon carcasses are transferred to terrestrial habitat by water movement and mink scavenging. There, carcasses are heavily consumed by terrestrial insects such as blowflies, which are in turn consumed by passerine birds such as the chucao and rayadito. Out-of-water carcasses are also scavenged by birds of prey (chimango caracara [*Milvago chimango*] and southern crested caracara [*Caracara plancus*]; Soto et al. 2007), culpeo foxes, and small rodents, including non-native house mice and black rats. The only taxa with multiple beneficial interactions are non-native trout and mink. The only taxon with a net negative interaction with Chinook is galaxiid fishes.

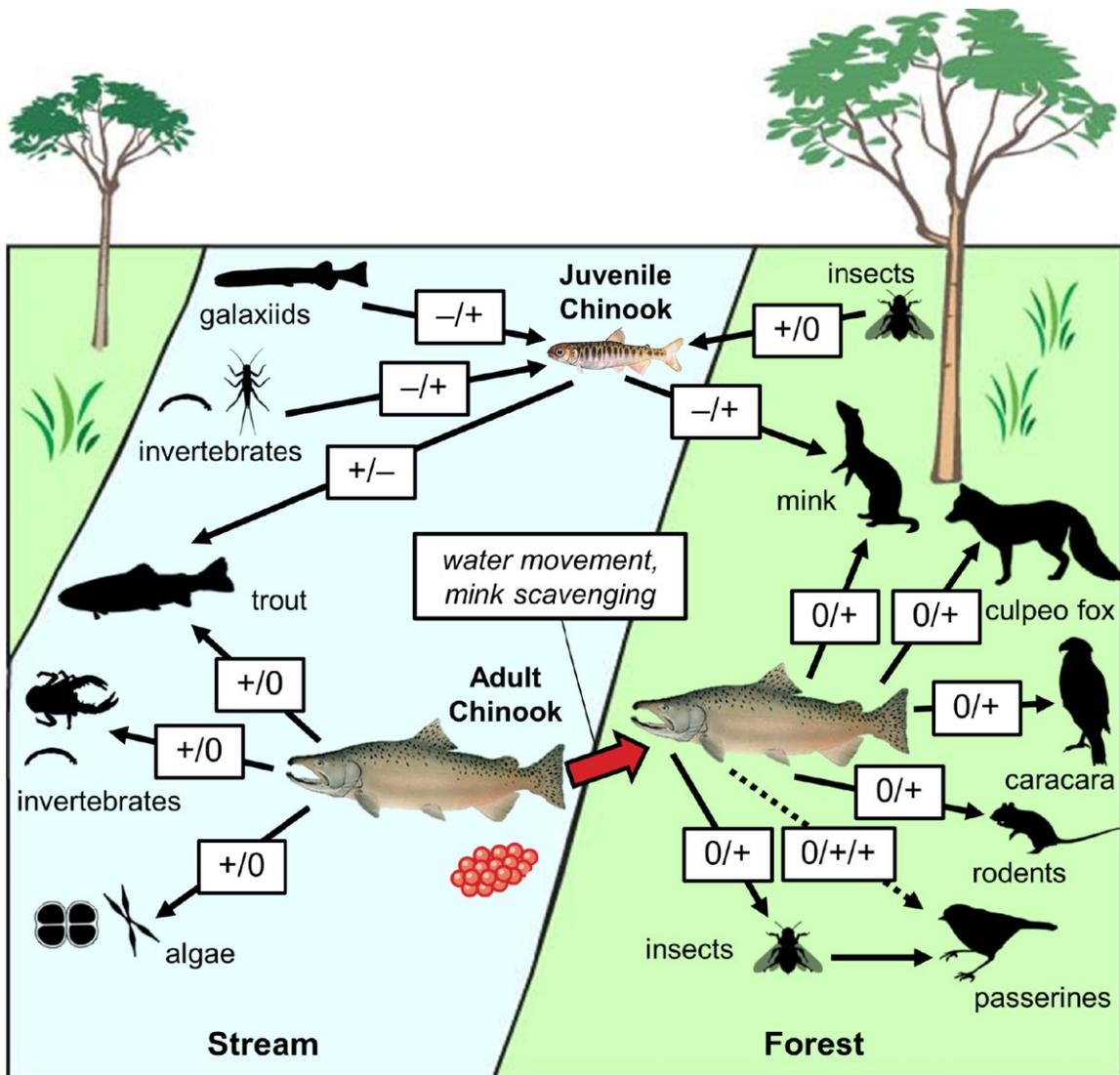


Figure 3.6 Trophic interactions involving Chinook salmon in streams and forests of Patagonia.

All documented interactions were classified following Simberloff and Von Holle (1999): '+/0' denotes interactions in which individuals of one species benefit whereas individuals of the other species are not affected; '+/-' denotes interactions in which individuals of one species benefit whereas individuals of the other species are negatively affected; and '0/+/' denotes a tri-trophic interaction whereby individuals from a third species benefit from the presence of the benefitting species in a '0/+' interaction. For terrestrial interactions, salmon correspond with the first taxon in each interaction (e.g., '0' in '0/+'), whereas they correspond with the second taxon in each freshwater interaction. *Black arrows* represent direct interactions, the *dashed arrow* represents an indirect interaction, and the *red arrow* represents the transfer of carcasses from streams to riparian habitat.

3.5. Discussion

The observations presented in this study reveal a multitude of trophic interactions involving Chinook salmon in Patagonia, including the re-emergence of historical

interactions from the native range of Pacific salmon. These interactions have emerged rapidly, with Chinook salmon being first reported in our study streams in the early 2000s (Correa and Gross 2008). The diverse taxa and trophic levels that interact with Chinook salmon in Patagonia suggest a potential for diverse impacts of salmon on Patagonian food webs.

The post-spawn fate of anadromous fish carcasses is mediated by a suite of physical and biological factors such as hydrology, hydromorphology, predation, and scavenging (Harding et al. 2019; Dunkle et al. 2020). For example, Pacific lamprey (*Entosphenus tridentatus*) carcasses are retained instream in depositional microhabitats whereas they are washed out onto riparian habitat alongside high-velocity stream segments (Dunkle et al. 2020), and predation by bears and wolves can transfer up to 23% of spawning Pacific salmon in a stream to the riparian zone (Harding et al. 2019). Here, the ratio of dead to live Chinook salmon observed was 68-89% at El Toqui, Huemules, and Jaramillo and only 19% at Ñirehuao. The relatively low number of carcasses found at Ñirehuao could be driven by the exceptionally high flows of water in this stream (mean discharge = 31.4 m³/s), which can flush carcasses downstream (Richey et al. 1975). We also found that 29-40% of carcasses were deposited out of water. Whereas the lack of bears and wolves in Patagonia should limit the number of salmon carcasses that are biologically transferred to riparian habitat, we show here that non-native mink can actively remove carcasses from streams via scavenging, and the same is likely true for other large scavengers such as foxes, dogs, and vultures. This active transport of carcasses should increase the degree to which marine-derived nutrients enter terrestrial food webs in Patagonia.

The novel interactions that emerge in invaded food webs can be predicted in part by the phylogenetic similarities between species in the invaded food web and species from the food web that the invader is native to (Pearse and Altermatt 2013). This influence of eco-evolutionary experience suggests that interactions from the native range of an invader may functionally re-emerge in invaded food webs via resident species that are closely related to interactors in the invader's native range. In Patagonia, we found that many species consume the nutrients provided by post-reproductive salmon, and that these positive effects extend to a variety of native taxa such as blowflies, beetles, passerine chucaos, culpeo foxes, and chironomids. All of these taxa are closely related to species in North America that similarly derive benefits from salmon consumption. For

example, North American blowflies are a dominant vector of salmon nutrients in terrestrial food webs, colonizing over 90% of carcasses (Hocking and Reimchen 2006) and numbering up to 50,000 larvae on individual carcasses (Meehan et al. 2005). Blowflies increase in abundance due to salmon consumption so much so that they have induced a phenological link between salmon spawning and the flowering of a plant (*Angelica genuflexa*) that blowflies pollinate as adults in Alaska (Lisi and Schindler 2011). Among streams in British Columbia, the abundance, nest density, and territory size of Pacific wrens (*Troglodytes pacificus*) – insectivorous passerines similar to chucaos – are positively associated with the abundance of spawning salmon (Wagner and Reynolds 2019; Wilcox et al. 2021). Like culpeo foxes in Patagonia, coyotes (*Canis latrans*) scavenge salmon carcasses in Alaska (Levi et al. 2015). Submerged salmon carcasses in Alaska are most heavily colonized by chironomid midge larvae (Chaloner et al. 2002), as was found here. These results indicate that many of the pathways of salmon nutrient incorporation in North American food webs have functionally re-emerged in South America via phylogenetically-similar native species, supporting the hypothesis that eco-evolutionary history mediates the interactions and impacts that stem from biological invasions (Pearse and Altermatt 2013; Carthey and Banks 2014; Saul and Jeschke 2015).

Most interactions among co-occurring non-native species are either neutral or antagonistic (Jackson 2015); however, many facilitative interactions have been documented and have raised concerns over their potential to increase the community-level impacts of invasive species (i.e., 'invasional meltdowns'; Simberloff and Von Holle 1999; Simberloff 2006). A mechanism that could promote this facilitation is an evolutionary history of coexistence (Best and Arcese 2009; Arismendi et al. 2020). Rainbow trout and mink coexist with Pacific salmon in their native range. There, they strongly benefit from the annual pulse of salmon eggs and carcasses (Ben-David 1997; Scheuerell et al. 2007) and also prey on juvenile salmon (Ben-David et al. 1997; Tabor et al 2004). Similarly, brown trout coexist with Atlantic salmon in their native range and strongly benefit from the consumption of Chinook salmon eggs in tributaries of the Laurentian Great Lakes (Hermann et al. 2020), where they are both introduced. In Patagonia, rainbow trout and brown trout consume salmon eggs and mink scavenge salmon carcasses during salmon spawning. The eco-evolutionary experience that trout and mink have with salmon likely means that they are pre-adapted for such consumption

and could consequently be key beneficiaries of the salmon invasion of Patagonia. Trout and mink are now widespread in Patagonia and negatively affect the abundance and distribution of many native species (Schüttler et al. 2009; Habit et al. 2010; Arismendi et al. 2012; Correa and Hendry 2012; Valenzuela et al. 2013). Other invasive species that benefit from salmon consumption in Patagonia include yellow jacket wasps, house mice, and black rats. It has also been speculated that Chinook in Chile might act as a vector for the invasive diatom *Didymosphenia geminata* (Bus Leone et al. 2014), though this remains untested. These observations add to the growing number of interactions among non-native species in Patagonia (Crego et al. 2016). As these interactions increase in strength and complexity, non-native species will continue to alter these otherwise minimally-impacted ecosystems.

The native aquatic fauna of Patagonia is characterized by low species richness and high levels of endemism, and many of the galaxiid fishes that dominate the native freshwater fish assemblage are imperiled (Habit and Cussac 2016). The interactions framework proposed here suggests that galaxiids are likely the 'loser' of the Chinook salmon invasion of Patagonia given that they are the only taxon with a net negative interaction with Chinook. Furthermore, galaxiids are likely to have an indirect negative interaction with salmon due to the positive effects of salmon on trout and mink, both of which are galaxiid predators (Arismendi et al. 2012; Valenzuela et al. 2013). On the other hand, galaxiids and other native fishes might benefit from consumption of salmon eggs and tissue; however, such consumption is likely limited because trout competitively exclude other stream fishes from salmon resources (Bailey and Moore 2020). Throughout the southern hemisphere, galaxiids have declined as a result of salmonid introductions (Townsend 2003; Habit et al. 2010; Shelton et al. 2015; Lintermans et al. 2020). Given that the potential for coexistence appears to be low, the protection of salmonid-free, hydrologically-isolated habitat should be an urgent priority for conservation efforts in Chile.

The interactions framework presented here provides the first assessment of the pathways through which Chinook salmon can impact terrestrial and freshwater food webs in Patagonia. All of the interacting taxa occur throughout much of the South American range of Chinook salmon, meaning the observed interactions likely take place across a large spatial scale. The list of interactors is certainly incomplete due to the limited scope of our field surveys. Other types of interactions that have not yet been

studied include responses to salmon-derived nutrients among riparian plants (e.g., Hocking and Reynolds 2011; Siemens et al. 2020; Kieran et al. 2021), consumption of juvenile salmon and salmon eggs by forest birds (e.g., Tonra et al. 2016), the transport of salmon-derived nutrients into terrestrial food webs through the emergence of stream insects (e.g., Francis et al. 2006), microbial interactions (discussed below), and bioturbation effects due to disturbance of the streambed (e.g., Moore and Schindler 2008). Moreover, the prevalence of these interactions likely varies spatially and temporally due to variation in physical and biological characteristics of ecosystems. For example, salmon-derived nutrients increased algal biomass in Ríos El Toqui, Huemules, and Jaramillo, whereas there was no such subsidy effect detected in Ñirehuao, the study stream with the greatest discharge (Muñoz et al. 2021). Despite these caveats, this interactions framework can help guide future research on population- and community-level impacts of non-native salmon in streams and forests.

Whereas our interactions framework focuses on macro-organisms, interactions with micro-organisms could be similarly consequential. In the native range of salmon, the internal microbiome of aquatic mayflies and terrestrial blowflies is influenced by the presence of salmon and the microbial assemblage associated with salmon carcasses (Pechal and Benbow 2016). Thus, as salmon create a novel link between marine and freshwater habitats in Patagonia, a novel assemblage of microbes might be incorporated by direct and indirect consumers of salmon. Future studies should expand on our interactions framework such that the microbial ecology of this invasion is better understood (e.g., Irgang et al. 2019).

The ecological consequences of these interactions will largely depend on how abundant salmon become in Patagonia. Monitoring of the abundance of Chinook salmon in Patagonia has been rare but will presumably grow given the emerging artisanal fishery for Chinook salmon in the coastal waters of southern Chile. An assessment of spawning numbers in the Río Toltén watershed in Chile estimated that over 12,000 adult Chinook returned to this watershed between 2014 and 2015 (Gomez-Uchida et al. 2014). These numbers are comparable to Chinook populations in British Columbia, where the annual spawner abundance in individual populations generally does not exceed a few tens of thousands (Gottesfeld et al. 2008) and is often less than 1,000 (Healey 1982). Without the other, more abundant species of Pacific salmon, the effects of salmon in Patagonia will be less pervasive than in North America. Nevertheless, the

freshwater ecosystems of southern South America are some of the most nutrient-limited systems in the world (Perakis and Hedin 2002; Dentener et al. 2006), meaning the novel inputs of marine-derived nutrients should be highly utilized by plants and animals (Sears et al. 2004). Moreover, recent evidence indicates that coho salmon (*O. kisutch*) have established self-sustaining populations in southern Chile (Górski et al. 2016; Maldonado-Márquez 2020; C. Correa, unpublished observations), suggesting that the abundance of Pacific salmon will continue to increase in the region. Going forward, expanded monitoring of the abundance and impacts of Patagonian salmon will be vital if managers are to balance the socio-economic benefits with the ecological costs of this invasion.

Chapter 4.

The local and global stability of Pacific salmon abundance³

4.1. Abstract

Ecological properties are hypothesized to stabilize across increasingly large spatial scales, with larger areas incorporating more asynchrony among local patches and thus more stability. We tested this hypothesis by quantifying the stability of Pacific salmon (*Oncorhynchus* spp.) abundance over the past six decades at two spatial scales: the North Pacific Ocean and Northern British Columbia (BC). The regional stability of annual salmon abundance was significantly higher in the North Pacific than in Northern BC, with asynchronous dynamics among patches increasing stability by an average of 170% in the North Pacific and 63% in Northern BC. Temporal variation in regional stability was primarily caused by shifting dominance of odd- and even-year pink (*O. gorbuscha*) salmon. At the North Pacific scale, artificial hatchery production had only a marginal effect on local stability in all jurisdictions except Japan. These results highlight the importance of spatial portfolios in the temporal maintenance of ecosystem services.

4.2. Introduction

The impact of humans on nature is increasingly pervasive, making it vital to understand the stability of biological systems and the services that they provide to humanity. Studies have consistently demonstrated that, at local spatial scales (e.g., within a grassland ecosystem), biodiversity is positively associated with the temporal stability of aggregate ecosystem properties such as total biomass and primary productivity (e.g., Naeem and Li 1997; Tilman et al. 2006; Hector et al. 2010; Hautier et al. 2015). This diversity-stability relationship occurs because species respond differentially to environmental heterogeneity and stochasticity, causing asynchronous dynamics among species through time and generating stability (i.e., invariability) of

³ A version of this chapter is being prepared for submission with the following authors list: Muñoz, N.J., Price, M.H.H., Godwin, S.C., Obrist, D.S., Dennert, A.M., Pendray, J.E., Hertz, E., Reynolds, J.D.

aggregate properties (Ives et al. 1999). Such research has revealed an emergent feature of biological systems that is analogous to that of financial investment portfolios: diversity in the individual components (e.g., species, populations, stock holdings) of a portfolio generates stability in the aggregate performance of the portfolio (e.g., community biomass, metapopulation abundance, return on investment) (Doak et al. 1998; Tilman et al. 1998; Schindler et al. 2015). Whereas diversity-stability relationships have enhanced our understanding of ecological functioning at local spatial scales, human societies often rely on the regional or global stability of ecosystem services such as fisheries and crop production (Brander 2007; Khoury et al. 2014). Applying this understanding to large spatial scales therefore requires explicit consideration of the spatial scaling of ecological properties (Levin 1992; Wang et al. 2017).

The link between ecological functioning at local and regional spatial scales has been the focus of a recent theoretical framework of temporal stability (Wang and Loreau 2014). This framework uses a metacommunity and metaecosystem approach, which designates spatially distinct sets of local communities and ecosystems that are connected by biotic factors such as dispersal and competition or abiotic factors such as climate (Loreau et al. 2003; Leibold et al. 2004). It posits that stability of an aggregate property at the metacommunity (i.e., regional) scale is influenced by two processes: i) temporal stability of the property within local communities (local stability), and ii) the degree to which temporal fluctuations in the property are synchronized among local communities (spatial synchrony). The core prediction of this framework is that ecological properties become increasingly stabilized across larger areas. This area-stability relationship is predicted to occur because larger areas (relative to smaller areas) should encompass more environmental heterogeneity and have reduced connectivity among local communities (both of which should reduce spatial synchrony) while also containing a greater regional pool of species (which should increase local species richness and, thus, local stability) (reviewed in Patrick et al. 2021). Previous applications of this framework have found partial support for an area-stability relationship (Catano et al. 2020; Patrick et al. 2021); however, this relationship has not yet been tested using metacommunities that are directly comparable (e.g., stability of the same set of species in smaller versus larger metacommunities).

Pacific salmon (*Oncorhynchus* spp.) are ideal species to study metacommunity and metaecosystem dynamics due to their migratory life histories, rich population

diversity, and importance to fisheries and wildlife. Once each year throughout Pacific North America and Asia, adult salmon return to natal streams to reproduce and die (Groot and Margolis 1991). Afterwards, juvenile salmon migrate from these streams to coastal and off-shelf habitats in the North Pacific Ocean. Salmon are broadly distributed in the North Pacific during the one to five years that individuals reside there, with North American and Asian stocks overlapping (Myers et al. 1990) and competing for shared prey resources (Bugaev et al. 2001; Johnson and Schindler 2008; Connors et al. 2020). The adult fish that are not captured by ocean fisheries return to their natal streams. In turn, these fish support a range of services in local communities and ecosystems, including the place-based fisheries of hundreds of coastal First Nation communities (Gayeski et al. 2018), ecosystem functioning through the delivery of marine-derived nutrients to aquatic and riparian consumers (Walsh et al. 2020), and ecotourism (e.g., PSF 2014).

Research on Pacific salmon has illustrated how the stability of natural resources can be influenced by human management practices. Salmon have rich inter- and intraspecific diversity in life histories (Groot and Margolis 1991), which act to stabilize their aggregate abundance via portfolio effects. For example, the sockeye (*O. nerka*) salmon stock complex in Bristol Bay, Alaska contains hundreds of discrete spawning populations, and asynchronous dynamics among these populations results in interannual stability of fisheries catch (Schindler et al. 2010) and contributes to economic stability in fishing communities (Cline et al. 2017). However, most commercial salmon fisheries involve mixed-stock fishing, whereby fisheries capture multiple stocks and species (Gayeski et al. 2018). Such mixed-stock fishing can erode diversity (and, thus, stability) because its lower level of selectivity allows for unproductive populations to be overfished (Moore et al. 2021). Indeed, portfolio effects have weakened over recent decades within salmon stock complexes in the southern portion of their range (Moore et al. 2010; Freshwater et al. 2019; Price et al. 2021; Sullaway et al. 2021), coincident with regional declines in abundance due to habitat loss, overfishing, and climate change (Gustafson et al. 2007). In response to this decline, large-scale hatchery production of salmon has been employed in many jurisdictions in order to achieve catch objectives while stabilizing populations (e.g., DFO 2021). However, whereas hatchery production may increase abundance for some populations, it may also negatively affect stability through the erosion of life history diversity (Satterthwaite & Carlson 2015), the

subsidization of mixed-stock fisheries (Meffe 1992), and by reducing the abundance of wild populations through competition (Connors et al. 2012; Connors et al. 2020; Ohlberger et al. 2021). As salmon populations continue to decline in many regions, a broad assessment of the influence of such management practices on salmon stability is needed.

The aims of this study were to i) use spatiotemporal reconstructions of Pacific salmon abundance to test the hypothesis that ecological properties stabilize across increasingly large areas (Levin 1992; Wang and Loreau 2014), and ii) assess the influence of species, local communities, hatcheries, and fisheries management on salmon stability. We aggregated the annual abundance of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon across the entire North Pacific Ocean and within Northern BC, Canada. At both spatial scales, we quantified the regional stability, local stability, and spatial synchrony of annual salmon abundance over the last six decades. We found that spatial asynchrony stabilized salmon abundance to a greater degree in the North Pacific than in Northern BC. We also found that large-scale hatchery production has only a marginal effect on the stability of salmon abundance throughout the North Pacific, whereas fisheries management in Northern BC has maintained the stability of escapement since the 1990s despite declines in abundance. These results support the predictions of Wang and Loreau (2014) and enhance our understanding of the drivers of salmon stability.

4.3. Methods

4.3.1. Salmon abundance data

To quantify the stability of Pacific salmon at two spatial scales, we used published reconstructions of adult pink, chum, and sockeye salmon abundance throughout the North Pacific (Ruggerone and Irvine 2018) and, at a smaller scale, within Northern BC (English et al. 2018). We included only pink, chum, and sockeye salmon in our analyses because abundance reconstructions in the North Pacific include only these three species, and also because these species comprise the vast majority of total Pacific salmon abundance (96% of total reported catch since the 1990s; NPAFC 2017). In the North Pacific data set, annual adult salmon abundance was reconstructed for the years 1952 to 2015 for each of 14 regions, encompassing the entire native range of Pacific

salmon (Ruggerone and Irvine 2018; Figure 4.1a). For each species, Ruggerone and Irvine (2018) estimated annual abundance as natural-origin (including fish produced by managed spawning channels), hatchery-origin, and total (natural- + hatchery-origin) abundance. We excluded one of the regions (Korea) from our analyses (leaving $n = 13$ regions) because Korea has no natural-origin salmon and produces only a small number of hatchery-origin chum salmon ($< 0.1\%$ of all hatchery-origin chum in the North Pacific since production in Korea began in 1971).

To assess how drivers of stability change across spatial scales, we ‘zoomed in’ on the Northern BC region from the North Pacific data set (Figure 4.1b). Within Northern BC, annual salmon abundance was reconstructed for 10 fishery Management Areas during the years 1954 to 2017 (English et al. 2018; Figure 4.1b). For each species, abundance was estimated as escapement (i.e., number of adults not caught by fisheries), catch (i.e., number of adults caught by fisheries), and total (i.e., escapement + catch). This data set has missing abundance estimates for some Management Areas during the years 1954-1959 and 2013-2017, as well as missing values throughout the time series for sockeye in Management Area 3 and pink in Management Area 10. To have a complete time series with no missing values, we included only the years 1960-2012 and we excluded sockeye in Management Area 3 and pink in Management Area 10. This data set does not distinguish between natural- and hatchery-origin abundance. The vast majority of salmon in this region are natural-origin, as enhancement programs in Northern BC typically use spawning channels and hatchery production is minor (with hatcheries contributing 1.6% of total Northern BC salmon abundance since the onset of hatchery production; Ruggerone and Irvine 2018).

4.3.2. Stability components

We used the framework developed by Wang and Loreau (2014) to quantify the stability of Pacific salmon abundance at two spatial scales (North Pacific and Northern BC). This framework considers a metacommunity composed of spatially distinct local communities. At the North Pacific scale, we consider a metacommunity (the North Pacific) composed of 13 local communities (regions spanning Pacific North America and Asia). At a finer scale, we then consider one of these local communities (Northern BC) as a metacommunity, itself composed of 10 local communities (Management Areas spanning BC’s central and north coasts).

Stability components (described below) were calculated in 10-year rolling windows throughout both time series (1952-2015 in the North Pacific, 1960-2012 in Northern BC). As such, these components incorporate the degree of year-to-year fluctuations in salmon abundance over successive 10-year periods of time. We chose a 10-year rolling window because it encompasses multiples of the average generation times of each salmon species. For example, the average age-at-maturity of chum and sockeye salmon in BC and Alaska is five years, whereas pink salmon exclusively return at age-2 (Quinn 2018). Trends in stability metrics over time were similar when 8- or 12-year rolling windows were used (Appendix Figure C1). Appendix Table C1 provides an overview of the model notation.

Following Wilcox et al. (2017), we inverted the coefficient of variation (CV) terms presented in Wang and Loreau (2014) such that stability terms represent the inverse of variability. Temporal stability of salmon abundance at the metacommunity level (i.e., in the North Pacific or Northern BC) is termed regional stability (γ_{stb}) and is calculated as:

$$\gamma_{stb} = \frac{\mu_M}{\sigma_M} \quad (1)$$

in which μ_M is the temporal mean and σ_M is the temporal standard deviation of total annual salmon abundance in metacommunity M . We obtained μ_M by summing the mean annual abundance of salmon in each local community.

Regional stability is influenced by two lower-level processes: i) local stability, and ii) spatial synchrony. Local stability (α_{stb}) is the average temporal stability of abundance at the local community level. This is obtained by first calculating the stability of each local community ($\alpha_{stb,i}$) as the inverse of the CV of salmon abundance in each local community. These local community-specific values are then weighted by local community abundance to obtain the average local stability at the metacommunity level:

$$\alpha_{stb} = \left(\sum_i \frac{\mu_i}{\mu_M} \times \frac{\sigma_i}{\mu_i} \right)^{-1} \quad (2)$$

in which μ_i is the temporal mean and σ_i is the temporal standard deviation of annual salmon abundance in local community i , and μ_M is the temporal mean of total annual salmon abundance in metacommunity M .

Spatial synchrony (ϕ) quantifies the similarity of temporal fluctuations in abundance among local communities and is calculated as:

$$\phi = \frac{\sum_{i,j} w_{ij}}{(\sum_i \sqrt{w_{ii}})^2} \quad (3)$$

in which w_{ij} is the temporal covariance in total annual abundance between communities i and j , and w_{ii} is the temporal variance of community i . Spatial synchrony ranges between 0 (perfect asynchrony) and 1 (perfect synchrony) and is influenced by both temporal synchrony of abundance among local communities as well as spatial unevenness in the mean and variance of abundance among local communities (Wang and Loreau 2014).

Spatial stabilization (τ) is inversely related to spatial synchrony and represents the degree to which stability is enhanced due to spatial dynamics (i.e., the increase in stability from the local community to the metacommunity level). This is calculated as the square root of $1/\phi$ and is equal to regional stability divided by local stability:

$$\tau = \sqrt{\frac{1}{\phi}} = \frac{Y_{stb}}{\alpha_{stb}} \quad (4)$$

Spatial stabilization is analogous to the portfolio effect (PE), which is most commonly calculated as the average CV of individual ‘assets’ (in this case, local communities) divided by the CV of the entire portfolio (in this case, the metacommunity) (Anderson et al. 2013):

$$PE = \frac{CV_L}{CV_M} \cong \frac{Y_{stb}}{\alpha_{stb}} \quad (5)$$

in which CV_L is the CV of annual salmon abundance in each local community averaged across local communities, and CV_M is the CV of annual salmon abundance in the metacommunity. Calculated like this, the portfolio effect is approximately equal to spatial stabilization (4). When it is calculated using a weighted mean (e.g., Freshwater et al. 2019), the portfolio effect is equal to spatial stabilization (4).

For the North Pacific, we sought to assess whether artificial hatchery production of salmon influences regional stability and its underlying components. Thus, we calculated stability components twice: once with natural-origin abundances, and once

with total (natural- + hatchery-origin) abundances. We could not calculate comparable stability components for hatchery-origin salmon only (i.e., excluding natural-origin salmon) due to a lack of hatchery production in some regions and years. For Northern BC, we sought to assess whether the stability of total abundance (i.e., escapement and catch combined) differs from that of escapement and catch alone. Consequently, we calculated stability components three times: once using total abundance (i.e., escapement + catch), once using escapement only, and once using catch only. All stability components were calculated and analyzed using R 4.0.0 (R Core Team 2020) (see below for code availability).

4.3.3. Statistical analysis

Using these stability components, we tested four hypotheses concerning the stability of annual salmon abundance (Table 4.1). To assess the stabilizing effect of spatial dynamics (Hypothesis 1), we first tested whether regional stability and spatial stabilization are greater in the North Pacific than in the Northern BC metacommunity. To do so, we used the `dabestr::dabest()` function in R (Ho et al. 2019) to calculate the bootstrapped mean and 95% confidence interval of the difference in regional stability and spatial stabilization between the two spatial scales, paired by year (i.e., 10-year window). We compared only the 10-year windows for which there were data from both spatial scales (i.e., between 1960 and 2012, excluding 1952-1959 and 2013-2015 from the North Pacific data). Next, we assessed how drivers of stability change across spatial scales. Within each spatial scale, we partitioned the variation in regional stability across all rolling windows between local stability and spatial synchrony, then compared the variance in regional stability explained by these two components in the North Pacific and the Northern BC metacommunities. We used the `vegan::varpart()` function in R (Oksanen et al. 2019) to quantify variance in regional stability explained by local stability, spatial synchrony, and covariance between these two components. This function uses linear regression to estimate the variance explained uniquely by each variable alone as well as the variance explained by their combination, with adjusted r^2 values as output. For both spatial scales, we used stability components derived from total abundance estimates.

Table 4.1 Hypotheses and prediction.

Hypothesis	Prediction	Explanation
1. Aggregate ecological properties stabilize hierarchically and across increasingly large spatial scales (Wang and Loreau 2014)	Regional stability (γ_{stb}) and spatial stabilization (τ) of annual salmon abundance are greater in the North Pacific than the Northern BC metacommunity	Larger regions (i.e., metacommunities) should incorporate more heterogeneity and stochasticity relative to smaller regions, increasing the degree to which ecological properties (e.g., salmon abundance) stabilize from local to regional scales
	In the North Pacific relative to the Northern BC metacommunity, local stability (α_{stb}) explains less and spatial synchrony (ϕ) explains more temporal variation in the regional stability of annual salmon abundance	In larger regions relative to smaller regions, local communities should contribute less to the regional stability of ecological properties, whereas asynchrony among local communities should contribute more
2. Stability of salmon abundance is influenced by species- and local community-specific dynamics	Species and local communities differ in their contributions to the regional stability (γ_{stb}) of annual salmon abundance	Variation among species (e.g., in age-at-maturity) and among local communities (e.g., in total salmon abundance, relative abundance of species, and environmental conditions) should result in differing contributions of those species and local communities to the overall stability of salmon abundance
3. Hatchery production stabilizes salmon abundance	Hatchery-origin salmon increase the regional stability (γ_{stb}) of annual salmon abundance in the North Pacific, as well as the stability of individual local communities ($\alpha_{stb,i}$)	Consistent, managed production of salmon should decrease annual variability in abundance
4. Fisheries management leads to greater stability of escapement relative to that of catch	The regional stability (γ_{stb}) of annual escapement is greater than that of catch in Northern BC	Fisheries management should prioritize stable catches in the long-term over the short-term, resulting in annual escapement being less variable than annual catch

To assess variation among species and among local communities in their influence on stability (Hypothesis 2), we calculated the contribution of each species and each local community to regional stability for both spatial scales. We also calculated the

contribution of species to local stability and spatial stabilization to infer the mechanism by which species contributed to regional stability. Using total abundance estimates, we excluded one species or one local community at a time, recalculated stability components, and quantified the contribution of each species or local community as the percentage change in stability components when that species or local community is excluded:

$$Contrib_k = \frac{component_{all} - component_{without k}}{component_{all}} \times 100 \quad (6)$$

in which k is a species or local community, $component_{all}$ is the stability component (i.e., local stability, spatial stabilization, or regional stability) including all species and local communities, and $component_{without k}$ is the stability component with k excluded. These measures of contribution were calculated for each rolling window. If an individual species or local community had a positive effect on stability in a given window, the contribution metric would be a positive value (and vice versa). To identify which process (i.e., local stability or spatial stabilization via chum, sockeye, or pink salmon) had the strongest influence on regional stability, the contribution of each species to local stability and spatial stabilization across rolling windows was compared with the temporal variation in regional stability by fitting bivariate linear regressions with the 'lm' function in R.

At the North Pacific scale, we assessed the influence of hatchery production on the stability of salmon abundance (Hypothesis 3) by using equation 6 to quantify the contribution of hatchery-origin salmon to stability across all rolling windows. To do so, we used the stability components derived from total abundance as $component_{all}$ and those derived from natural-origin abundance as $component_{without k}$. We assessed region-wide effects by calculating hatchery contributions to regional stability. We then assessed how hatchery production affects stability at local levels by calculating contributions to the stability of individual local communities ($\alpha_{stb,i}$).

Lastly, at the Northern BC scale, we assessed whether fisheries management leads to the stability of escapement being greater than that of catch (Hypothesis 4). To do so, we compared the regional stability of annual salmon escapement with that of catch across all rolling windows using the `dabestr::dabest()` function in R.

4.4. Results and Discussion

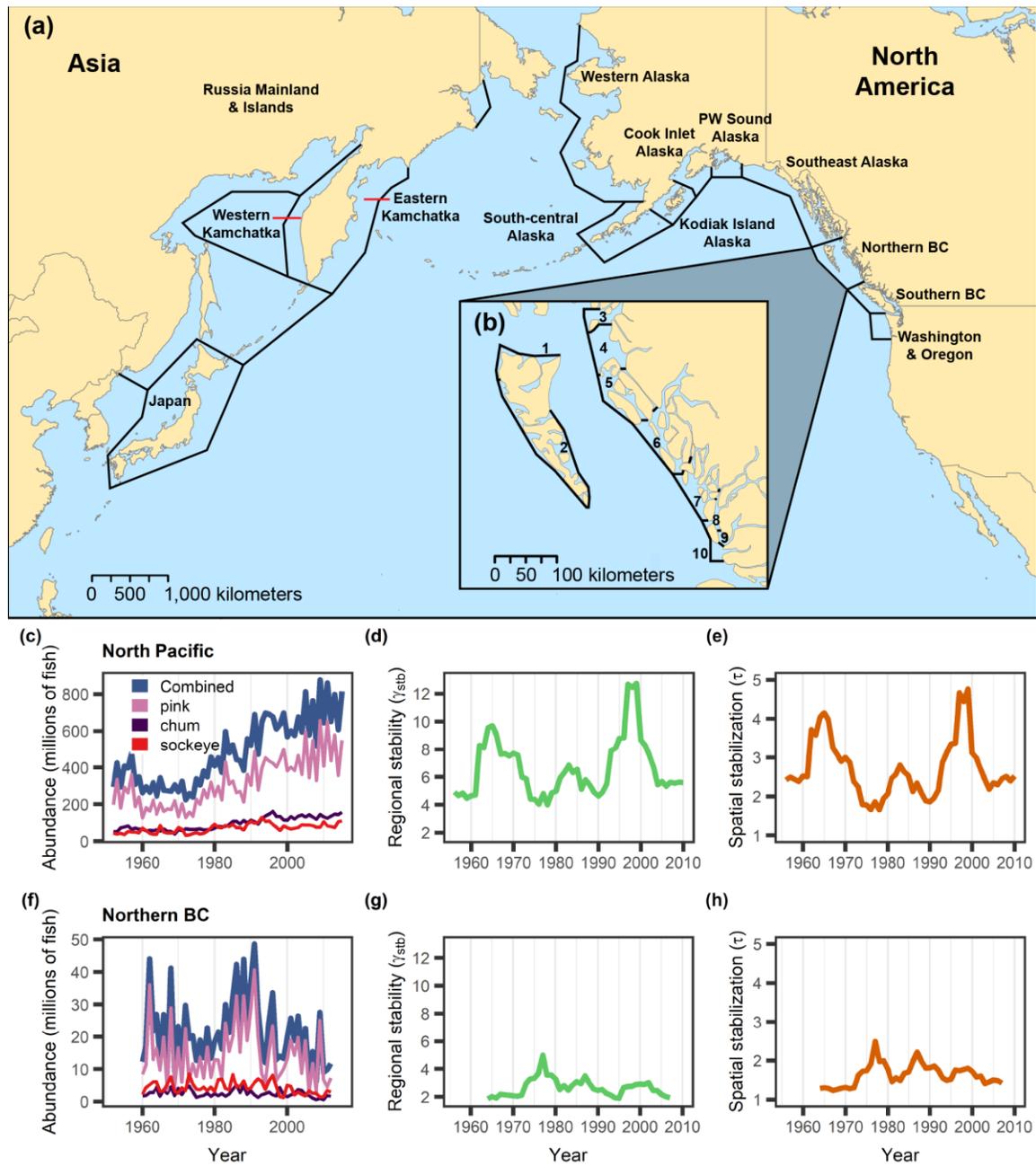


Figure 4.1 Map of regions throughout (a) the North Pacific and (b) Northern British Columbia (BC), and the abundance and stability of salmon in (a-c) the North Pacific, and (d-f) Northern BC.

The annual abundance of pink (pink lines), chum (purple lines), and sockeye salmon (red lines) was reconstructed between 1952-2015 in the North Pacific (Ruggerone and Irvine 2018) and 1960-2012 in Northern BC (English et al. 2018). Regional stability (green) and spatial stabilization (orange) of total annual salmon abundance were calculated in 10-year rolling windows throughout both time series. The plotted year values for these stability components correspond with the middle year of each rolling window (e.g., 1990 for 1986-1995).

The total annual abundance of salmon in the North Pacific during 1952 to 2015 increased from a low of 225 million fish near the beginning of the time series to over 800 million fish by the end of the series (Ruggerone and Irvine 2018; Figure 4.1c). Conversely, in Northern BC during 1960 to 2012, salmon abundance varied annually from 6 million to 49 million fish but reached several of the lowest returns on record towards the end of the time series (English et al. 2018; Figure 4.1f). Across both time series, chum, sockeye, and pink salmon respectively represented 20, 14, and 66% of total salmon abundance in the North Pacific, and 12, 20, and 68% in Northern BC, with pink salmon being much more annually variable than chum and sockeye (Figure 4.1c, f).

4.4.1. Hypothesis 1: Stability across spatial scales

Across 10-year rolling windows, both the regional stability (γ_{stb}) and spatial stabilization (τ) of total annual salmon abundance were significantly higher in the North Pacific than the Northern BC metacommunity (Figures. 4.1, C2). In the North Pacific, the mean \pm SD of regional stability was 6.62 ± 2.12 , with three distinct peaks in stability throughout the time series (Figure 4.1d). In Northern BC, regional stability averaged 2.65 ± 0.63 and also peaked three times during the series (Figure 4.1g). Spatial stabilization ranged between 1.66 and 4.76 (mean = 2.70 ± 0.75) in the North Pacific and between 1.23 and 2.49 (mean = 1.63 ± 0.28) in Northern BC (Figure 4.1e, h). Thus, over the course of the time series, asynchronous dynamics among local communities increased the stability of annual salmon abundance by 66% to 376% in the North Pacific and by 23% to 149% in Northern BC.

At the North Pacific scale, local stability (α_{stb}) explained 16% of the temporal variation in regional stability, whereas spatial synchrony (ϕ) explained 63% (Figure 4.2a, b). At the Northern BC scale, local stability and spatial synchrony respectively explained 34% and 47% of the variation in regional stability (Figure 4.2c, d). Spatial synchrony was therefore the strongest driver of regional stability at both spatial scales, but the influence of local stability grew from the larger spatial scale to the smaller (3.9 times less important than spatial synchrony in the North Pacific, 1.4 times less important in Northern BC).

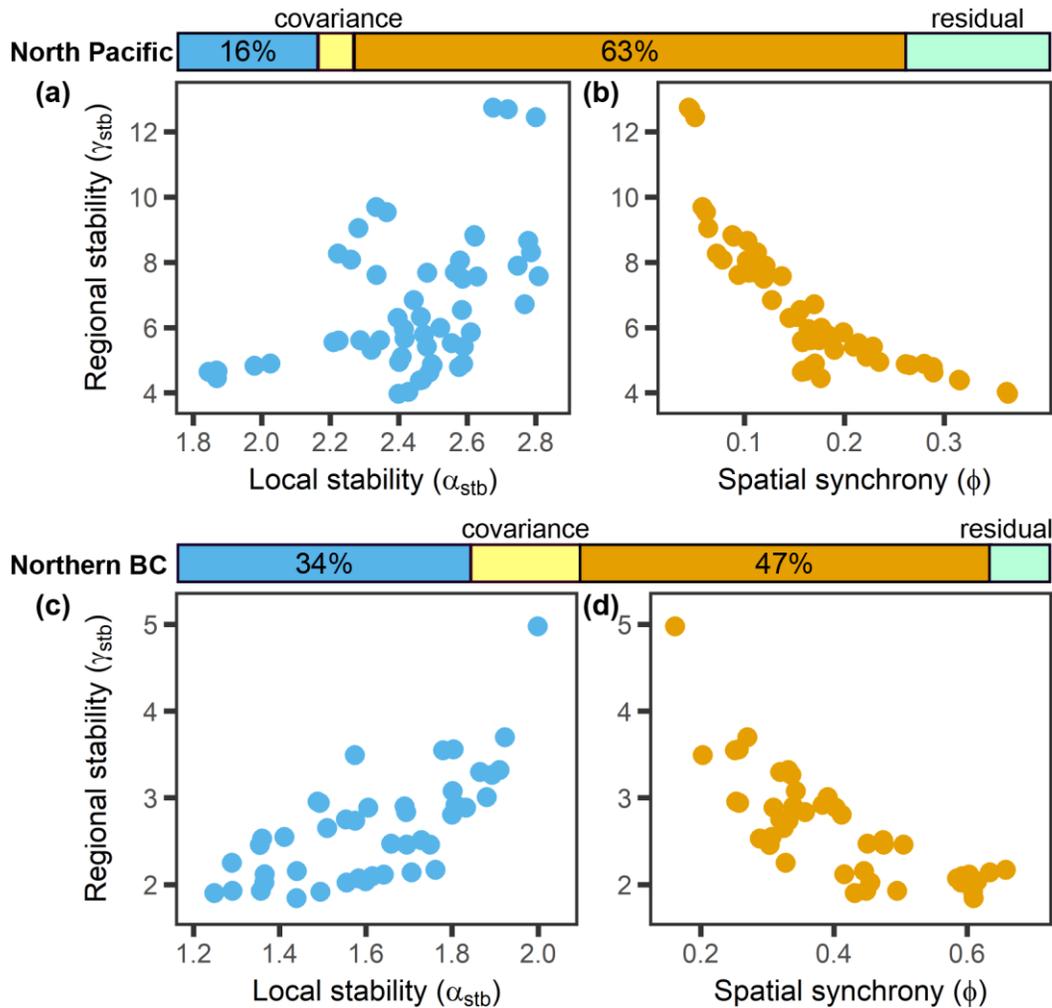


Figure 4.2 The relative influence of local stability (blue) and spatial synchrony (orange), as well as covariance between these two components, on the regional stability of total annual salmon abundance in (a,b) the North Pacific and (c,d) Northern British Columbia (BC).

Stability components were calculated in 10-year rolling windows between 1952-2015 in the North Pacific and 1960-2012 in Northern BC. Each point represents an individual 10-year window. Bars represent the amount of variation in regional stability explained by local stability, spatial synchrony, and covariance between these two components, as well as residual variation.

The regional stability of ecological properties is hypothesized to be determined by local stability and spatial synchrony, with properties becoming increasingly stabilized across larger areas due to more asynchrony among local communities (Wang and Loreau 2014). Applying this framework to the largest spatial and temporal scale to date, we found that: i) the regional stability and spatial stabilization of Pacific salmon abundance are significantly higher in the North Pacific relative to Northern BC; ii) spatial synchrony and local stability explain the vast majority of temporal variation in regional

stability at both spatial scales; and iii) regional stability is determined by spatial synchrony to a greater extent in the North Pacific than in Northern BC. These results support the core predictions of Wang and Loreau (2014) and confirm the importance of spatial portfolios in the maintenance of ecological functioning at regional scales (e.g., Thorson et al. 2018; Okamoto et al. 2020).

Previous applications of this framework have similarly found that local stability and spatial synchrony are key drivers of regional stability, however the relative importance of these drivers has varied across studies. Using herbaceous plant abundance data from 62 study sites around the world, Wilcox et al. (2017) found that local stability and spatial synchrony respectively explained 63% and 24% of the variation in regional stability among study sites. Conversely, Catano et al. (2020) quantified the stability of passerine bird biomass across 35 conservation regions spanning North America and found that local stability and spatial synchrony respectively explained 17% and 58% of the variation in regional stability, closely corresponding with the relative effect of these drivers found at the North Pacific scale here. This variation among studies is likely related to the size of study units: the metacommunities used by Wilcox et al. (2017) encompass much smaller areas (0.24 to 144 ha) than those used by Catano et al. (2020) (500 to 1.1 million ha) and those used here. Collectively, increasing stability due to spatial asynchrony from smaller to larger areas would further support the predictions of Wang and Loreau (2014). Future studies should integrate such results to examine cross-system patterns in the spatial scaling of stability and the factors that shape area-stability relationships (Wang et al. 2017).

4.4.2. Hypothesis 2: Variation among species and local communities

Chum and sockeye salmon had a relatively consistent and positive effect on regional stability in both the North Pacific (chum contribution = $18.4\% \pm 6.6\%$, sockeye contribution = $7.7\% \pm 8.2\%$) and Northern BC (chum contribution = $7.0\% \pm 4.3\%$, sockeye contribution = $16.8\% \pm 7.4\%$; Figure 4.3). Conversely, pink salmon had a highly variable effect on regional stability throughout the time series in both metacommunities, being mostly negative but at times having the most positive effect of all three species (contribution in the North Pacific = $-36.6\% \pm 57.1\%$, contribution in Northern BC = $-36.9\% \pm 36.6\%$; Figure 4.3). This pattern can be explained by i) pink salmon having a strongly negative effect on local stability (Figure C3a, b), and ii) pink salmon shifting

between periods of high and low spatial synchrony (Figure C3c, d). Temporal variation in regional stability was most strongly associated with the contribution of pink salmon to spatial stabilization ($r^2 = 0.39$ in the North Pacific, $r^2 = 0.37$ in Northern BC; Figures C4, C5). This relationship indicates that the peaks in regional stability throughout the time series were driven by highly asynchronous dynamics of pink salmon among local communities, whereas the lows in regional stability correspond (in part) with highly synchronous dynamics of pink salmon. This pattern holds across both spatial scales, although peaks in regional stability in Northern BC were also associated with increased spatial stabilization caused by sockeye salmon dynamics ($r^2 = 0.19$; Figure C5e).

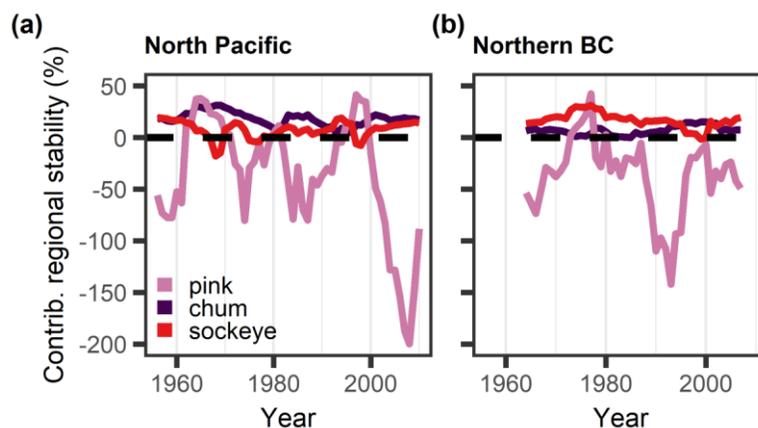


Figure 4.3 The percent contribution of pink (pink lines), chum (purple lines), and sockeye salmon (red lines) to the regional stability of total annual salmon abundance in (a) the North Pacific and (b) Northern British Columbia (BC).

Contributions were calculated as the percentage change in regional stability due to the inclusion of the species in every 10-year rolling window. Values above zero (dashed line) represent a positive effect on regional stability (and vice versa).

At both spatial scales, contributions to regional stability varied widely among local communities and, in several cases, within local communities over time (Figures C6, C7). In general, neutral contributions to regional stability occurred in local communities with low numbers of salmon (Figures C8, C9). Negative contributions occurred when both i) local community salmon abundance was dominated by pink salmon, and ii) odd-years had much greater pink salmon abundance relative to even-years (Figures C8, C9). For example, at the Northern BC scale, Management Area 4 (i.e., ocean waters surrounding the Skeena River) was the greatest contributor to regional stability before the 1990s (Figure C7) and, during this period, sockeye, odd-year pink, and even-year pink salmon

all were similarly abundant there (Figure C9). However, a large spike in pink abundance followed by greater dominance of odd-year over even-year pink salmon resulted in Management Area 4 having largely negative or neutral effects on regional stability during the 1990s and 2000s.

The large effect of pink salmon on the regional stability of annual salmon abundance is likely due to their numerical dominance and unique life history. Whereas all other species of Pacific salmon vary in age-at-maturity within a population cohort, pink salmon exhibit an obligate two-year life cycle. As such, odd- and even-year pink salmon represent genetically distinct lineages that often have divergent levels of abundance among sympatric populations (Heard 1991). Such annually divergent abundances within local communities explain the largely negative effect of pink salmon on local stability, whereas spatial variation in the dominance of odd- or even-year cohorts explain the major effect of pink salmon on regional stability via spatial asynchrony. Indeed, the peaks in regional stability and spatial stabilization that we found at the North Pacific scale here correspond with the occurrence of even-year dominance in North America (i.e., the mid-1950s to mid-1970s, mid-1980s, late 1990s) (Irvine et al. 2014). These periods of even-year dominance in North America regionally stabilized salmon abundance via spatial asynchrony because odd-years have dominated in Asia since the 1950s (Irvine et al. 2014). An exception to this odd-year dominance in Asia is Western Kamchatka, which switched from odd-year to even-year dominance in the mid-1980s (Figure C8) and subsequently had the most positive contribution to regional stability of any local community (Figure C6).

Several lines of evidence indicate that odd-year pink salmon are adapted to warmer environments than are even-year pink salmon (Nagata et al. 2007; Krkošek et al. 2011; Beacham et al. 2012), which could explain recent increases in odd-year abundance relative to even-years (Irvine et al. 2014). Within Northern BC, even-year cohorts have historically been more abundant than odd-year cohorts (Ricker 1962, Heard 1991); however, most even-year stocks in BC have been declining or stable since 1950 while most odd-year stocks have been increasing (Irvine et al. 2014). An increasing dominance of odd-year fish with rising ocean temperatures would progressively destabilize annual salmon abundance in Northern BC and the North Pacific.

In contrast with pink salmon, sockeye and chum salmon contribute positively to the local stability of annual salmon abundance (Figure C3a, b). In the North Pacific, sockeye and chum have modestly increased in abundance since the 1950s, with this increase being largely influenced by enhanced productivity of sockeye in Alaska and increased hatchery production of chum in Japan (Ruggerone and Irvine 2018). Conversely, numerous populations of these two species have declined in the southern portion of their range, particularly along the central and north coasts of BC (Price et al. 2017). Indeed, wild sockeye populations from the Skeena River (i.e., Management Area 4) declined by 56% to 99% over the past century (Price et al. 2019), resulting in diminished population diversity and an eroded portfolio within the watershed (Price et al. 2021). Given the importance of sockeye and chum to the local stability of annual salmon abundance, a reversal in these declines would promote local stability.

4.4.3. Hypothesis 3: Influence of hatcheries

Across the North Pacific, the contribution of hatchery-origin salmon to regional stability varied throughout the time series (mean = 10.7% ± 6.3%) despite the annual abundance of hatchery-origin salmon increasing by an order of magnitude during this period (Figure 4.4a, b). The effect of hatchery production on the stability of salmon abundance in individual local communities ($\alpha_{stb,i}$) was generally modest (Figure 4.4; Table C2) and appeared to be related to the relative abundance of natural- and hatchery-origin salmon (Figure C10). Minor (4-12% mean contribution since the onset of hatchery production) increases in stability occurred in every local community that: i) had low to intermediate numbers of natural-origin salmon (3 to 22 million adult fish annually on average), and ii) produced low to intermediate numbers of hatchery fish (0.4 to 5 million adults annually), including Washington & Oregon, Southern BC, Cook Inlet Alaska, and Kodiak Island Alaska. A major (49% mean contribution) increase in stability occurred in Japan, which had the second lowest number of natural-origin salmon (5 million fish annually) but the highest number of hatchery fish (38 million fish annually). Conversely, Southeast Alaska and Russia Mainland & Islands produced high numbers of hatchery fish between 1990 and 2015 (11 and 26 million annually, respectively) but, having the highest numbers of natural-origin salmon of any two local communities during this time, there was only a marginal (10 and 5% mean contribution, respectively) effect of hatcheries on stability. Prince William (PW) Sound Alaska produced the second

highest number of hatchery salmon (28 million annually) but achieved only a 12% mean contribution to stability. Other local communities (Northern BC, South-Central Alaska, Western Alaska, Eastern Kamchatka, and Western Kamchatka) had no or negligible hatchery production.

Hatchery production of salmon can impact wild salmon populations negatively at large spatial scales due to competition in the North Pacific (Connors et al. 2020) and, at more local scales, through the introduction of maladaptive genotypes (Neff et al. 2011), increased fisheries mortality due to mixed-stock fisheries (Hilborn and Eggers 2000), and competition in nearshore habitats (Ohlberger et al. 2021). Thus, the benefits of hatchery production must be carefully weighed against its costs. Enhancing temporal stability of salmon abundance would be a valuable benefit of hatcheries for economic outcomes in fishing communities (Hilborn et al. 2003; Cline et al. 2017). Whereas we found support for the hypothesis that hatchery production has a positive influence on the stability of annual salmon abundance at the regional (North Pacific) scale, we also found that this stabilizing effect is concentrated in only one local community (Japan), and that hatchery production has only a marginal effect on stability in areas that produce large quantities of hatchery fish, including PW Sound Alaska, Southeast Alaska, and Russia Mainland & Islands. The success of Japanese hatcheries in stabilizing salmon abundance is undoubtedly related to the severe depletion and extirpation of wild salmon populations in Japan by the early 1900s (Nagata et al. 2012). In an analysis of the economic performance of several enhancement programs (including pink salmon in PW Sound Alaska and chum salmon in Japan), Hilborn (1998) found that the chum salmon program in Japan was the only one to produce a net biological and economic benefit and concluded that enhancement programs aimed at augmenting existing stocks for commercial purposes are unlikely to be beneficial. Similarly, our findings suggest that large-scale hatchery production in areas with viable salmon stocks does not greatly improve the stability of salmon abundance. The stabilization of salmon populations is typically a key objective of hatchery programs (e.g., DFO 2021), but our results suggest that the efficacy of hatcheries in achieving this objective is questionable.

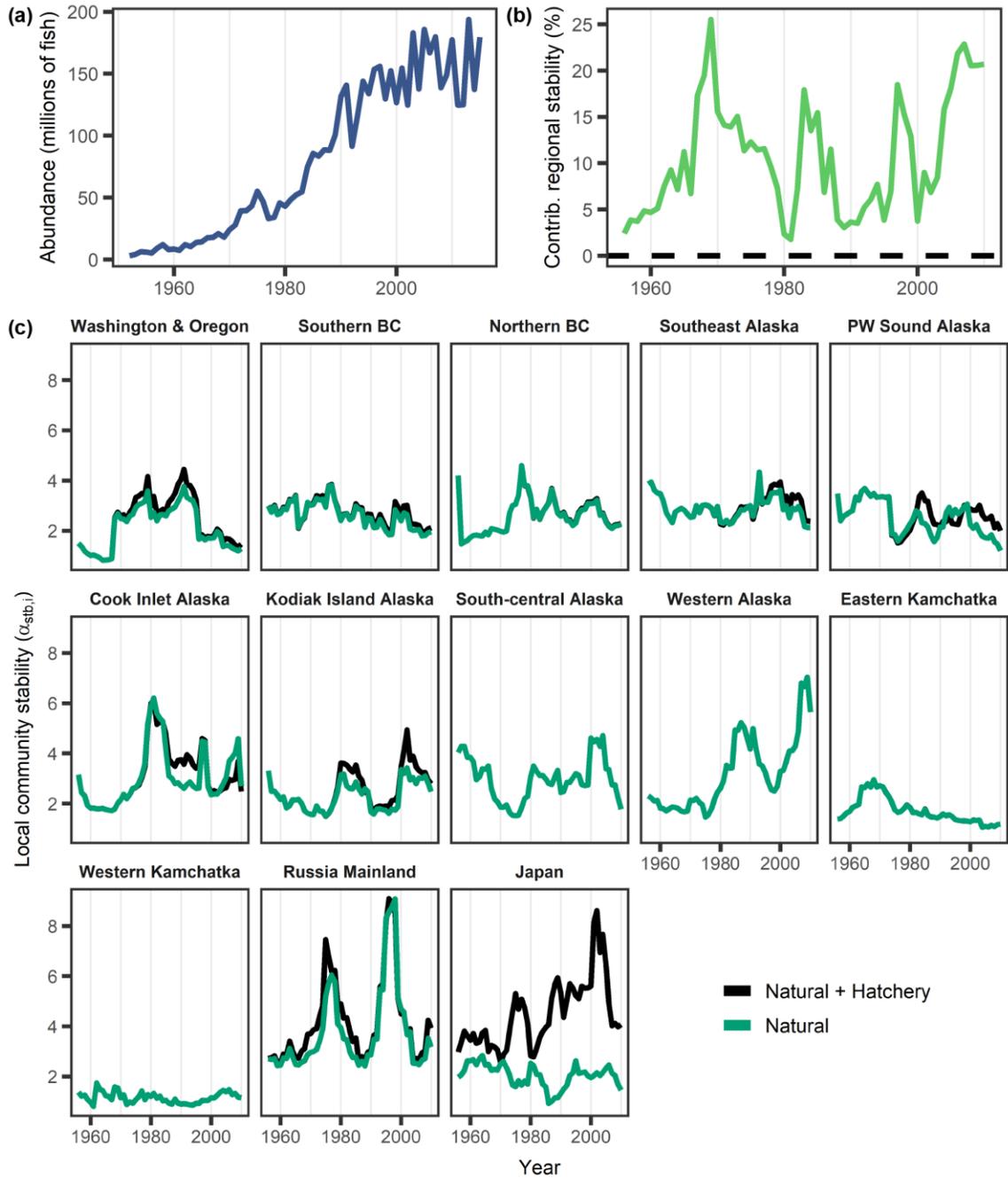


Figure 4.4 (a) Annual abundance of hatchery-origin salmon in the North Pacific between 1952 and 2015; (b) contribution of hatchery-origin salmon to the regional stability of total annual salmon abundance in the North Pacific; and (c) temporal stability of annual salmon abundance in individual local communities ($\alpha_{stb,i}$) throughout the North Pacific.

Local community stability was calculated in 10-year rolling windows for natural-origin salmon abundance (green lines) and for total (natural- plus hatchery-origin) salmon abundance (black lines). In (b) and (c), year values correspond with the middle year of each rolling window. In (b), values above zero (dotted line) represent positive contributions to stability. Abundance data are from Ruggerone and Irvine (2018).

The goal of salmon hatchery programs range between the conservation of at-risk populations and the augmentation of fishing opportunities, with many programs falling between these two extremes such that they aim to enhance fisheries catch while also aiming to promote the persistence of wild stocks (Naish et al. 2008). Because hatchery production strictly for conservation purposes is relatively minor, the beneficiaries of any stabilization of salmon abundance due to hatchery production should primarily be fishing communities and not recipient ecosystems in which salmon spawn. Such benefits to fisheries occurs in Japan, where hatchery production of salmon provides a temporally stable resource for fishing communities. However, this stabilization of salmon abundance does not occur in other regions, including those in which hatcheries produce salmon solely for fisheries enhancement (e.g., Russia, Prince William Sound Alaska) and those in which hatchery production aims to augment fisheries catch as well as the stability of wild stocks (e.g., most regions in Pacific North America).

4.4.4. Hypothesis 4: Influence of fisheries management

Between 1960 and the mid 1990s in Northern BC, catch and escapement of salmon were approximately equal, with catch typically being higher than escapement in abundant years but lower than escapement in less-abundant years (Figure 4.5a). In the mid 1990s, DFO adopted more conservative exploitation rates (Walters et al. 2019), resulting in escapement consistently exceeding catch between 1997 and 2012. Throughout the time series, the regional stability of annual escapement (mean = 3.20 ± 0.89) was significantly higher than that of catch (mean = 2.05 ± 0.45 ; Figures 4.5b, C11).

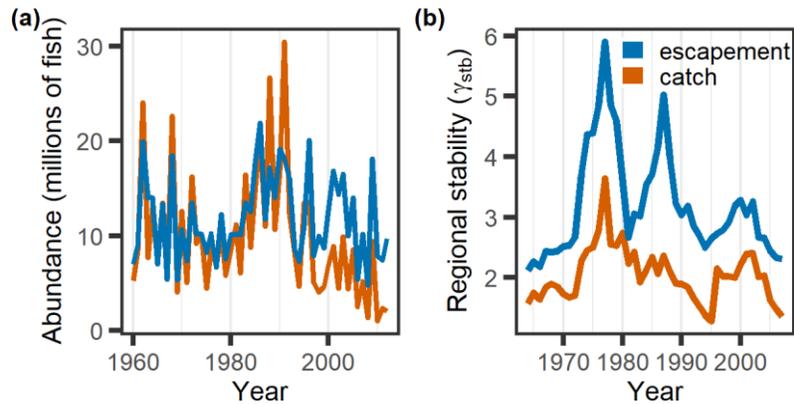


Figure 4.5 The (a) abundance and (b) regional stability of annual salmon escapement (blue) and catch (orange) in Northern British Columbia.

Regional stability was calculated in 10-year rolling windows between 1960 and 2012. In (b), plotted year values correspond with the middle year of each rolling window. Escapement and catch data are from English et al. (2018).

The greater stability of annual escapement relative to catch suggests that, since 1960, fisheries management in Northern BC has achieved greater stability of salmon returns to local ecosystems than of commercial catch. This is particularly evident after the mid-1990s, when more conservative exploitation rates ensured stable escapement of salmon despite declines in abundance. In addition to being important to the long-term sustainability of these salmon populations, this maintenance of escapement throughout the time series suggests reliable provisioning of salmon to local ecosystems and place-based fisheries. However, it is important to consider the deeper historical context when assessing the performance of fisheries management. For salmon populations in this region, the magnitude of decline is much larger when using a baseline abundance from 1913–1923 (i.e., at the onset of industrial fishing) compared to the 1960s (Price et al. 2019). High exploitation rates prior to the mid-1990s likely reduced population diversity within stock complexes (Walters et al. 2008; Price et al. 2021), which would ultimately contribute to the more variable catches observed toward the end of the time series (Schindler et al. 2010). Although the stability of annual escapement (and, thus, the reliability of local ecosystem services) has not declined since 1960, this time period does not capture the full extent of human impacts on salmon abundance.

4.4.5. Conclusions

Our results address the spatial ecology of salmon and can help inform efforts to stabilize salmon populations. Namely, managers should aim to ensure a spatial portfolio of habitat options are available for salmon, both at regional scales (e.g., among Management Areas) and local scales. For example, asynchronous dynamics among Management Areas increase the stability of annual salmon abundance in Northern BC by an average of 63%. Although the contribution of any one Management Area changes over time, ensuring that all Management Areas have the potential for productive salmon populations will foster temporal stability of salmon and salmon fisheries in Northern BC. This also applies at more local scales: hotspots of salmon productivity within a watershed change through time (Brennan et al. 2019), meaning streams that do not currently host productive salmon populations may do so in the future if left intact.

Our analysis supports the prediction that spatial asynchrony stabilizes ecological properties across increasingly large areas (Wang and Loreau 2014) and reveals insights into how biological uniqueness can differentially affect local and regional stability. For example, Western Kamchatka had the lowest local stability of annual salmon abundance of any local community in the North Pacific (Figure 4.4), yet after the mid-1980s it was the greatest contributor to regional stability due to its unique abundance of even-year pink salmon (Figure C6). The multi-scale framework presented in Wang and Loreau (2014) is a tool that can be applied by scientists, conservation practitioners, and resource managers to diagnose past and future changes in ecological stability across a wide range of spatial scales. Given the pervasiveness of habitat loss, climate change, and extinction and the large spatial scales over which management decisions are often made, this tool can inform efforts to maintain ecological stability.

Chapter 5.

General Discussion

My thesis addresses the ecological impacts of Chinook salmon in Patagonia as well as the drivers of ecological stability across spatial scales. A strength of this thesis is that it has both applied and theoretical relevance. For example, the results from Chapters 2 and 3 can help inform managers and policy-makers in Chile regarding how to move forward with non-native salmon, but also speak more broadly to the role of salmon in food webs and the novel trophic interactions that emerge following biological invasions. Similarly, Chapter 4 provides insights into the influence of hatchery production and fisheries management on salmon stability, but also tests a general hypothesis regarding the behaviour of ecological systems. Here, I reflect on these chapters and address future research directions.

In Chapter 2, I used spatial and temporal variation in the presence of Chinook salmon to test whether Patagonian salmon subsidize stream algae through the delivery of marine-derived nutrients. I found that marine-derived nutrients were incorporated by biofilms and increased algal biomass in three out of four streams examined with salmon populations. Frankly, the clear effect of salmon on algal biomass came as a surprise. Upon seeing the low densities of spawning Chinook salmon during my first field season in 2016, I became doubtful that I would be able to detect an effect of salmon on algal biomass. This doubt was magnified by my experience counting pink and chum salmon in Heiltsuk territory in September 2015. There, I walked streams that were considerably smaller than those studied in Patagonia, yet some streams bore over 10,000 spawners. Thus, I was surprised to find a clear signature of marine-derived nutrient incorporation and an increase in algal biomass upon analyzing the data from this first field season. The large effect of salmon (relative to their numbers) is presumably tied to the high degree of nutrient limitation known to occur in Patagonia (Perakis and Hedin 2002). Indeed, Patagonia is one of the few regions on Earth that receives no or little nitrogen input from human sources, making it pristine relative to the global increase in nitrogen deposition rates that have occurred due to fossil fuel combustion, fertilizer production, and land use change (Holland et al. 1999; Dentener et al. 2006).

In Chapter 3, I combined field-based observations with a literature search to summarize the trophic interactions that have emerged in Patagonia following the establishment of Chinook salmon. I found that a diverse group of native and non-native taxa interact with salmon in Patagonia, and that the taxa that benefit from consuming salmon-derived resources are taxonomically or functionally similar to those that do so in the native range of salmon. The initial motivation behind this chapter was more of a practical one, to gather data that could guide future studies of population-level impacts of Patagonian salmon. While this chapter does that, a broader relevance of these observations became clear when recognizing the similarity of the species that benefit from salmon consumption in Patagonia and those that do so in North America. Ecologists have sought to predict the trophic interactions that emerge following novel combinations of species due to biological invasions, and studies have shown that evolutionary history mediates emergent trophic interactions (Ricciardi and Atkinson 2004; Pearse and Altermatt 2013; Saul and Jeschke 2015; Schittko et al. 2020). The observations presented in this chapter support these findings, albeit qualitatively. I believe that this chapter is an important contribution because it describes previously undescribed ecological interactions. Such natural history observations are entering a “renaissance” due to statistical and technological advances (e.g., camera trapping) allowing observations to be more systematic than anecdotal and, thus, more capable of revealing patterns in nature (Tosa et al. 2021).

In Chapter 4 I used six decades of annual Pacific salmon abundance data from two spatial scales to test the hypothesis that ecological properties stabilize across increasingly large spatial scales (Wang and Loreau 2014). I found support for this hypothesis and also found that pink salmon drive temporal variation in the regional stability of salmon abundance, that hatchery production generally has only a marginal effect on salmon stability in jurisdictions throughout the North Pacific, and that the stability of annual salmon escapement in northern BC has not declined since the 1960s despite declines in total salmon abundance. This chapter adds to the growing body of research on metacommunity stability and portfolio effects. Research on Pacific salmon has been at the forefront of this field (e.g., Schindler et al. 2010), which comes as no surprise given the remarkable inter- and intra-specific diversity of salmon as well as their importance to people and wildlife. Research on the stability and portfolio performance of salmon has typically been conducted within or among stocks of the same species (e.g.,

Schindler et al. 2010, Freshwater et al. 2019; Moore et al. 2021; Price et al. 2021; Sullaway et al. 2021). Such an approach makes practical sense for informing or studying the effects of fisheries management given that different species of salmon are targeted and managed separately. Conversely, in this chapter I investigated the stability of the aggregate abundance of the three most common salmon species. In the context of testing the hypothesis of Wang and Loreau (2014), using aggregate abundance instead of the abundance of an individual species was preferable because it allowed testing this hypothesis with a more biologically complex system. However, the overall stability of Pacific salmon abundance also has applied relevance; mixed-stock salmon fisheries catch and substantially impact non-target salmon species (Walters et al. 2008), making the overall stability of salmon informative in terms of the performance of salmon resource management.

Stability in Ecology and Resource Management

The framework of spatial stability within metacommunities applied in Chapter 4 (Wang and Loreau 2014) may be useful as a tool to diagnose past and future changes in ecological stability while allowing scientists to test theoretical questions regarding the effects of local and regional biodiversity. To date, this framework has been used to test the theorized influence of local stability, spatial synchrony, local species (alpha) diversity, and spatial turnover of species (beta diversity) on the regional stability of annual plant abundance in 62 long-term study sites (Wilcox et al. 2017), annual bird biomass throughout North America (Catano et al. 2020), and the abundance of four different taxonomic groups in four different metacommunities (terrestrial beetles in Phoenix, Arizona; aquatic macrophytes in the Upper and Lower Chesapeake Bay; stream fishes throughout Maryland) (Patrick et al. 2021). Moreover, both Catano et al. (2020) and Patrick et al. (2021) used structural equation modeling to assess the effects of climatic or environmental heterogeneity and both found that such heterogeneity increased regional stability by increasing spatial asynchrony. These studies illustrate the flexibility of this framework and its potential utility to ecologists.

Future studies of Pacific salmon stability could apply this framework in the context of climate change. Climatic conditions such as sea surface temperature and the Pacific Decadal Oscillation have ocean-scale effects on salmon, with warmer conditions generally benefitting the productivity of northern stocks while reducing that of southern

stocks (Mantua et al. 1997; Mueter et al. 2002; Connors et al. 2020). Future studies could build on our analysis at the North Pacific scale by incorporating climatic data and the spatial relationships among local communities to model how past climatic change has affected the local and regional stability of salmon abundance throughout the North Pacific.

The stability of ecological properties is valued by people because of the reliability of ecosystem services that it entails. As such, this framework is likely to be of use to resource managers and economists for understanding patterns in the economic stability of human communities. For example, Cline et al. (2017) combined fisheries catch and revenue data from 105 Alaskan fishing communities to assess the drivers of economic stability during climatic and market shifts. They found that communities with the greatest diversity of fishing opportunities did not experience the loss of revenue that most communities experienced following regime shifts. The framework presented in Wang and Loreau (2014) could be similarly combined with natural resource revenue data to identify the biological and spatial correlates of economic stability.

Salmon in Patagonia: Outlook and Opportunities

Managing the invasion

The data presented in Chapters 2 and 3 represent a significant advance in our understanding of how Chinook salmon are ecologically impacting aquatic and riparian ecosystems in Patagonia. We now know that marine-derived nutrients stimulate algal biomass in streams, and that a wide variety of trophic interactions have emerged with juvenile and adult salmon. However, what do these findings mean in the broader context of managing this invasion?

In terms of the desirability of wild salmon in Patagonia, the ecological effects and interactions described here add to the ecological change that is occurring in Patagonia due to the establishment of non-native species (e.g., Schüttler et al. 2009; Habit et al. 2010; Crego et al. 2016; Reid et al. 2021). As such, it is reasonable and perhaps apt to view Chinook salmon as “invasive” and requiring management action to mitigate their impacts. An alternative interpretation of these data is that the ecological effect of salmon is actually beneficial in that it could stimulate ecosystem productivity and increase the

abundance of some plants and animals. Indeed, the delivery of marine-derived nutrients is considered a key part of the ecological integrity of stream and forest food webs in the native range of salmon (Willson and Halupka 1995; Darimont et al. 2010), and beneficial ecological effects are one of the principal motivations for the conservation of non-native species (Schlaepfer et al. 2011). However, I do not believe that this is an ecologically sound argument. The highly endemic flora and fauna of Patagonia exist in a region with globally unique levels of nutrient poverty (Holland et al. 1999), and the novel input of marine-derived nutrients will inevitably create “winners” and “losers” such that some species are more capable of capitalizing on salmon nutrients (e.g., Bailey and Moore 2020) and subsequently have greater competitive or predatory effects on other species (Sears et al. 2004).

The primary socio-economic benefits of wild salmon in Patagonia are derived via artisanal and recreational fisheries. Unfortunately, there is a paucity of information concerning the economic value of Patagonian salmon due to the ongoing legal invisibility of the species (Cid-Aguayo et al. 2021). There are clearly some economic benefits to the recreational fishery of Chinook salmon; tourism is the major industry in most parts of Patagonia (Guala et al. 2021), and the recreational fishing of trout and salmon is seemingly responsible for a significant portion of this tourism.

The lack of acknowledgement of this invasion by Chilean regulatory frameworks is a major impediment to both the mitigation of ecological impacts and the sustainable use of this resource. Salmon aquaculture companies (the most prominent of which are Norwegian-owned) have successfully lobbied the government to have all salmon in Chilean waters be considered private property (Cid-Aguayo et al. 2021). It is imperative that Chilean law catches up to the ecological reality of Patagonia and that managers create a strategy for addressing this invasion.

A monitoring program that provides stock-specific abundance estimates will a key first step towards understanding the ecological costs and socio-economic benefits of Patagonian salmon (while also being foundational to effective fisheries management). Research on the effect of salmon on stream nutrient budgets would contextualize the significance of this novel resource linkage, while study of population-level consequences of the trophic interactions described here would clarify potential food web effects. Particularly relevant in terms of ecological impacts of salmon would be study of their

effect on rainbow trout, brown trout, and mink populations. These three invaders strongly benefit from salmon subsidies in their native range (Ben-David et al. 1997; Scheuerell et al. 2007; Hermann et al. 2020) and diminish native animal populations in Patagonia (Schüttler et al. 2009; Habit et al. 2010; Correa and Hendry 2012; Valenzuela et al. 2013). The interaction between salmon, trout, and mink could be detrimental to galaxiid fishes, which have declined in abundance due to trout (Habit et al. 2010; Correa and Hendry 2012), are preyed upon by mink (Valenzuela et al. 2013) and sub-adult Chinook (Ibarra et al. 2011; Bravo et al. 2019), and, for most species, are at risk of extinction (Habit and Cussac 2016).

The results from Chapter 2 indicate that waterfalls represent geophysical barriers that limit the longitudinal extent of salmon impacts in watersheds. Such barriers may create opportunities for the conservation of aquatic ecosystems and species in Patagonia (Reid et al. 2021). Indeed, lakes that are hydrologically isolated from river systems due to physical barriers still host abundant populations of native galaxiids (Correa and Hendry 2012; Habit et al. 2012). Unfortunately, such salmonid-free water bodies are increasingly rare, with rainbow and brown trout being the most abundant freshwater fishes in southern Chile (Soto et al. 2007; Habit et al. 2010) and having been introduced to many stream reaches and lakes that would be otherwise inaccessible to them. Nevertheless, waterways upstream of barriers to salmon migration may prove to be effective targets for conservation actions aimed at the recovery of at-risk aquatic taxa in Patagonia (Reid et al. 2021).

Insights into salmon ecology

The introduction to and rapid colonization of Patagonia by Chinook salmon provides a natural experiment with which questions in the evolutionary and landscape ecology of salmon may be tested. Initial research efforts have characterized the genetic diversity within and among populations (Correa and Moran 2017; Musleh et al. 2020), which can aid in future studies of adaptive evolution. Particularly insightful may be the study of juvenile life history diversity across latitudinal and hydrologic gradients. In the native range of Chinook salmon, the relative frequency of “stream-type” (>1-year freshwater residents) and “ocean-type” (2 or 3-month freshwater residents) life history pathways within populations varies by latitude and distance to the ocean (Taylor 1990) and appears to be adaptively associated with hydrologic regime (Beechie et al. 2006).

Whether such environmental variables are similarly associated with juvenile life history diversity among Patagonian populations (particularly among those with the same introduction origin) would offer insight into the environmental adaptation of Chinook salmon and the role of phenotypic plasticity and rapid evolution. Moreover, an interesting characteristic of Patagonian Chinook salmon is that their northern range limit occurs at nearly the same latitude as their southern range limit in North America (39° S and 38° N, respectively). Studies of the environmental drivers of this limit (e.g., stream or ocean productivity, temperature, rainfall) would enhance our understanding of the habitat requirements of Chinook salmon and may be insightful regarding the vulnerability of Chinook salmon to climate change.

Concluding remarks

Studying salmon in Patagonia has been an enriching experience, both professionally and personally. While spending so much time in remote streams surrounded by these beautiful fish, it has also confronted me with some challenging questions. How can such a spectacular phenomenon – the return of adults to their birthplace, the steadfast maintenance and protection of their redds, their sacrifice for the next generation – be “bad”? What makes a species “good”? Why do we conserve species, and how do we decide which ones receive our consideration? Impartially, I know that salmon are likely to have negative consequences for some native species in Patagonia. Indeed, while conducting snorkel surveys in salmon streams in the Aysén watershed, the only fish I observed after many hours underwater were salmon and trout. There does not appear to be “space” for native fishes in such heavily invaded streams, and if salmon exacerbate this displacement of at-risk species then, logically and ethically, I believe that these impacts should be mitigated. Nevertheless, I could not prescribe such action without feeling some remorse. Such is the challenge of this invasion.

The ecological change occurring in Patagonia due to non-native species mirrors some of the socio-economic change occurring there. Industrial development is growing in the region, with salmon farms expanding southward (Niklitschek et al. 2013) and there is a constant economic pressure for large-scale hydropower development (Cussac et al. 2016). Fortunately, globally unique conservation practices are well underway in the region (Martínez-Harms et al. 2021). More than half of the terrestrial habitat in Chilean

Patagonia is intact and protected, and over 40% of its coastal waters have some level of protection. I hope that my doctoral research contributes to ecological knowledge in Patagonia and that others can build on this work in efforts to conserve its unique natural heritage.

References

- Alò, D., Correa, C., Samaniego, H., Krabbenhoft, C.A., Turner, T.F., 2019. Otolith microchemistry and diadromy in Patagonian river fishes. *PeerJ* 7, e6149.
- Anderson, S.C., Cooper, A.B., Dulvy, N.K., 2013. Ecological prophets: quantifying metapopulation portfolio effects. *Methods in Ecology and Evolution* 4, 971–981. <https://doi.org/10.1111/2041-210X.12093>
- André, E.R., Hecky, R.E., Duthie, H.C., 2003. Nitrogen and phosphorus regeneration by cichlids in the littoral zone of Lake Malawi, Africa. *Journal of Great Lakes Research* 29, 190–201.
- Araya, M., Niklitschek, E.J., Secor, D.H., Piccoli, P.M., 2014. Partial migration in introduced wild chinook salmon (*Oncorhynchus tshawytscha*) of southern Chile. *Estuarine, Coastal and Shelf Science* 149, 87–95.
- Arismendi, I., González, J., Soto, D., Penaluna, B., 2012. Piscivory and diet overlap between two non-native fishes in southern Chilean streams. *Austral Ecology* 37, 346–354. <https://doi.org/10.1111/j.1442-9993.2011.02282.x>
- Arismendi, I., Penaluna, B.E., Jara, C.G., 2020. Introduced beaver improve growth of non-native trout in Tierra del Fuego, South America. *Ecology and Evolution* 10, 9454–9465. <https://doi.org/10.1002/ece3.6636>
- Arismendi, I., Soto, D., 2012. Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from southern Chile. *Knowledge and Management of Aquatic Ecosystems* 405, 01. <https://doi.org/10.1051/kmae/2012009>
- Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P., Quinn, T.P., 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91, 1445–1454. <https://doi.org/10.1890/09-0790.1>
- Atlas, W.I., Palen, W.J., Courcelles, D.M., Munshaw, R.G., Monteith, Z.L., 2013. Dependence of stream predators on terrestrial prey fluxes: food web responses to subsidized predation. *Ecosphere* 4, art69. <https://doi.org/10.1890/ES12-00366.1>
- Bailey, C.J., Moore, J.W., 2020. Resource pulses increase the diversity of successful competitors in a multi-species stream fish assemblage. *Ecosphere* 11, e03211. <https://doi.org/10.1002/ecs2.3211>
- Beacham, T.D., McIntosh, B., MacConnachie, C., Spilsted, B., White, B.A., 2012. Population structure of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia and Washington, determined with microsatellites. *Fishery Bulletin* 110, 242–256.

- Beechie, T., Buhle, E., Ruckelshaus, M., Fullerton, A., Holsinger, L., 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130, 560–572.
- Ben-David, M., 1997. Timing of reproduction in wild mink: the influence of spawning Pacific salmon. *Canadian Journal of Zoology* 75, 376–382.
<https://doi.org/10.1139/z97-047>
- Ben-David, M., Hanley, T.A., Klein, D.R., Schell, D.M., 1997. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. *Canadian Journal of Zoology* 75, 803–811. <https://doi.org/10.1139/z97-102>
- Benjamin, J.R., Bellmore, J.R., Watson, G.A., 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. *Freshwater Science* 35, 810–825.
<https://doi.org/10.1086/686686>
- Benjamin, J.R., Bellmore, J.R., Whitney, E., Dunham, J.B., 2020. Can nutrient additions facilitate recovery of Pacific salmon? *Canadian Journal of Fisheries and Aquatic Sciences* 77, 1601–1611. <https://doi.org/10.1139/cjfas-2019-0438>
- Bentley, K.T., Schindler, D.E., Armstrong, J.B., Zhang, R., Ruff, C.P., Lisi, P.J., 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. *Ecosphere* 3, art113.
<https://doi.org/10.1890/ES12-00231.1>
- Best, R.J., Arcese, P., 2009. Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders. *Oecologia* 159, 139–150. <https://doi.org/10.1007/s00442-008-1172-1>
- Brander, K.M., 2007. Global fish production and climate change. *Proceedings of the National Academy of Sciences* 104, 19709.
<https://doi.org/10.1073/pnas.0702059104>
- Bravo, S., Silva, M.T., Ciancio, J., Whelan, K., 2019. Size structure, age, and diets of introduced Chinook salmon (*Oncorhynchus tshawytscha*) inhabiting the Palena River, Chilean Patagonia. *Latin American Journal of Aquatic Research* 47, 129–137.
- Brennan Sean R., Schindler Daniel E., Cline Timothy J., Walsworth Timothy E., Buck Greg, Fernandez Diego P., 2019. Shifting habitat mosaics and fish production across river basins. *Science* 364, 783–786.
<https://doi.org/10.1126/science.aav4313>
- Bugaev, V.F., Welch, D.W., Selifonov, M.M., Grachev, L.E., Eveson, J.P., 2001. Influence of the marine abundance of pink (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. *Fisheries Oceanography* 10, 26–32. <https://doi.org/10.1046/j.1365-2419.2001.00150.x>

- Bus Leone, P., Cerda, J., Sala, S., Reid, B., 2014. Mink (*Neovison vison*) as a natural vector in the dispersal of the diatom *Didymosphenia geminata*. *Diatom Research* 29, 259–266. <https://doi.org/10.1080/0269249X.2014.890957>
- Carthey, A.J.R., Banks, P.B., 2014. Naïveté in novel ecological interactions: lessons from theory and experimental evidence. *Biological Reviews* 89, 932–949. <https://doi.org/10.1111/brv.12087>
- Catano, C.P., Fristoe, T.S., LaManna, J.A., Myers, J.A., 2020. Local species diversity, β -diversity and climate influence the regional stability of bird biomass across North America. *Proceedings of the Royal Society B* 287, 20192520. <https://doi.org/10.1098/rspb.2019.2520>
- Chalde, T., Fernández, D.A., 2017. Early migration and estuary stopover of introduced Chinook salmon population in the Lapataia River Basin, southern Tierra del Fuego Island. *Estuarine, Coastal and Shelf Science* 199, 49–58. <https://doi.org/10.1016/j.ecss.2017.09.030>
- Chaloner, D.T., Lamberti, G.A., Cak, A.D., Blair, N.L., Edwards, R.T., 2007. Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. *Freshwater Biology* 52, 478–490. <https://doi.org/10.1111/j.1365-2427.2006.01715.x>
- Chaloner, D.T., Wipfli, M.S., 2002. Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. *Journal of the North American Benthological Society* 21, 430–442. <https://doi.org/10.2307/1468480>
- Chaloner, D.T., Wipfli, M.S., Caouette, J.P., 2002. Mass loss and macroinvertebrate colonisation of Pacific salmon carcasses in south-eastern Alaskan streams. *Freshwater Biology* 47, 263–273. <https://doi.org/10.1046/j.1365-2427.2002.00804.x>
- Christie, K.S., Reimchen, T.E., 2008. Presence of salmon increases passerine density on Pacific Northwest streams. *The Auk* 125, 51–59. <https://doi.org/10.1525/auk.2008.125.1.51>
- Ciancio, J.E., Pascual, M.A., Botto, F., Frere, E., Iribarne, O., 2008. Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. *Limnology and Oceanography* 53, 788–798. <https://doi.org/10.4319/lo.2008.53.2.0788>
- Ciancio, J.E., Rossi, C.R., Pascual, M., Anderson, E., Garza, J.C., 2015. The invasion of an Atlantic Ocean river basin in Patagonia by Chinook salmon: new insights from SNPs. *Biological Invasions* 17, 2989–2998. <https://doi.org/10.1007/s10530-015-0928-x>

- Cid-Aguayo, B., Ramirez, A., Sepúlveda, M., Gomez-Uchida, D., 2021. Invasive Chinook salmon in Chile: stakeholder perceptions and management conflicts around a new common-use resource. *Environmental Management* 68, 814–823.
<https://doi.org/10.1007/s00267-021-01528-0>
- Cline, T.J., Schindler, D.E., Hilborn, R., 2017. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nature Communications* 8, 14042.
<https://doi.org/10.1038/ncomms14042>
- Connors, B., Malick, M.J., Ruggerone, G.T., Rand, P., Adkison, M., Irvine, J.R., Campbell, R., Gorman, K., 2020. Climate and competition influence sockeye salmon population dynamics across the Northeast Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 77, 943–949.
<https://doi.org/10.1139/cjfas-2019-0422>
- Connors, B.M., Braun, D.C., Peterman, R.M., Cooper, A.B., Reynolds, J.D., Dill, L.M., Ruggerone, G.T., Krkošek, M., 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics: Competition, climate, disease, and salmon. *Conservation Letters* 5, 304–312. <https://doi.org/10.1111/j.1755-263X.2012.00244.x>
- Correa, C., Gross, M.R., 2008. Chinook salmon invade southern South America. *Biological Invasions* 10, 615–639. <https://doi.org/10.1007/s10530-007-9157-2>
- Correa, C., Hendry, A.P., 2012. Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. *Ecological Applications* 22, 828–842.
- Correa, C., Moran, P., 2017. Polyphyletic ancestry of expanding Patagonian Chinook salmon populations. *Scientific reports* 7, 1–13.
- Crego, R.D., Jiménez, J.E., Rozzi, R., 2016. A synergistic trio of invasive mammals? Facilitative interactions among beavers, muskrats, and mink at the southern end of the Americas. *Biological Invasions* 18, 1923–1938.
<https://doi.org/10.1007/s10530-016-1135-0>
- Cussac, V.E., Habit, E., Ciancio, J., Battini, M.A., Riva Rossi, C., Barriga, J.P., Baigún, C., Crichigno, S., 2016. Freshwater fishes of Patagonia: conservation and fisheries. *Journal of Fish Biology* 89, 1068–1097.
<https://doi.org/10.1111/jfb.13008>
- Darimont, C.T., Bryan, H.M., Carlson, S.M., Hocking, M.D., MacDuffee, M., Paquet, P.C., Price, M.H.H., Reimchen, T.E., Reynolds, J.D., Wilmers, C.C., 2010. Salmon for terrestrial protected areas. *Conservation Letters* 3, 379–389.
<https://doi.org/10.1111/j.1755-263X.2010.00145.x>

- Darwall, W.R.T., Freyhof, J., 2016. Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity, in: Closs, G.P., Krkosek, M., Olden, J.D. (eds.), Conservation of freshwater fishes. Cambridge University Press, Cambridge, UK, pp 1–36. <https://doi.org/10.1017/CBO9781139627085.002>
- David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E., Loeuille, N., 2017. Chapter One - Impacts of invasive species on food webs: a review of empirical data, in: Bohan, D.A., Dumbrell, A.J., Massol, F. (eds.), Advances in ecological research. Academic Press, Boston, USA, pp. 1–60. <https://doi.org/10.1016/bs.aecr.2016.10.001>
- Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W.M., Marconi, V., McRae, L., Baumgartner, L.J., Brink, K., Claussen, J.E., Cooke, S.J., 2020. The Living Planet Index (PLI) for migratory freshwater fish: technical report. World Fish Migration Foundation, the Netherlands.
- Dentener, F., Drevet, J., Lamarque, J.F., Bey, I., Eickhout, B., Fiore, A.M., Hauglustaine, D., Horowitz, L.W., Krol, M., Kulshrestha, U.C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Van Noije, T., Atherton, C., Bell, N., Bergman, D., Butler, T., Cofala, J., Collins, B., Doherty, R., Ellingsen, K., Galloway, J., Gauss, M., Montanaro, V., Müller, J.F., Pitari, G., Rodriguez, J., Sanderson, M., Solomon, F., Strahan, S., Schultz, M., Sudo, K., Szopa, S., Wild, O., 2006. Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation: Multimodal global deposition. Global Biogeochemical Cycles 20, GB4003. <https://doi.org/10.1029/2005GB002672>
- DFO (Fisheries and Oceans Canada), 2021. Pacific Salmon Strategy Initiative. URL <https://www.dfo-mpo.gc.ca/campaign-campagne/pss-ssp/index-eng.html> (accessed 1.17.22).
- Di Prinzio, C.Y., Arismendi, I., 2018. Early development and diets of non-native juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in an invaded river of Patagonia, southern South America. Austral Ecology 43, 732–741. <https://doi.org/10.1111/aec.12597>
- Di Prinzio, C.Y., Pascual, M.A., 2008. The establishment of exotic Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific rivers of Chubut, Patagonia, Argentina. Annales de Limnologie - International Journal of Limnology 44, 25–32. <https://doi.org/10.1051/limn:2008020>
- Di Prinzio, C.Y., Rossi, C.R., Ciancio, J., Garza, J.C., Casaux, R., 2015. Disentangling the contributions of ocean ranching and net-pen aquaculture in the successful establishment of Chinook salmon in a Patagonian basin. Environmental Biology of Fishes 98, 1987–1997. <https://doi.org/10.1007/s10641-015-0418-0>
- Diaz, M., Pedrozo, F., Reynolds, C., Temporetti, P., 2007. Chemical composition and the nitrogen-regulated trophic state of Patagonian lakes. Limnologica 37, 17–27. <https://doi.org/10.1016/j.limno.2006.08.006>

- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability-diversity relationships in community ecology. *Ecology* 79, 264–276.
- Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., Svenning, J.-C., 2016. Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences* 113, 868.
<https://doi.org/10.1073/pnas.1502549112>
- Downes, B.J., Barmuta, L.A., Fairweather, P.G., Faith, D.P., Keough, M.J., Lake, P.S., Mapstone, B.D., Quinn, G.P., 2002. *Monitoring ecological impacts: concepts and practice in flowing waters*. Cambridge University Press.
- Dunkle, M.R., Lampman, R.T., Jackson, A.D., Caudill, C.C., 2020. Factors affecting the fate of Pacific lamprey carcasses and resource transport to riparian and stream macrohabitats. *Freshwater Biology* 65, 1429–1439.
<https://doi.org/10.1111/fwb.13510>
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10, 1135–1142.
<https://doi.org/10.1111/j.1461-0248.2007.01113.x>
- Elton, C., 1958. *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, USA.
- English, K., Peacock, D., Challenger, W., Noble, C., Beveridge, I., Robichaud, D., Beach, K., Hertz, E., Connors, K., 2014. North and central coast salmon escapement, catch, run size and exploitation rate estimates for each salmon conservation unit for 1954-2017. Pacific Salmon Foundation.
- Ewel, J.J., O'Dowd, D.J., Bergelson, J., Daehler, C.C., D'Antonio, C.M., Gómez, L.D., Gordon, D.R., Hobbs, R.J., Holt, A., Hopper, K.R., Hughes, C.E., LaHart, M., Leakey, R.R.B., Lee, W.G., Loope, L.L., Lorence, D.H., Louda, S.M., Lugo, A.E., McEvoy, P.B., Richardson, D.M., Vitousek, P.M., 1999. Deliberate introductions of species: benefits can be reaped, but risks are high. *BioScience* 49, 619–630.
<https://doi.org/10.2307/1313438>
- Field, R.D., Reynolds, J.D., 2011. Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proceedings of the Royal Society B: Biological Sciences* 278, 3081–3088.
<https://doi.org/10.1098/rspb.2010.2731>
- Field, R.D., Reynolds, J.D., 2013. Ecological links between salmon, large carnivore predation, and scavenging birds. *Journal of Avian Biology* 44, 009–016.
<https://doi.org/10.1111/j.1600-048X.2012.05601.x>

- Flecker, A.S., McIntyre, P.B., Moore, J.W., Anderson, J.T., Taylor, B.W., Hall, R.O., 2010. Migratory fishes as material and process subsidies in riverine ecosystems. *American Fisheries Society Symposium* 73, 559–592.
- Francis, T.B., Schindler, D.E., Moore, J.W., 2006. Aquatic insects play a minor role in dispersing salmon-derived nutrients into riparian forests in southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 2543–2552. <https://doi.org/10.1139/f06-144>
- Freshwater, C., Anderson, S.C., Holt, K.R., Huang, A., Holt, C.A., 2019. Weakened portfolio effects constrain management effectiveness for population aggregates. *Ecological Applications* 29, e01966. <https://doi.org/10.1002/eap.1966>
- Gayeski, N.J., Stanford, J.A., Montgomery, D.R., Lichatowich, J., Peterman, R.M., Williams, R.N., 2018. The failure of wild salmon management: need for a place-based conceptual foundation. *Fisheries* 43, 303–309. <https://doi.org/10.1002/fsh.10062>
- Gende, S.M., Edwards, R.T., Willson, M.F., Wipfli, M.S., 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* 52, 917–928. [https://doi.org/10.1641/0006-3568\(2002\)052\[0917:PSIAAT\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2)
- Gomez-Uchida, D., Aedo, G., Ernst, B., Canales-Aguirre, C., Ferrada-Fuentes, S., Cañas, M., Cañas, D., Cadiz, M., Musleh, S., Rivara, P., 2014. Estudio biológico pesquero y sanitario de la población de salmón Chinook en la cuenca del río Toltén en la Región de la Araucanía. *FIPA* 87, 2016.
- Gomez-Uchida, D., Cañas-Rojas, D., Riva-Rossi, C.M., Ciancio, J.E., Pascual, M.A., Ernst, B., Aedo, E., Musleh, S.S., Valenzuela-Aguayo, F., Quinn, T.P., Seeb, J.E., Seeb, L.W., 2018. Genetic signals of artificial and natural dispersal linked to colonization of South America by non-native Chinook salmon (*Oncorhynchus tshawytscha*). *Ecology and Evolution* 8, 6192–6209. <https://doi.org/10.1002/ece3.4036>
- González, C.R., Llanos, L., Oses, C., Elgueta, M., 2017. Calliphoridae from Chile: key to the genera and species (Diptera: Oestroidea). *Anales del Instituto de la Patagonia* 45, 19–27.
- Górski, K., González, J., Vivancos, A., Habit, E., Ruzzante, D., 2017. Young-of-the-year Coho Salmon *Oncorhynchus kisutch* recruit in fresh waters of remote Patagonian fjords in southern Chile (51°S). *Biological Invasions* 19, 1127–1136. <https://doi.org/10.1007/s10530-016-1341-9>
- Gottesfeld, A., Hassan, M., Tunnicliffe, J., 2008. Salmon Bioturbation and Stream Process. *American Fisheries Society Symposium* 65, 175–193.
- Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., MacNeil, M.A., 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559, 250–253. <https://doi.org/10.1038/s41586-018-0202-3>

- Gresh, T., Lichatowich, J., Schoonmaker, P., 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25, 15–21.
- Groot, G., Margolis, L., 1991. *Pacific salmon life histories*. UBC press, Vancouver, Canada.
- Guala, C., Velosa, K., Farías, A., Sariego, F., 2021. Caracterización del desarrollo turístico asociado a las áreas silvestres protegidas de la Patagonia chilena, in: Castilla, J.C., Armesto, J.J., Martínez-Harms, M.J. (eds.) *Conservación en la Patagonia Chilena: evaluación del conocimiento, oportunidades y desafíos*. Ediciones UC, Santiago, Chile, pp. 575–598.
- Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., Hard, J.J., 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology* 21, 1009–1020. <https://doi.org/10.1111/j.1523-1739.2007.00693.x>
- Habit, E., Cussac, V., 2016. Conservation of the freshwater fauna of Patagonia: an alert to the urgent need for integrative management and sustainable development. *Journal of Fish Biology* 89, 369–370.
- Habit, E., Gonzalez, J., Ruzzante, D.E., Walde, S.J., 2012. Native and introduced fish species richness in Chilean Patagonian lakes: inferences on invasion mechanisms using salmonid-free lakes. *Diversity and Distributions* 18, 1153–1165. <https://doi.org/10.1111/j.1472-4642.2012.00906.x>
- Habit, E., Piedra, P., Ruzzante, D.E., Walde, S.J., Belk, M.C., Cussac, V.E., Gonzalez, J., Colin, N., 2010. Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecology and Biogeography* 19, 697–710. <https://doi.org/10.1111/j.1466-8238.2010.00541.x>
- Harding, J.M.S., Harding, J.N., Field, R.D., Pendray, J.E., Swain, N.R., Wagner, M.A., Reynolds, J.D., 2019. Landscape structure and species interactions drive the distribution of salmon carcasses in coastal watersheds. *Frontiers in Ecology and Evolution* 7, 192.
- Harding, J.N., Harding, J.M.S., Reynolds, J.D., 2014. Movers and shakers: nutrient subsidies and benthic disturbance predict biofilm biomass and stable isotope signatures in coastal streams. *Freshwater Biology* 59, 1361–1377. <https://doi.org/10.1111/fwb.12351>

- Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., Lind, E.M., MacDougall, A.S., Stevens, C.J., Bakker, J.D., Buckley, Y.M., Chu, C., Collins, S.L., Daleo, P., Damschen, E.I., Davies, K.F., Fay, P.A., Firn, J., Gruner, D.S., Jin, V.L., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Li, W., McCulley, R.L., Melbourne, B.A., Moore, J.L., O'Halloran, L.R., Prober, S.M., Risch, A.C., Sankaran, M., Schuetz, M., Hector, A., 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508, 521–525. <https://doi.org/10.1038/nature13014>
- Healey, M.C., 1982. Catch, escapement and stock-recruitment for British Columbia chinook salmon since 1951. Government of Canada, Fisheries and Oceans.
- Heard, W.R., 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*), in Groot, G., Margolis, L. (eds.) *Pacific salmon life histories*. UBC Press, Vancouver, Canada, pp. 119–230.
- Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmborg, C., Pereira, J.S., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B., Loreau, M., 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91, 2213–2220. <https://doi.org/10.1890/09-1162.1>
- Hermann, N.T., Chaloner, D.T., Gerig, B.S., Lamberti, G.A., 2020. Ecological consequences of Great Lakes salmon subsidies for stream-resident brook and brown trout. *Canadian Journal of Fisheries and Aquatic Sciences* 77, 1758–1771. <https://doi.org/10.1139/cjfas-2020-0086>
- Hilborn, R., 1998. The economic performance of marine stock enhancement projects. *Bulletin of Marine Science* 62, 661–674.
- 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. [https://doi.org/10.1577/1548-8659\(2000\)129<0333:AROTHP>2.0.CO;2](https://doi.org/10.1577/1548-8659(2000)129<0333:AROTHP>2.0.CO;2)
- Hilborn, R., Quinn, T.P., Schindler, D.E., Rogers, D.E., 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences* 100, 6564–6568. <https://doi.org/10.1073/pnas.1037274100>
- Hillebrand, H., 2009. Meta-analysis of grazer control of periphyton biomass across aquatic ecosystems. *Journal of Phycology* 45, 798–806. <https://doi.org/10.1111/j.1529-8817.2009.00702.x>
- Ho, J., Tumkaya, T., Aryal, S., Choi, H., Claridge-Chang, A., 2019. Moving beyond P values: data analysis with estimation graphics. *Nature Methods* 16, 565–566. <https://doi.org/10.1038/s41592-019-0470-3>

- Hocking, M.D., Reimchen, T.E., 2006. Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 2076–2086. <https://doi.org/10.1139/f06-110>
- Hocking, M.D., Reimchen, T.E., 2002. Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. *BMC Ecology* 2, 4. <https://doi.org/10.1186/1472-6785-2-4>
- Hocking, M.D., Reynolds J.D., 2011. Impacts of salmon on riparian plant diversity. *Science* 331, 1609–1612. <https://doi.org/10.1126/science.1201079>
- Holland, E.A., Dentener, F.J., Braswell, B.H., Sulzman, J.M., 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46, 7–43.
- Holtgrieve, G.W., Schindler, D.E., 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology* 92, 373–385. <https://doi.org/10.1890/09-1694.1>
- Holtgrieve, G.W., Schindler, D.E., Gowell, C.P., Ruff, C.P., Lisi, P.J., 2010. Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology* 55, 2598–2611. <https://doi.org/10.1111/j.1365-2427.2010.02489.x>
- Hood, E., Fellman, J.B., Edwards, R.T., D'Amore, D.V., Scott, D., 2019. Salmon-derived nutrient and organic matter fluxes from a coastal catchment in southeast Alaska. *Freshwater Biology* 64, 1157–1168.
- Ibarra, J., Habit, E., Barra, R., Solís, K., 2011. Juveniles de salmón Chinook (*Oncorhynchus tshawytscha* Walbaum, 1792) en ríos y lagos de la Patagonia chilena. *Gayana* 75, 17–25.
- Irgang, R., Poblete-Morales, M., Gomez-Uchida, D., Avendaño-Herrera, R., 2019. First description of health status and associated bacterial diversity from nonnative Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum 1792) naturalised in a large river system from southern Chile. *Bulletin of the European Association of Fish Pathologists* 39, 60–69.
- Irvine, J.R., Michielsens, C.J.G., O'Brien, M., White, B.A., Folkes, M., 2014. Increasing dominance of odd-year returning pink salmon. *Transactions of the American Fisheries Society* 143, 939–956. <https://doi.org/10.1080/00028487.2014.889747>
- Ivan, L.N., Rutherford, E.S., Johengen, T.H., 2011. Impacts of adfluvial fish on the ecology of two Great Lakes tributaries. *Transactions of the American Fisheries Society* 140, 1670–1682. <https://doi.org/10.1080/00028487.2011.642233>
- Ives A. R., Gross K., Klug J. L., 1999. Stability and variability in competitive communities. *Science* 286, 542–544. <https://doi.org/10.1126/science.286.5439.542>

- Jackson, M.C., 2015. Interactions among multiple invasive animals. *Ecology* 96, 2035–2041. <https://doi.org/10.1890/15-0171.1>
- Jackson, M.C., Wasserman, R.J., Grey, J., Ricciardi, A., Dick, J.T.A., Alexander, M.E., 2017. Novel and disrupted trophic links following invasion in freshwater ecosystems, in: Bohan, D.A., Dumbrell, A.J., Massol, F. (eds.), *Advances in ecological research*. Academic Press, Boston, USA pp. 55–97. <https://doi.org/10.1016/bs.aecr.2016.10.006>
- Janetski, D.J., Chaloner, D.T., Moerke, A.H., Levi, P.S., Lamberti, G.A., 2014. Novel environmental conditions alter subsidy and engineering effects by introduced Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 71, 502–513. <https://doi.org/10.1139/cjfas-2013-0292>
- Janetski, D.J., Chaloner, D.T., Tiegs, S.D., Lamberti, G.A., 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* 159, 583–595. <https://doi.org/10.1007/s00442-008-1249-x>
- Johnson, S.P., Schindler, D.E., 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecological Research* 24, 855–863. <https://doi.org/10.1007/s11284-008-0559-0>
- Kaylor, M.J., White, S.M., Sedell, E.R., Warren, D.R., 2020. Carcass additions increase juvenile salmonid growth, condition, and size in an interior Columbia River Basin tributary. *Canadian Journal of Fisheries and Aquatic Sciences* 77, 703–715. <https://doi.org/10.1139/cjfas-2019-0215>
- Khoury, C.K., Bjorkman, A.D., Dempewolf, H., Ramirez-Villegas, J., Guarino, L., Jarvis, A., Rieseberg, L.H., Struik, P.C., 2014. Increasing homogeneity in global food supplies and the implications for food security. *Proceedings of the National Academy of Sciences* 111, 4001. <https://doi.org/10.1073/pnas.1313490111>
- Kieran, C.N., Obrist, D.S., Muñoz, N.J., Hanly, P.J., Reynolds, J.D., 2021. Links between fluctuations in sockeye salmon abundance and riparian forest productivity identified by remote sensing. *Ecosphere* 12, e03699. <https://doi.org/10.1002/ecs2.3699>
- Kohler, A.E., Pearsons, T.N., Zendt, J.S., Mesa, M.G., Johnson, C.L., Connolly, P.J., 2012. Nutrient enrichment with salmon carcass analogs in the Columbia River basin, USA: a stream food web analysis. *Transactions of the American Fisheries Society* 141, 802–824. <https://doi.org/10.1080/00028487.2012.676380>
- Kondolf, G.M., Wolman, M.G., 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 29, 2275–2285. <https://doi.org/10.1029/93WR00402>
- Krkošek, M., Hilborn, R., Peterman, R.M., Quinn, T.P., 2011. Cycles, stochasticity and density dependence in pink salmon population dynamics. *Proceedings of the Royal Society B: Biological Sciences* 278, 2060–2068. <https://doi.org/10.1098/rspb.2010.2335>

- Lamberti, G.A., Resh, V., 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macro invertebrates. *Freshwater Biology* 15, 21–30. <https://doi.org/10.1111/j.1365-2427.1985.tb00693.x>
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology: The metacommunity concept. *Ecology Letters* 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lessard, J.L., Merritt, R.W., 2006. Influence of marine-derived nutrients from spawning salmon on aquatic insect communities in southeast Alaskan streams. *Oikos* 113, 334–343. <https://doi.org/10.1111/j.2006.0030-1299.14512.x>
- Levi, T., Wheat, R.E., Allen, J.M., Wilmers, C.C., 2015. Differential use of salmon by vertebrate consumers: implications for conservation. *PeerJ* 3, e1157. <https://doi.org/10.7717/peerj.1157>
- Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73, 1943–1967. <https://doi.org/10.2307/1941447>
- Lintermans, M., Geyle, H.M., Beatty, S., Brown, C., Ebner, B.C., Freeman, R., Hammer, M.P., Humphreys, W.F., Kennard, M.J., Kern, P., Martin, K., Morgan, D.L., Raadik, T.A., Unmack, P.J., Wager, R., Woinarski, J.C.Z., Garnett, S.T., 2020. Big trouble for little fish: identifying Australian freshwater fishes in imminent risk of extinction. *Pacific Conservation Biology* 26, 365–377.
- Lisi, P.J., Schindler, D.E., 2011. Spatial variation in timing of marine subsidies influences riparian phenology through a plant-pollinator mutualism. *Ecosphere* 2, art101. <https://doi.org/10.1890/ES11-00173.1>
- Loreau, M., Mouquet, N., Holt, R.D., 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6, 673–679. <https://doi.org/10.1046/j.1461-0248.2003.00483.x>
- Maldonado-Márquez, A., Contador, T., Rendoll-Cárcamo, J., Moore, S., Pérez-Troncoso, C., Gomez-Uchida, D., Harrod, C., 2020. Southernmost distribution limit for endangered Peladillas (*Aplochiton taeniatus*) and non-native coho salmon (*Oncorhynchus kisutch*) coexisting within the Cape Horn biosphere reserve, Chile. *Journal of Fish Biology* 96, 1495–1500. <https://doi.org/10.1111/jfb.14309>
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78, 1069–1080. [https://doi.org/10.1175/1520-0477\(1997\)078<1069:APICOW>2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2)

- Martínez-Harms, M.J., Armesto, J.J., Castilla, J.C., Astorga, A., Aylwin, J., Buschmann, A.H., Castro, V., Daneri, G., Fernández, M., Fuentes-Castillo, T., Gelcich, S., González, H.E., Hucke-Gaete, R., Marquet, P.A., Morello, F., Nahuelhual, L., Pliscoff, P., Reid, B., Rozzi, R., Guala, C., Tecklin, D., 2021. A systematic evidence map of conservation knowledge in Chilean Patagonia. *Conservation Science and Practice* 4, e575.
- Meehan, E.P., Seminet-Reneau, E.E., Quinn, T.P., 2005. Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *American Midland Naturalist* 153, 142–151. [https://doi.org/10.1674/0003-0031\(2005\)153\[0142:BPOPSF\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2005)153[0142:BPOPSF]2.0.CO;2)
- Meffe, G.K., 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. *Conservation Biology* 6, 350–354.
- Meyerson, L.A., Mooney, H.A., 2007. Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 5, 199–208. [https://doi.org/10.1890/1540-9295\(2007\)5\[199:IASIAE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2)
- Mitchell, N.L., Lamberti, G.A., 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnology and Oceanography* 50, 217–227. <https://doi.org/10.4319/lo.2005.50.1.0217>
- Mollot, G., Pantel, J.H., Romanuk, T.N., 2017. The effects of invasive species on the decline in species richness: a global meta-analysis, in: Bohan, D.A., Dumbrell, A.J., Massol, F. (eds.), *Advances in Ecological Research*. Academic Press, Boston, USA, pp. 61–83. <https://doi.org/10.1016/bs.aecr.2016.10.002>
- Moore, J.W., Connors, B.M., Hodgson, E.E., 2021. Conservation risks and portfolio effects in mixed-stock fisheries. *Fish and Fisheries* 22, 1024–1040. <https://doi.org/10.1111/faf.12567>
- Moore, J.W., McClure, M., Rogers, L.A., Schindler, D.E., 2010. Synchronization and portfolio performance of threatened salmon: Synchronization of salmon populations. *Conservation Letters* 3, 340–348. <https://doi.org/10.1111/j.1755-263X.2010.00119.x>
- Moore, J.W., Schindler, D.E., 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology* 77, 275–284. <https://doi.org/10.1111/j.1365-2656.2007.01336.x>
- Morris, M.R., Stanford, J.A., 2011. Floodplain succession and soil nitrogen accumulation on a salmon river in southwestern Kamchatka. *Ecological Monographs* 81, 43–61. <https://doi.org/10.1890/08-2296.1>
- Mueter, F.J., Peterman, R.M., Pyper, B.J., 2011. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 456–463. <https://doi.org/10.1139/f02-020>

- Muñoz, N.J., Reid, B., Correa, C., Neff, B.D., Reynolds, J.D., 2021. Non-native Chinook salmon add nutrient subsidies and functional novelty to Patagonian streams. *Freshwater Biology* 66, 495–508. <https://doi.org/10.1111/fwb.13655>
- Musleh, S.S., Seeb, L.W., Seeb, J.E., Ernst, B., Neira, S., Harrod, C., Gomez-Uchida, D., 2020. Mixed-stock analyses of migratory, non-native Chinook salmon at sea and assignment to natal sites in fresh water at their introduced range in South America. *Biological Invasions* 22, 3175–3182.
- Myers, K.W., Walker, R.V., Fowler, S., Dahlberg, Michael L., 1990. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1989. International North Pacific Fisheries Commission FRI-UW-9009 University of Washington, Seattle, USA.
- Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. *Nature* 390, 507–509. <https://doi.org/10.1038/37348>
- Nagata, M., Ando, D., Fujiwara, M., Miyakoshi, Y., Sawada, M., Shimada, H., Asami, H., 2007. A shift in pink salmon dominance in the Okhotsk Sea of Hokkaido in relation to coastal environments during early sea life. *North Pacific Anadromous Fish Commission Bulletin* 4, 237–249.
- Nagata, M., Miyakoshi, Y., Urabe, H., Fujiwara, M., Sasaki, Y., Kasugai, K., Torao, M., Ando, D., Kaeriyama, M., 2012. An overview of salmon enhancement and the need to manage and monitor natural spawning in Hokkaido, Japan. *Environmental Biology of Fishes* 94, 311–323. <https://doi.org/10.1007/s10641-011-9882-3>
- Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., Hilborn, R., 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology* 53, 61–194.
- Naiman, R.J., Bilby, R.E., Schindler, D.E., Helfield, J.M., 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5, 399–417. <https://doi.org/10.1007/s10021-001-0083-3>
- Narum, S.R., Gallardo, P., Correa, C., Matala, A., Hasselman, D., Sutherland, B.J.G., Bernatchez, L., 2017. Genomic patterns of diversity and divergence of two introduced salmonid species in Patagonia, South America. *Evolutionary Applications* 10, 402–416. <https://doi.org/10.1111/eva.12464>
- 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.

- Niklitschek, E.J., Soto, D., Lafon, A., Molinet, C., Toledo, P., 2013. Southward expansion of the Chilean salmon industry in the Patagonian Fjords: main environmental challenges. *Reviews in Aquaculture* 5, 172–195.
<https://doi.org/10.1111/raq.12012>
- Nunn, N., Qian, N., 2010. The Columbian exchange: a history of disease, food, and ideas. *Journal of Economic Perspectives* 24, 163–188.
<https://doi.org/10.1257/jep.24.2.163>
- Ohlberger, J., Ward, E.J., Brenner, R.E., Hunsicker, M.E., Haught, S.B., Finnoff, D., Litzow, M.A., Schwoerer, T., Ruggerone, G.T., Hauri, C., 2021. Non-stationary and interactive effects of climate and competition on pink salmon productivity. *Global Change Biology* gcb.16049. <https://doi.org/10.1111/gcb.16049>
- Okamoto, D.K., Hessing-Lewis, M., Samhoury, J.F., Shelton, A.O., Stier, A., Levin, P.S., Salomon, A.K., 2020. Spatial variation in exploited metapopulations obscures risk of collapse. *Ecological Applications* 30, e02051.
- O’Keefe, T.C., Edwards, R.T., 2003. Evidence for hyporheic transfer and removal of marine-derived nutrients in a sockeye stream in Southwest Alaska. *American Fisheries Society Symposium* 34, 99–110.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., 2020. vegan: community ecology package. R package version 2.5-6. 2019.
- Ormazabal, C., 1993. The conservation of biodiversity in Chile. *Revista Chilena de Historia Natural* 66, 383–402.
- Patrick, C.J., McCluney, K.E., Ruhi, A., Gregory, A., Sabo, J., Thorp, J.H., 2021. Multi-scale biodiversity drives temporal variability in macrosystems. *Frontiers in Ecology and the Environment* 19, 47–56. <https://doi.org/10.1002/fee.2297>
- Pearse, I.S., Altermatt, F., 2013. Predicting novel trophic interactions in a non-native world. *Ecology Letters* 16, 1088–1094. <https://doi.org/10.1111/ele.12143>
- Pechal, J.L., Benbow, M.E., 2016. Microbial ecology of the salmon necrobiome: evidence salmon carrion decomposition influences aquatic and terrestrial insect microbiomes. *Environmental Microbiology* 18, 1511–1522.
<https://doi.org/10.1111/1462-2920.13187>
- Perakis, S.S., Hedin, L.O., 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415, 416–419.
<https://doi.org/10.1038/415416a>
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18, 293–320.
<https://doi.org/10.1146/annurev.es.18.110187.001453>

- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28, 289–316.
<https://doi.org/10.1146/annurev.ecolsys.28.1.289>
- Power, M.E., 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71, 897–904.
<https://doi.org/10.2307/1937361>
- Price, M.H.H., Connors, B.M., Candy, J.R., McIntosh, B., Beacham, T.D., Moore, J.W., Reynolds, J.D., 2019. Genetics of century-old fish scales reveal population patterns of decline. *Conservation Letters* 12, e12669.
<https://doi.org/10.1111/conl.12669>
- Price, M.H.H., English, K.K., Rosenberger, A.G., MacDuffee, M., Reynolds, J.D., 2017. Canada's Wild Salmon Policy: an assessment of conservation progress in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 74, 1507–1518.
<https://doi.org/10.1139/cjfas-2017-0127>
- Price, M.H.H., Moore, J.W., Connors, B.M., Wilson, K.L., Reynolds, J.D., 2021. Portfolio simplification arising from a century of change in salmon population diversity and artificial production. *Journal of Applied Ecology* 58, 1477–1486.
<https://doi.org/10.1111/1365-2664.13835>
- PSF (Pacific Salmon Foundation), 2014. Economic dimensions of British Columbia's Pacific salmon resource. Available at <https://waves-vagues.dfo-mpo.gc.ca/Library/357876.pdf>
- Quinn, T.P., 2018. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle, USA.
- Quinn, T.P., Helfield, J.M., Austin, C.S., Hovel, R.A., Bunn, A.G., 2018. A multidecade experiment shows that fertilization by salmon carcasses enhanced tree growth in the riparian zone. *Ecology* 99, 2433–2441. <https://doi.org/10.1002/ecy.2453>
- R Core Team, 2020. *R: A language and environment for statistical computing*. Vienna, Austria.
- Rand, P.S., Hall, C.A.S., McDowell, W.H., Ringler, N.H., Kennen, J.G., 1992. Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 2377–2385.
<https://doi.org/10.1139/f92-262>
- Reid, B., Astorga, A., Madriz, R.I., Correa, C., 2021. Estado del conocimiento y conservación de los ecosistemas dulceacuícolas de la Patagonia occidental austral, in: Castilla, J.C., Armesto, J.J., Martínez-Harms, M.J. (eds.) *Conservación en la Patagonia Chilena: evaluación del conocimiento, oportunidades y desafíos*. Ediciones UC, Santiago, Chile, pp 429–471.

- Reimchen, T.E., 2017. Diverse ecological pathways of salmon nutrients through an litact marine-terrestrial interface. *The Canadian Field-Naturalist* 131, 350–368. <https://doi.org/10.22621/cfn.v131i4.1965>
- Rex, J.F., Petticrew, E.L., 2008. Delivery of marine-derived nutrients to streambeds by Pacific salmon. *Nature Geoscience* 1, 840–843. <https://doi.org/10.1038/ngeo364>
- Ricciardi, A., Atkinson, S.K., 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems: Distinctiveness magnifies impact of invaders. *Ecology Letters* 7, 781–784. <https://doi.org/10.1111/j.1461-0248.2004.00642.x>
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83, 263–282. <https://doi.org/10.1890/13-0183.1>
- Richey, J.E., Perkins, M.A., Goldman, C.R., 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. *Journal of the Fisheries Research Board of Canada* 32, 817–820. <https://doi.org/10.1139/f75-109>
- Ricker, W.E., 1962. Regulation of the abundance of pink salmon populations. Institute of Fisheries, University of British Columbia, Vancouver, Canada, pp. 155–206.
- Risse-Buhl, U., Trefzger, N., Seifert, A.-G., Schönborn, W., Gleixner, G., Küsel, K., 2012. Tracking the autochthonous carbon transfer in stream biofilm food webs. *FEMS Microbiology Ecology* 79, 118–131. <https://doi.org/10.1111/j.1574-6941.2011.01202.x>
- Rosemond, A.D., Mulholland, P.J., Brawley, S.H., 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 66–75. <https://doi.org/10.1139/f99-181>
- Rüegg, J., Chaloner, D.T., Ballantyne, F., Levi, P.S., Song, C., Tank, J.L., Tiegs, S.D., Lamberti, G.A., 2020. Understanding the relative roles of salmon spawner enrichment and disturbance: a high-frequency, multi-habitat field and modeling approach. *Frontiers in Ecology and Evolution* 8, 19.
- 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: Dynamics, Management, and Ecosystem Science* 10, 152–168. <https://doi.org/10.1002/mcf2.10023>
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B* 274, 1237–1243. <https://doi.org/10.1098/rspb.2006.0444>

- Satterthwaite, W.H., Carlson, S.M., 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* 72, 1860–1875. <https://doi.org/10.1139/cjfas-2015-0169>
- Saul, W.-C., Jeschke, J.M., 2015. Eco-evolutionary experience in novel species interactions. *Ecology Letters* 18, 236–245. <https://doi.org/10.1111/ele.12408>
- Scherson, R.A., Albornoz, A.A., Moreira-Muñoz, A.S., Urbina-Casanova, R., 2014. Endemicity and evolutionary value: a study of Chilean endemic vascular plant genera. *Ecology and Evolution* 4, 806–816. <https://doi.org/10.1002/ece3.960>
- Scheuerell, M.D., Moore, J.M., Schindler, D.E., Harvey, C.J., 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology* 52, 1944–1956. <https://doi.org/10.1111/j.1365-2427.2007.01823.x>
- Schindler, D.E., Armstrong, J.B., Bentley, K.T., Jankowski, K., Lisi, P.J., Payne, L.X., 2013. Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters* 9, 20130048. <https://doi.org/10.1098/rsbl.2013.0048>
- Schindler, D.E., Armstrong, J.B., Reed, T.E., 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13, 257–263. <https://doi.org/10.1890/140275>
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612. <https://doi.org/10.1038/nature09060>
- Schittko, C., Bernard-Verdier, M., Heger, T., Buchholz, S., Kowarik, I., von der Lippe, M., Seitz, B., Joshi, J., Jeschke, J.M., 2020. A multidimensional framework for measuring biotic novelty: How novel is a community? *Global Change Biology* 26, 4401–4417. <https://doi.org/10.1111/gcb.15140>
- Schlaepfer, M.A., Sax, D.F., Olden, J.D., 2011. The potential conservation value of non-native species. *Conservation Biology* 25, 428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schuldt, J.A., Hershey, A.E., 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society* 14, 259–268. <https://doi.org/10.2307/1467778>
- Schüttler, E., Klenke, R., McGehee, S., Rozzi, R., Jax, K., 2009. Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. *Biological Conservation* 142, 1450–1460. <https://doi.org/10.1016/j.biocon.2009.02.013>

- Sears, A., Holt, R., Polis, G., 2004. Feast and famine in food webs: the effects of pulsed productivity, in Polis, G.A., Power, M.E., Huxel, G.R. (eds.) Food webs at the landscape level. University of Chicago Press, Chicago, USA, pp 359–386
- Shelton, J.M., Samways, M.J., Day, J.A., 2015. Predatory impact of non-native rainbow trout on endemic fish populations in headwater streams in the Cape Floristic Region of South Africa. *Biological Invasions* 17, 365–379. <https://doi.org/10.1007/s10530-014-0735-9>
- Siemens, L.D., Dennert, A.M., Obrist, D.S., Reynolds, J.D., 2020. Spawning salmon density influences fruit production of salmonberry (*Rubus spectabilis*). *Ecosphere* 11, e03282. <https://doi.org/10.1002/ecs2.3282>
- Simberloff, D., 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9, 912–919. <https://doi.org/10.1111/j.1461-0248.2006.00939.x>
- Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21–32. <https://doi.org/10.1023/A:1010086329619>
- Soto, D., Arismendi, I., Di Prinzio, C.Y., Jara, F., 2007. Establishment of Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific basins of southern South America and its potential ecosystem implications. *Revista Chilena de la Historia Natural* 80, 81–98.
- Steinman, A.D., Lamberti, G.A., Leavitt, P.R., Uzarski, D.G., 2017. Biomass and pigments of benthic algae, in: Hauer, F.R., Lamberti, G.A. (eds.), *Methods in stream ecology*. Academic Press, Boston, USA, pp. 223–241. <https://doi.org/10.1016/B978-0-12-416558-8.00012-3>
- Sullaway, G.H., Shelton, A.O., Samhouri, J.F., 2021. Synchrony erodes spatial portfolios of an anadromous fish and alters availability for resource users. *Journal of Animal Ecology* 90, 2692–2703. <https://doi.org/10.1111/1365-2656.13575>
- Swain, N.R., Hocking, M.D., Harding, J.N., Reynolds, J.D., 2014. Effects of salmon on the diet and condition of stream-resident sculpins. *Canadian Journal of Fisheries and Aquatic Sciences* 71, 521–532. <https://doi.org/10.1139/cjfas-2013-0159>
- Tabor, R.A., Celedonia, M.T., Mejia, F., Piaskowski, R.M., Low, D.L., 2004. Predation of juvenile Chinook salmon by predatory fishes in three areas of the Lake Washington basin. US Fish and Wildlife Service, Lacey, USA.
- Taylor, E.B., 1990. Environmental correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 37, 1–17.

- Thorson, J.T., Scheuerell, M.D., Olden, J.D., Schindler, D.E., 2018. Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes. *Proceedings of the Royal Society B* 285, 20180915.
- Tilman, D., Lehman, C.L., Bristow, C.E., 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *The American Naturalist* 151, 277–282. <https://doi.org/10.1086/286118>
- Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441, 629–632. <https://doi.org/10.1038/nature04742>
- Tonra, C.M., Sager-Fradkin, K., Marra, P.P., 2016. Barriers to salmon migration impact body condition, offspring size, and life history variation in an avian consumer. *Ecography* 39, 1056–1065. <https://doi.org/10.1111/ecog.02014>
- Tosa, M.I., Dzedzic, E.H., Appel, C.L., Urbina, J., Massey, A., Ruprecht, J., Eriksson, C.E., Dolliver, J.E., Lesmeister, D.B., Betts, M.G., Peres, C.A., Levi, T., 2021. The rapid rise of next-generation natural history. *Frontiers in Ecology and Evolution* 9, 698131.
- Townsend, C.R., 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology* 17, 38–47. <https://doi.org/10.1046/j.1523-1739.2003.02017.x>
- Valdovinos, C., 2006. Invertebrados dulceacuícolas, in CONAMA (ed.) *Biodiversidad en Chile*. Ocho Libros, Santiago, Chile, pp 202–223.
- Valenzuela, A.E., Rey, A.R., Fasola, L., Samaniego, R.A.S., Schiavini, A., 2013. Trophic ecology of a top predator colonizing the southern extreme of South America: Feeding habits of invasive American mink (*Neovison vison*) in Tierra del Fuego. *Mammalian Biology* 78, 104–110.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 2011. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 130–137. <https://doi.org/10.1139/f80-017>
- Verspoor, J.J., Braun, D.C., Stubbs, M.M., Reynolds, J.D., 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. *Ecosphere* 2, art18. <https://doi.org/10.1890/ES10-00011.1>
- Vitousek, P.M., 1996. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies, in Samson, F.B., Knopf, F.L. (eds.), *Ecosystem management: selected readings*. Springer, New York, USA, pp 183–191. https://doi.org/10.1007/978-1-4612-4018-1_17

- Vitule, J.R.S., Freire, C.A., Vazquez, D.P., Nuñez, M.A., Simberloff, D., 2012. Revisiting the potential conservation value of non-native species. *Conservation Biology* 26, 1153–1155.
- Wagner, M.A., Reynolds, J.D., 2019. Salmon increase forest bird abundance and diversity. *PLOS ONE* 14, e0210031.
<https://doi.org/10.1371/journal.pone.0210031>
- Walsh, J.C., Pendray, J.E., Godwin, S.C., Artelle, K.A., Kindsvater, H.K., Field, R.D., Harding, J.N., Swain, N.R., Reynolds, J.D., 2020. Relationships between Pacific salmon and aquatic and terrestrial ecosystems: implications for ecosystem-based management. *Ecology* 101, e03060. <https://doi.org/10.1002/ecy.3060>
- Walters, C., English, K., Korman, J., Hilborn, R., 2019. The managed decline of British Columbia's commercial salmon fishery. *Marine Policy* 101, 25–32.
<https://doi.org/10.1016/j.marpol.2018.12.014>
- Walters, C.J., Lichatowich, J.A., Peterman, R.M., Reynolds, J.D., 2008. Report of the Skeena independent science review panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment 15.
- Wang, S., Loreau, M., 2014. Ecosystem stability in space: α , β and γ variability. *Ecology Letters* 17, 891–901. <https://doi.org/10.1111/ele.12292>
- Wang, S., Loreau, M., Arnoldi, J.-F., Fang, J., Rahman, K.Abd., Tao, S., de Mazancourt, C., 2017. An invariability-area relationship sheds new light on the spatial scaling of ecological stability. *Nature Communications* 8, 15211.
<https://doi.org/10.1038/ncomms15211>
- White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* 12, 443–455.
<https://doi.org/10.1111/j.1366-9516.2006.00265.x>
- Wilcox, K.A., Wagner, M.A., Reynolds, J.D., 2021. Salmon subsidies predict territory size and habitat selection of an avian insectivore. *PLOS ONE* 16, e0254314.
<https://doi.org/10.1371/journal.pone.0254314>
- Wilcox, K.R., Tredennick, A.T., Koerner, S.E., Grman, E., Hallett, L.M., Avolio, M.L., La Pierre, K.J., Houseman, G.R., Isbell, F., Johnson, D.S., Alatalo, J.M., Baldwin, A.H., Bork, E.W., Boughton, E.H., Bowman, W.D., Britton, A.J., Cahill, J.F., Collins, S.L., Du, G., Eskelinen, A., Gough, L., Jentsch, A., Kern, C., Klanderud, K., Knapp, A.K., Kreyling, J., Luo, Y., McLaren, J.R., Megonigal, P., Onipchenko, V., Prev y, J., Price, J.N., Robinson, C.H., Sala, O.E., Smith, M.D., Soudzilovskaia, N.A., Souza, L., Tilman, D., White, S.R., Xu, Z., Yahdjian, L., Yu, Q., Zhang, P., Zhang, Y., 2017. Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters* 20, 1534–1545.
<https://doi.org/10.1111/ele.12861>

- Willson, M.F., Halupka, K.C., 1995. Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* 9, 489–497. <https://doi.org/10.1046/j.1523-1739.1995.09030489.x>
- Wipfli, M.S., Hudson, J., Caouette, J., 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1503–1511. <https://doi.org/10.1139/f98-031>

Appendix A.

Supporting Information for Chapter 2

Table A1. Characteristics of the Impact (i.e. downstream) and Control (i.e. upstream) sites used in the Control-Impact study.

Stream name	Distance between sites (km)	Tile depth on sampling date (cm)		Open canopy at each tile (%)		Temperature during study (°C)		Biomass sample size		Isotope sample size	
		Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control
El Toqui	1.5	17.7 ± 3	15.3 ± 3	97 ± 4	97 ± 3	N/A	N/A	7	8	7	7
Ñirehuao	9.2	27.0 ± 3	25.0 ± 4	92 ± 12	92 ± 9	8.28 ± 3.12*	8.02 ± 3.09*	5	12	5	8
Emperador	2.2	25.1 ± 3	24.4 ± 2	88 ± 13	86 ± 13	N/A	N/A	9	7	6	6
Jaramillo	2.1	16.6 ± 4	17.8 ± 2	93 ± 8	90 ± 10	10.06 ± 1.52*	10.03 ± 1.41*	9	5	6	4

* Note: Temperatures were recorded until May 28 in Ñirehuao and May 1 in Jaramillo. The additional four weeks of cold May temperatures explain the lower mean temperature of Ñirehuao. Problems with logger and data retrieval prevented temperatures in El Toqui and Emperador from being recorded.

Table A2. Sampling characteristics of the Before-After-Control-Impact study.

Stream name	Period	Distance between sites (km)	Tile depth on sampling date (cm)		Open canopy at each tile (%)		Tile incubation time (days)		Biomass sample size		Isotope sample size	
			Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control
Ñirehuao	Before	9.2	13.3 ± 3	13.7 ± 5	93 ± 11	87 ± 17	36	36	8	12	6	12
	After	9.2	26.4 ± 4	36.4 ± 5	90 ± 12	89 ± 12	35	34	14	13	14	14
Huemules	Before	3.9	18.0 ± 4	15.2 ± 4	97 ± 3	98 ± 3	30	30	11	13	10	10
	After	3.9	26.9 ± 3	25.9 ± 3	98 ± 3	98 ± 4	35	35	12	12	12	13

Table A3. Effects of site, stream, and period on biofilm biomass and isotopic traits in the Before-After-Control-Impact study of Chinook salmon in Patagonia, southern Chile. The results of linear models are summarized for effects on biofilm isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) as well as algal biomass (chl *a*), total biofilm biomass (AFDM), and percent of total biomass composed of chl *a* (chl *a* %). Significant effects ($P < 0.05$) are bolded.

Trait	df	SS	F	P
$\delta^{13}\text{C}$				
<i>site</i>	1	0.30	0.34	0.562
<i>period</i>	1	71.5	81.6	< 0.001
<i>stream</i>	1	13.8	15.7	< 0.001
<i>site</i> × <i>period</i>	1	0.36	0.41	0.524
<i>site</i> × <i>stream</i>	1	1.60	1.83	0.180
<i>period</i> × <i>stream</i>	1	50.8	58.0	< 0.001
<i>site</i> × <i>period</i> × <i>stream</i>	1	48.6	55.6	< 0.001
<i>residual</i>	83	72.7		
$\delta^{15}\text{N}$				
<i>site</i>	1	1.39	11.0	0.001
<i>period</i>	1	9.17	72.8	< 0.001
<i>stream</i>	1	0.64	5.09	0.027
<i>site</i> × <i>period</i>	1	0.28	2.23	0.139
<i>site</i> × <i>stream</i>	1	0.44	3.49	0.065
<i>period</i> × <i>stream</i>	1	4.76	37.8	< 0.001
<i>site</i> × <i>period</i> × <i>stream</i>	1	2.78	22.1	< 0.001
<i>residual</i>	83	10.5		
chl <i>a</i>				
<i>site</i>	1	0.07	34.2	< 0.001
<i>period</i>	1	1.67	873	< 0.001
<i>stream</i>	1	0.16	86.0	< 0.001
<i>site</i> × <i>period</i>	1	0.02	10.5	0.002
<i>site</i> × <i>stream</i>	1	0.01	5.11	0.026
<i>period</i> × <i>stream</i>	1	0.14	75.2	< 0.001
<i>site</i> × <i>period</i> × <i>stream</i>	1	0.00	0.01	0.904
<i>residual</i>	87	0.17		
AFDM				
<i>site</i>	1	0.05	17.2	< 0.001
<i>period</i>	1	0.46	167	< 0.001
<i>stream</i>	1	0.05	19.3	< 0.001
<i>site</i> × <i>period</i>	1	0.03	9.69	0.003

Trait	df	SS	F	P
<i>site × stream</i>	1	0.00	0.74	0.391
<i>period × stream</i>	1	0.07	23.9	< 0.001
<i>site × period × stream</i>	1	0.00	0.76	0.385
<i>residual</i>	87	0.24		
chl a %				
site	1	0.06	35.8	< 0.001
period	1	1.95	1259	< 0.001
stream	1	0.09	59.6	< 0.001
site × period	1	0.01	8.42	0.005
site × stream	1	0.02	9.84	0.002
period × stream	1	0.06	40.4	< 0.001
site × period × stream	1	0.00	3.01	0.086
<i>residual</i>	87	0.13		

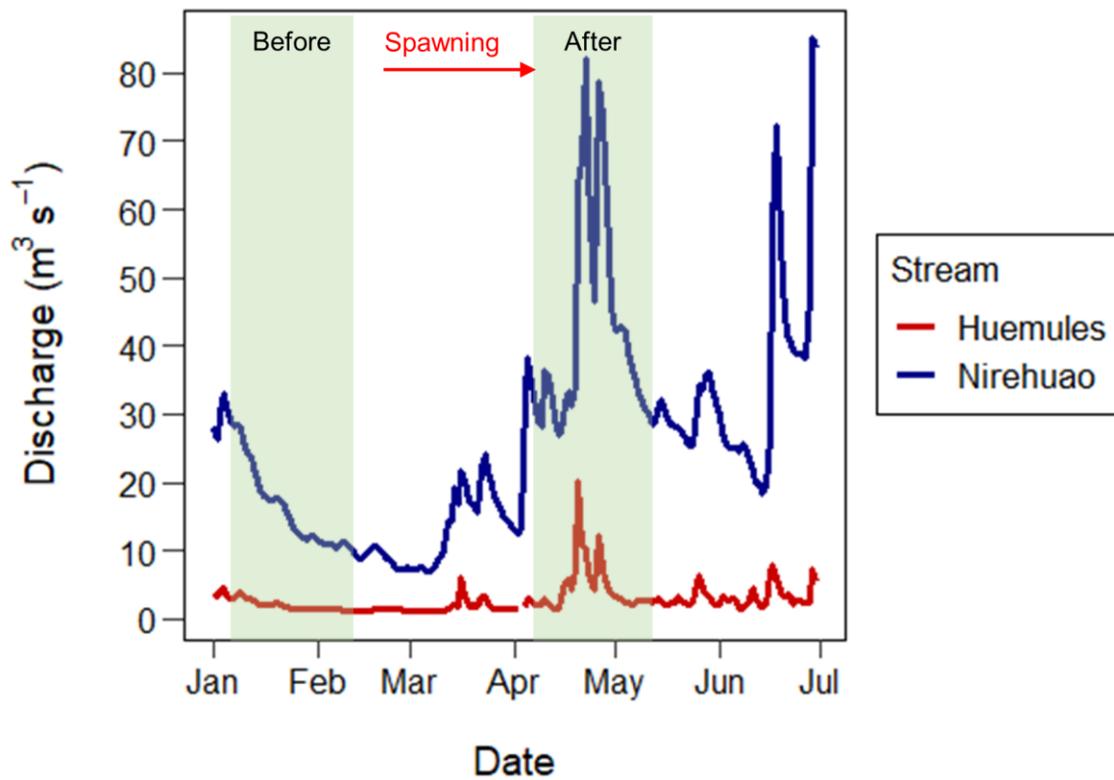


Figure A1. Stream hydrographs throughout the Before-After-Control-Impact study, with reference to the timing of tile deployment during the Before and After periods as well as the onset of salmon spawning.

Daily discharge data were obtained from the Government of Chile's hydrologic monitoring program.

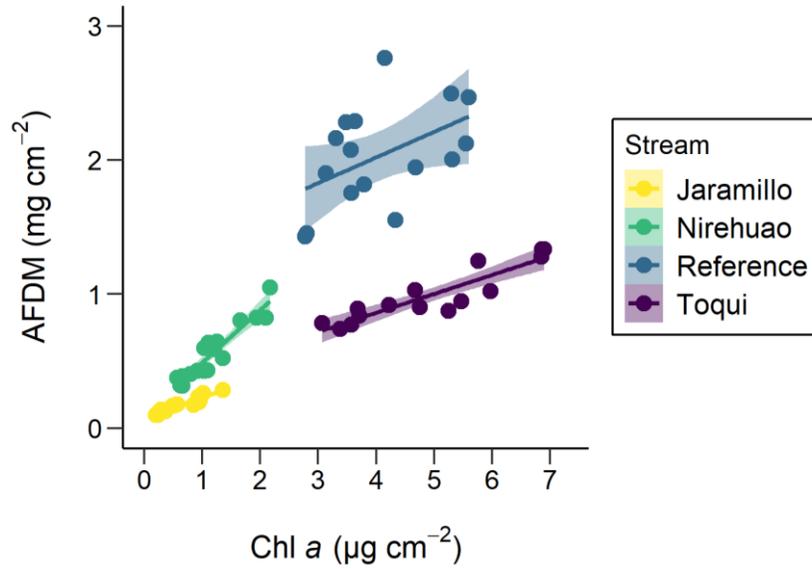


Figure A2. Relationship between algal biomass (chl a) and total biofilm biomass (AFDM) among streams in the Control-Impact study.

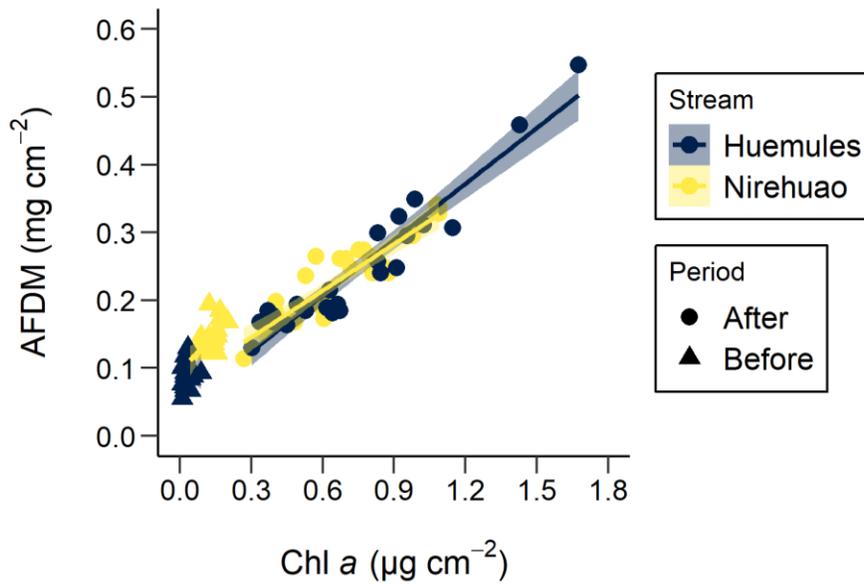


Figure S3. Relationship between algal biomass (chl a) and total biofilm biomass (AFDM) among streams and periods in the Before-After-Control-Impact study.

Appendix B.

Supporting Information for Chapter 3

Table B1. The nature and type of all documented Chinook salmon interactions with freshwater or riparian taxa in Patagonia.

Interacting taxon	Salmon life stage	Interaction type	Nature of Interaction	Source
Mink (<i>Neovison vison</i>)	Adult	0/+	Scavenging (carcasses)	This study
Culpeo fox (<i>Lycalopex culpaeus</i>)	Adult	0/+	Scavenging (carcasses)	This study
Rodents (<i>Rattus rattus</i> , <i>Mus musculus</i> , <i>Oligoryzomys longicaudatus</i>)	Adult	0/+	Scavenging (carcasses)	This study
Terrestrial insects (e.g., Calliphoridae, Silphidae)	Adult	0/+	Scavenging (carcasses)	This study
Stream invertebrates (e.g., Chironomidae, <i>Aegla</i> spp.)	Adult	0/+	Scavenging (carcasses or spilt eggs)	This study; Soto et al. 2007; Arismendi and Soto 2012
Passerine birds (<i>Scelorchilis rubecula</i> , <i>Aphrastura spinicauda</i>)	Adult	0/+/+	Predation of carcass-associated insects	This study
Stream algae	Adult	0/+	Nutrient subsidy	Muñoz et al. 2021
Trout (<i>Salmo trutta</i> , <i>Oncorhynchus mykiss</i>)	Adult	0/+	Scavenging (spilt eggs)	Soto et al. 2007; Arismendi and Soto 2012
Caracara (<i>Milvago chimango</i> , <i>Caracara plancus</i>)	Adult	0/+	Scavenging (carcasses)	Soto et al. 2007
Terrestrial invertebrates (e.g. Diptera, Hymenoptera, Trichoptera)	Juvenile	+/0	Terrestrial prey subsidy	Chalde and Fernandez 2017; Di Prinzio and Arismendi 2018
Stream invertebrates (e.g., Ephemeroptera, Plecoptera, Diptera, Coleoptera, <i>Hyalella</i> spp.)	Juvenile	+/-	Predator-prey	Ibarra et al. 2011; Chalde and Fernandez 2017; Di Prinzio and Arismendi 2018; Bravo et al. 2019

Interacting taxon	Salmon life stage	Interaction type	Nature of Interaction	Source
Galaxiids (e.g., <i>Galaxias maculatus</i>)	Juvenile	+/-	Predator-prey	Ibarra et al. 2011; Bravo et al. 2019
Trout (<i>Salmo trutta</i> , <i>Oncorhynchus mykiss</i>)	Juvenile	-/+	Predator-prey	Inferred from Tabor et al. 2004
Mink (<i>Neovison vison</i>)	Juvenile	-/+	Predator-prey	Inferred from Ben-David et al. 1997

When the interacting taxon is composed of multiple taxa, the most prominent interactors are listed as examples. For each interaction type, Chinook salmon is represented by the first taxon (e.g. '0' in '0/+').



Figure B1. Terrestrial invertebrates on out-of-water carcasses, including (a, b) adult blowflies (Calliphoridae: *Calliphora vicina*), (c) adult March flies (Bibionidae: *Dilophus* spp.), and (d) non-native yellow jacket wasps (Vespidae: *Vespula* spp.).



Figure B2. Camera trap photo of an out-of-water salmon carcass covered by dozens of beetles.

Beetles observed on carcasses included carrion beetles (Silphidae: *Oxelytrum* spp. and *Nicrophorus* spp.), predatory beetles (Staphylinidae and Carabidae: *Ceroglossus* spp.), and Darwin's beetle (Lucanidae: *Chiasognathus grantii*).



Figure B3. Weeks after the end of spawning, underwater carcasses were covered with a thick, mould-like biofilm, similar to what occurs in their native range.

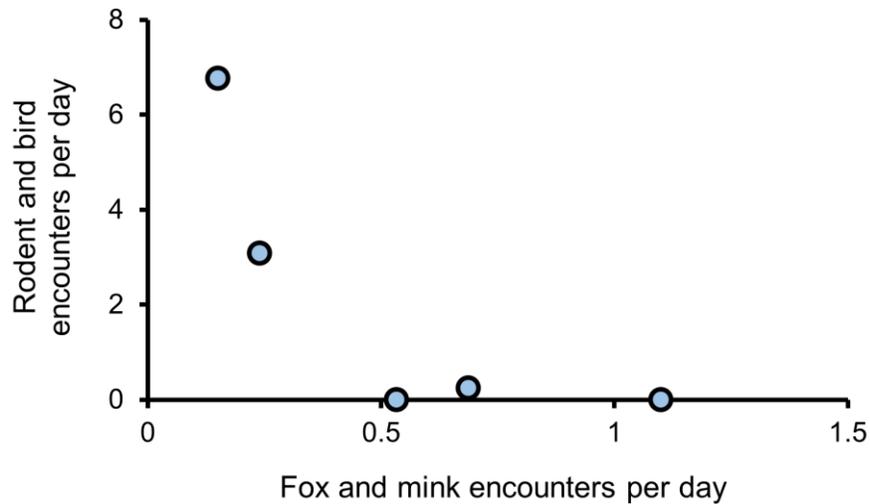


Figure B4. Among streams and years, the combined carcass encounters per camera day of culpeo foxes and mink relative to that of rodents (colilargos, black rats, and/or house mice) and passerine birds (chucaos and thorn-tailed rayaditos).

Each data point represents an individual stream in an individual year (three streams surveyed in 2016, two streams surveyed in 2018).



Figure B5. The transfer of a Chinook salmon carcass from stream to streambank by an American mink in Río El Toqui, southern Chile.

Pictured are stills from video footage showing the mink (a) submerging its head to feed on the underwater carcass, (b) removing carcass flesh and attempting to dislodge the carcass from underneath a log, and (c) feeding on the carcass on the streambank after having removed it from the water.

Appendix C.

Supporting Information for Chapter 4

Table C1. Overview of model notation.

Symbol	Name	Description
<i>Primary terms</i>		
γ_{stb}	regional stability	temporal stability of abundance at the metacommunity level
α_{stb}	local stability	average temporal stability of abundance at the local community level
$\alpha_{stb,i}$	local community stability	temporal stability of abundance within each local community
Φ	spatial synchrony	similarity in temporal fluctuations in abundance among local communities
τ	spatial stabilization	increase in stability from the local to metacommunity level; analogous to portfolio effect
<i>Contrib</i>	contribution	percentage change in stability component when a subset (e.g., pink salmon) is excluded
<i>Secondary terms</i>		
μ		temporal mean of total annual abundance
σ		temporal standard deviation of total annual abundance
w		temporal covariance in total annual abundance
<i>CV</i>		coefficient of variation
<i>Subscripts</i>		
M		metacommunity (e.g., North Pacific)
L		all local communities (e.g., Japan, etc.)
i and j		indexes for local community
k		index for species or local community

Table C2. Contribution of hatchery-origin salmon to the stability of individual local communities ($\alpha_{stb,i}$) in the North Pacific.

Local community	Contribution to $\alpha_{stb,i}$ (%) [*]	Hatchery production of salmon (millions of fish) [†]	Percentage of total abundance (%) [‡]
Washington & Oregon	8.1 ± 5.8	annual: 0.44 (1959-2015) total: 25.1	14.4
Southern BC	4.3 ± 3.8	annual: 1.8 (1957-2015) total: 105	7.4
Northern BC	1.2 ± 0.9	annual: 0.35 (1979-2015) total: 12.9	1.6
Southeast Alaska	4.7 ± 6.3	annual: 7.9 (1978-2015) total: 302	9.2
PW Sound Alaska	11.5 ± 20	annual: 27.5 (1977-2015) total: 1071	63.9
Cook Inlet Alaska	3.6 ± 17	annual: 1.3 (1977-2015) total: 52.4	13.4
Kodiak Island Alaska	12.1 ± 8.6	annual: 5.1 (1977-2015) total: 198	18.9
South-central Alaska	0	annual: 0 total: 0	0
Western Alaska	0.03 ± 0.1	annual: 0.02 (1981-2003) total: 0.51	0.04
Eastern Kamchatka	0.14 ± 0.05	annual: 0.08 (1974-2015) total: 3.5	0.1
Western Kamchatka	0.10 ± 0.05	annual: 0.06 (1972-2015) total: 2.7	0.1
Russia mainland	9.6 ± 8.4	annual: 15.0 (1952-2015) total: 958	13.0
Japan	49.3 ± 21	annual: 37.6 (1952-2015) total: 2405	87.9

* Contribution (mean ± SD) was calculated using only the rolling windows in which there was hatchery production.

† Annual hatchery production is the mean annual abundance of hatchery-origin salmon during the period of hatchery production in each local community. This period is indicated in brackets. Data from Ruggerone and Irvine (2018).

‡ Calculated as the percent of total salmon abundance composed of hatchery-origin salmon during the period of hatchery production (i.e., excluding years in which there was no hatchery production).

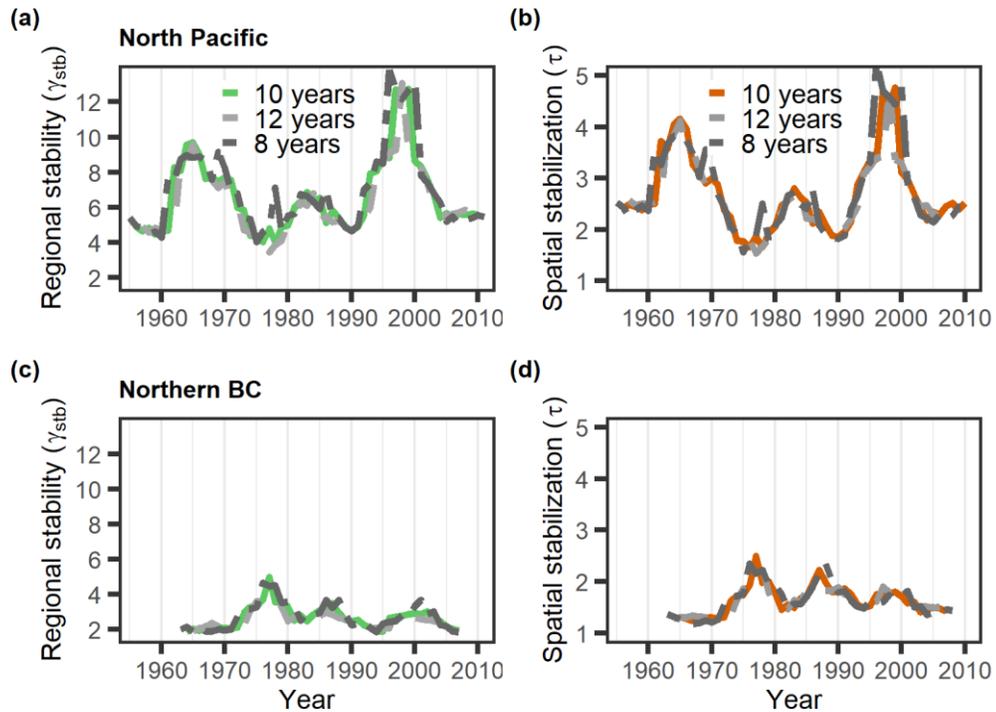


Figure C1. Stability components of annual salmon abundance calculated in 8-year (dark grey dashed lines), 10-year (coloured solid lines), and 12-year (light grey dashed lines) rolling windows in (a,b) the North Pacific and (c,d) Northern British Columbia (BC).

The regional stability (a,c; green lines) and spatial stabilization (b,d; orange lines) of total annual salmon abundance were calculated between 1952–2015 in the North Pacific and 1960–2012 in Northern BC. The plotted year values for these stability components correspond with the middle year of each rolling window.

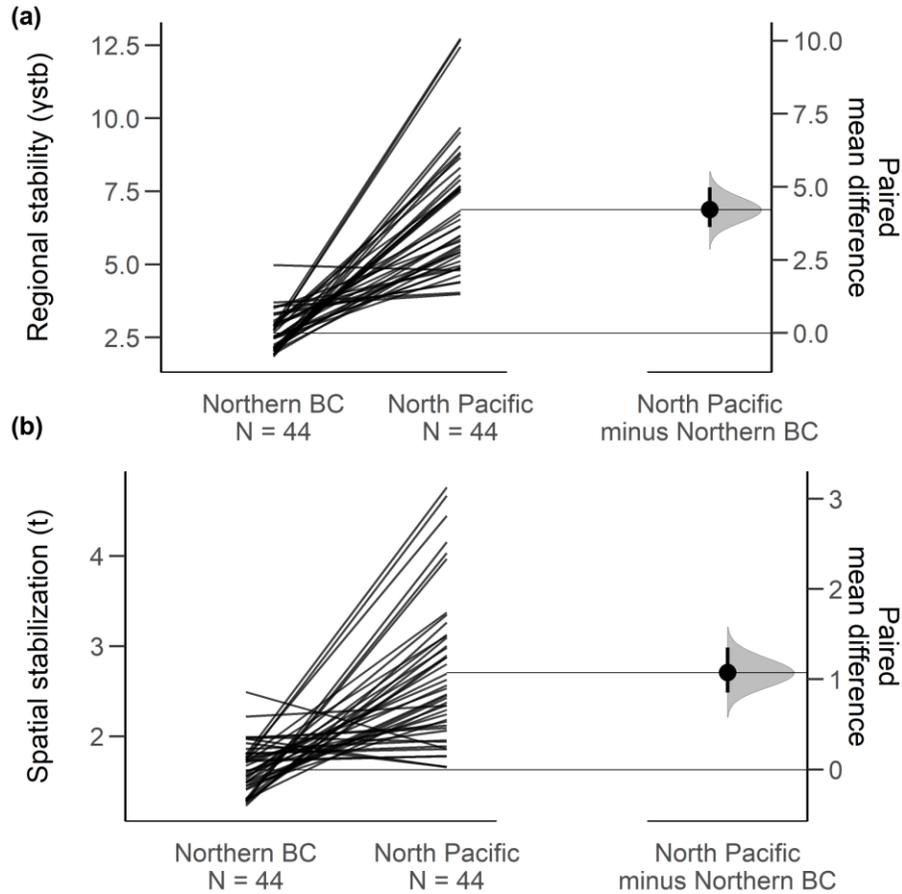


Figure C2. Comparisons of (a) regional stability and (b) spatial stabilization of total annual salmon abundance in the North Pacific and Northern BC metacommunities, paired by year (i.e., 10-year rolling window).

The bootstrapped mean difference between metacommunities is represented by the point on the right side of the plots, and the 95% confidence interval of this difference is indicated by the vertical line around the mean difference. For both stability components, the 95% confidence intervals do not cross the zero-difference line at the bottom of the panels' right side, indicating that the stability components are significantly higher in the North Pacific than in Northern BC.

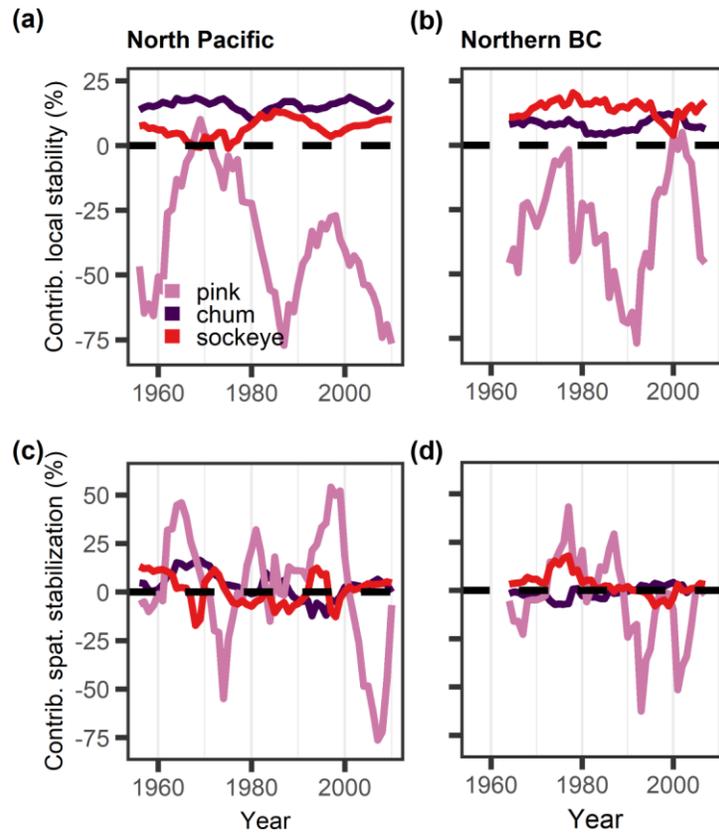


Figure C3. The contribution of pink (pink lines), chum (purple lines), and sockeye salmon (red lines) to the (a,b) local stability and (c,d) spatial stabilization of total annual salmon abundance in (a,c) the North Pacific and (b,d) Northern British Columbia (BC).

Contributions were calculated as the percentage change in the stability component due to the inclusion of the species in every 10-year rolling window. Values above zero (dashed line) represent a positive effect on the stability component (and vice versa).

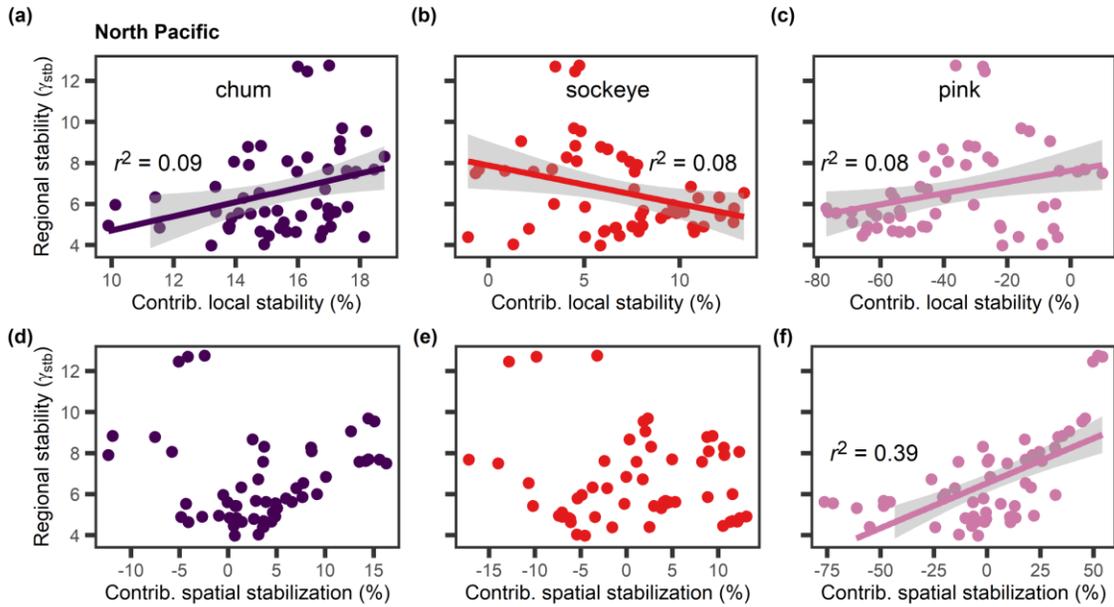


Figure C4. Associations between temporal variation in the regional stability of total annual salmon abundance in the North Pacific and the contributions of (a,d) chum, (b,e) sockeye, and (c,f) pink salmon to (a-c) local stability and (d-f) spatial stabilization. r^2 values are shown for every significant ($p < 0.05$) association.

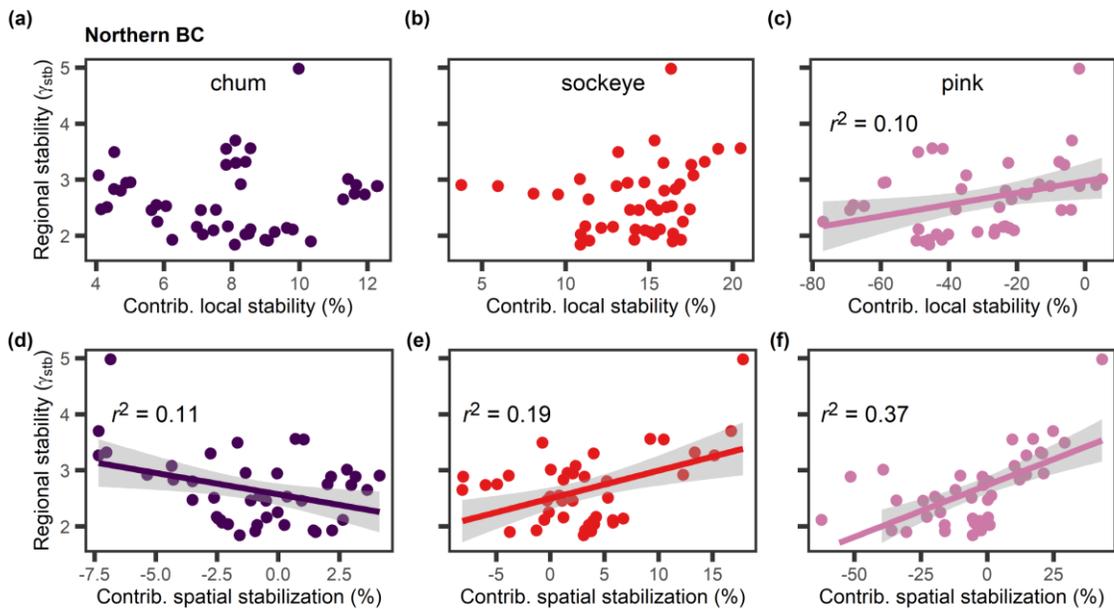


Figure C5. Associations between temporal variation in the regional stability of total annual salmon abundance in Northern BC and the contributions of (a,d) chum, (b,e) sockeye, and (c,f) pink salmon to (a-c) local stability and (d-f) spatial stabilization. r^2 values are shown for every significant ($p < 0.05$) association.

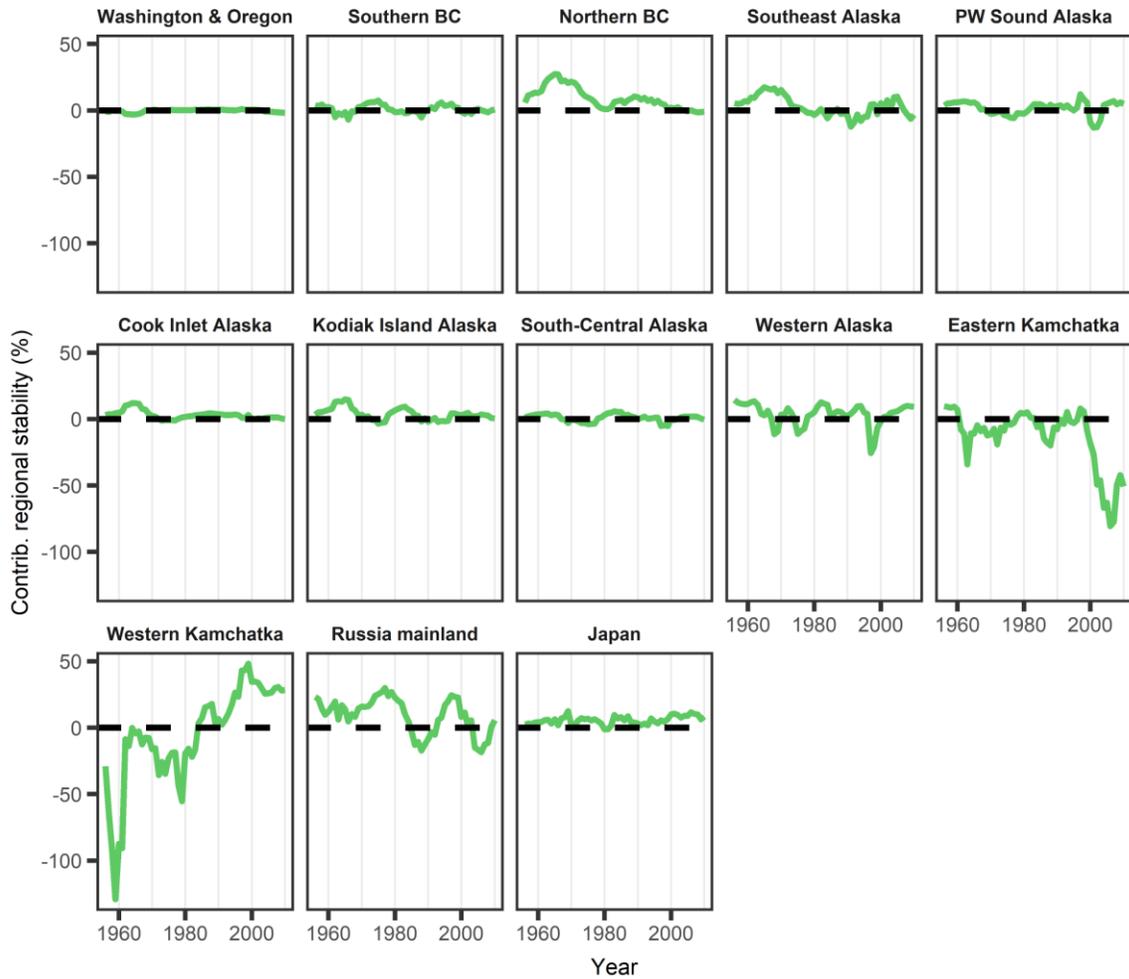


Figure C6. Contribution to the regional stability of total annual salmon abundance among local communities in the North Pacific. Contributions were calculated as the percentage change in regional stability due to the inclusion of the local community in every 10-year rolling window. Values above zero (dashed line) represent a positive effect on regional stability (and vice versa). The plotted year values correspond with the middle year of each rolling window.

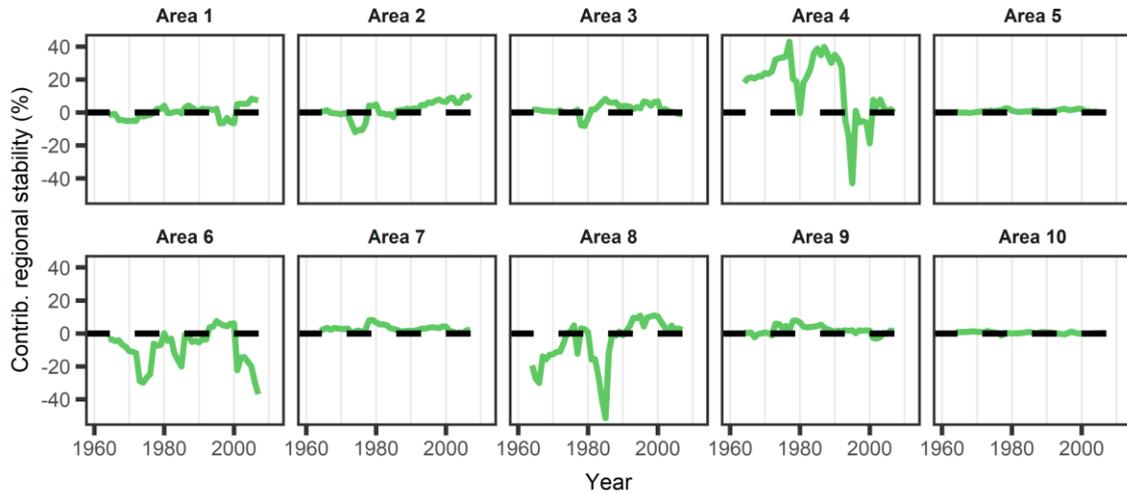


Figure C7. Contribution to the regional stability of total annual salmon abundance among local communities (i.e., Management Areas) in Northern British Columbia.

Contributions were calculated as the percentage change in regional stability due to the inclusion of the local community in every 10-year rolling window. Values above zero (dashed line) represent a positive effect on regional stability (and vice versa). The plotted year values correspond with the middle year of each rolling window.

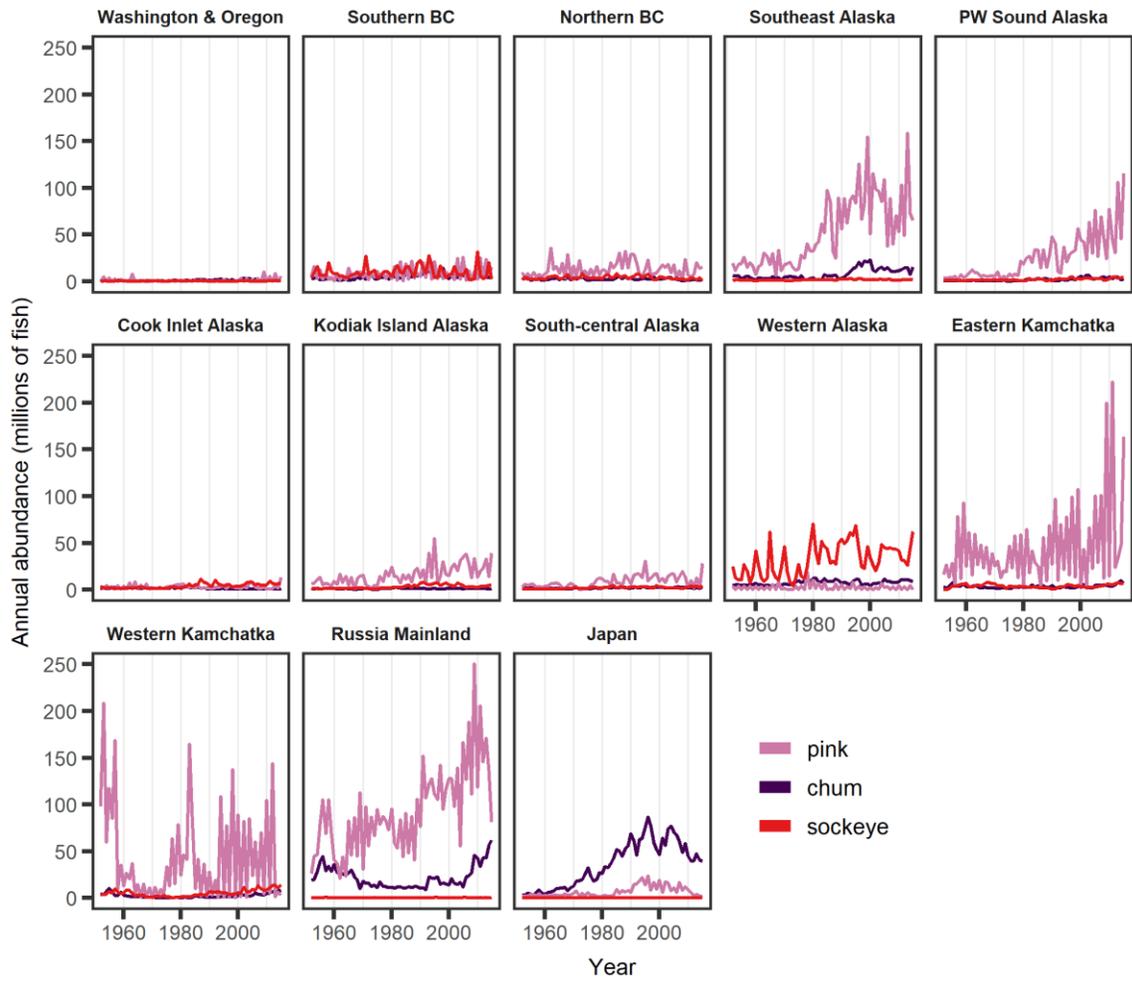


Figure C8. Total annual abundance of pink salmon (pink lines), chum salmon (purple lines), and sockeye salmon (red lines) in local communities throughout the North Pacific between 1952 to 2015.
 Data are from Ruggerone and Irvine (2018).

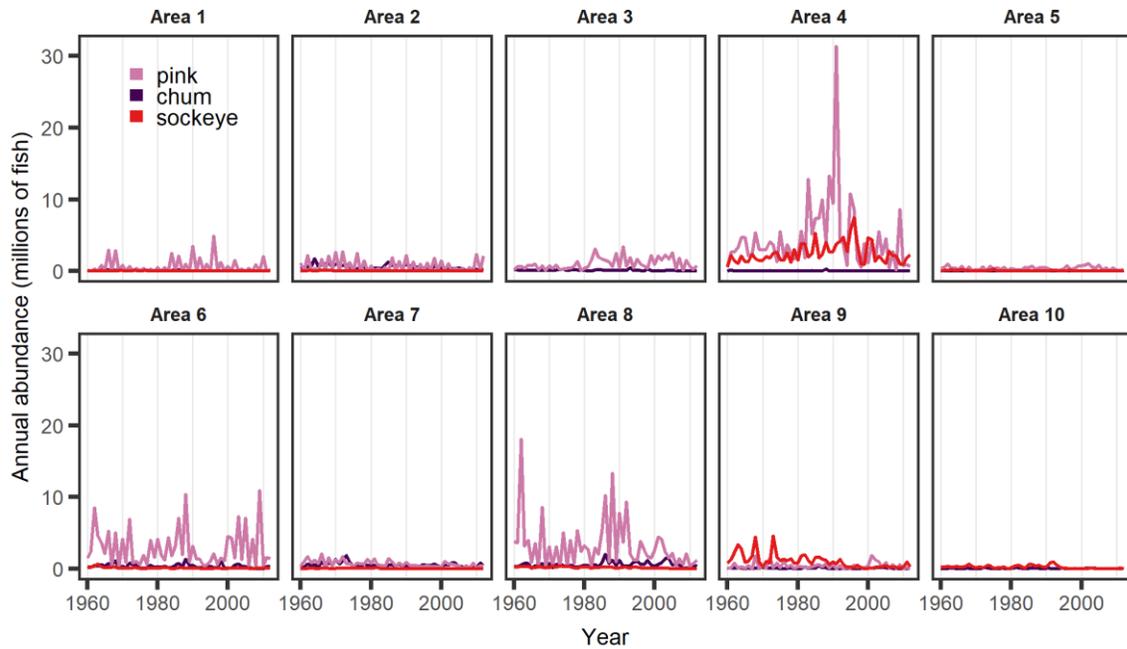


Figure C9 Total annual abundance between 1960 to 2010 of pink salmon (pink lines), chum salmon (purple lines), and sockeye salmon (red lines) in local communities (i.e., Management Areas) in the coastal waters of Northern British Columbia.

Sockeye in Management Area 3 and pink in Management Area 10 were excluded from the analysis due to missing abundance estimates. Data are from English et al. (2018).

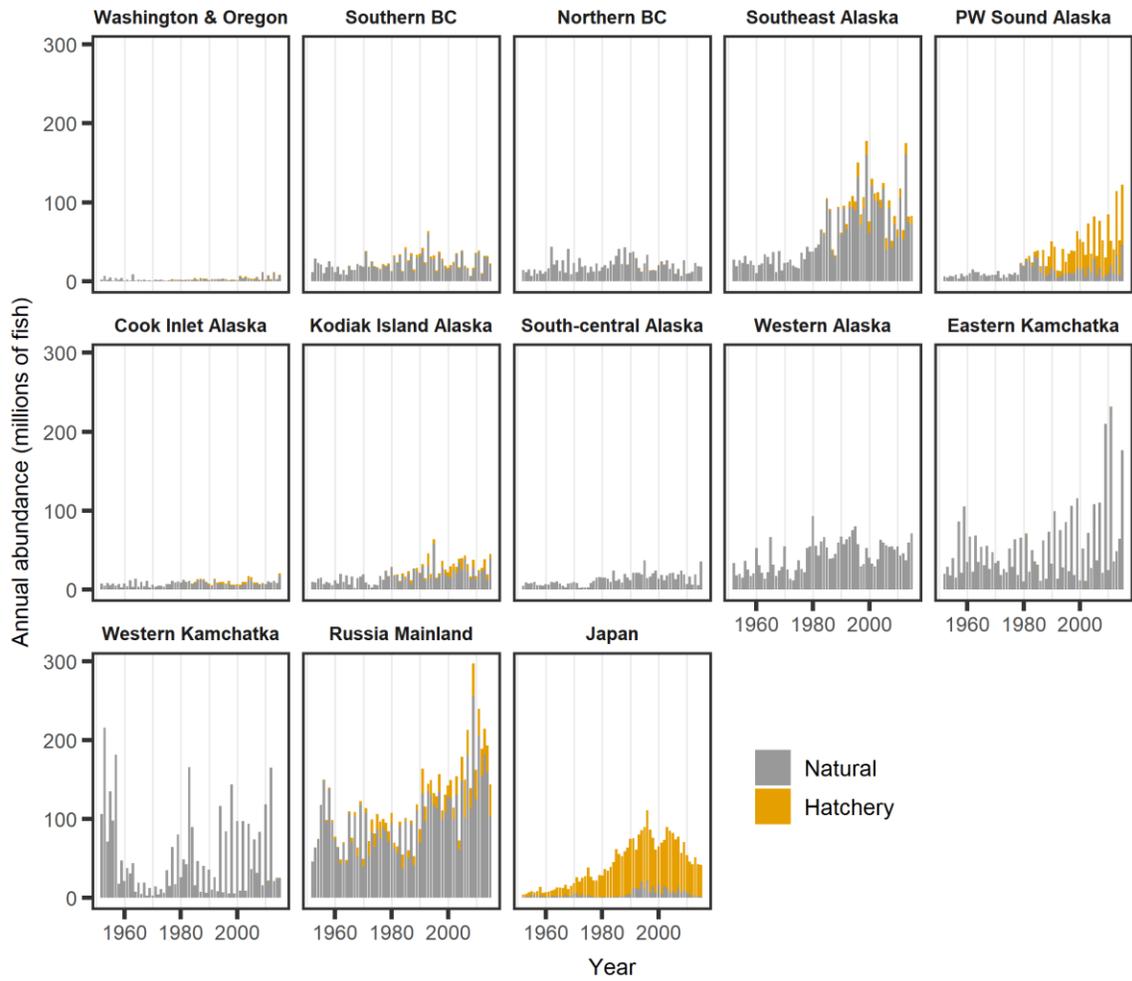


Figure C10. Annual abundance between 1952 to 2015 of natural-origin (grey) and hatchery-origin (orange) salmon in local communities throughout the North Pacific.

Data are from Ruggerone and Irvine (2018).

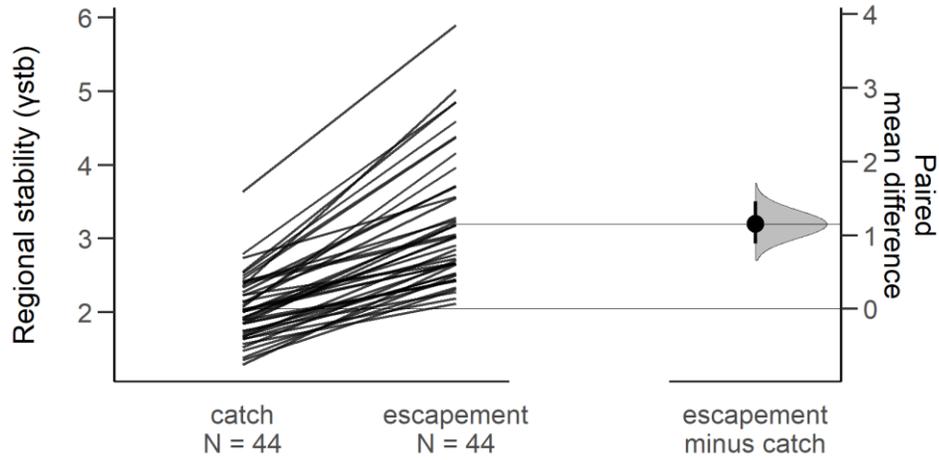


Figure C11. Bootstrapped mean difference between the regional stability of annual salmon catch and that of salmon escapement in Northern British Columbia, paired by year (i.e., 10-year rolling window).

The 95% confidence interval does not cross the zero-difference line at the bottom of the panels' right side, indicating that the stability of escapement is significantly higher than that of catch.

Appendix D.

Salmon in Clear and Present Danger⁴

During the summer of 2019, record heat events caused thousands of adult Pacific salmon to die of heat stress while migrating to their spawning grounds throughout Alaska (1). These die-offs come as many rivers in western North America have started transitioning to a regime of lower summer flows and higher temperatures during the salmon migration and spawning season (2). This transition, driven by warmer air temperatures and reduced snow and ice, will increase in severity and pervasiveness during the next few decades (3). Marine heat waves are also increasing in frequency (4), causing poor marine survival of many salmon populations (5). The threat of climate change is here and demands action now.

Curtailling the rise of global air temperatures by reducing carbon emissions is vital for salmon conservation. Aside from emission reductions, we urge federal governments to prioritize climate change resilience in fisheries and environmental policy. This means protecting evolutionarily unique populations of salmon as well as diverse landscapes that naturally vary in hydrology (6, 7). It also means that the remaining hotspots of salmon productivity must be safeguarded against degradation.

One such region is the watersheds of Bristol Bay, Alaska, where the controversial Pebble Mine has been proposed (8). Bristol Bay supports the most abundant sockeye salmon populations in the world, with a wild salmon fishery that provides 12,000 jobs and generates \$1.5 billion annually (9) while providing food security for rural Alaskans. However, the U.S. Environmental Protection Agency recently overturned its previous conclusion that the mine would cause irreparable harm to this ecosystem (10); barring congressional intervention, the final permitting decision is expected from the U.S. Army Corps of Engineers in early 2020.

Habitat destruction has driven the collapse of wild salmon fisheries from California to Washington, where 93% of wild salmon abundance has been lost (11).

⁴ A version of this appendix appears as Muñoz, N.J., Reynolds, J.D., Moore, J.W., Neff, B.D., 2019. Salmon in clear and present danger. *Science* 366, 582.

Intact habitat confers resilience to environmental change; the Pebble Mine would erode resilience when it is needed most. The warming caused by global carbon emissions will continue to kill salmon (12) and will kill the jobs and food security that salmon provide if our governments do not give them a fighting chance.

Supplementary References for Appendix D

1. M. C. Martin, "Warm waters across Alaska cause salmon die-offs" *Juneau Empire* (2019); www.juneauempire.com/news/warm-waters-across-alaska-cause-salmon-die-offs/.
2. P. W. Mote, A. F. Hamlet, M. P. Clark, D. P. Lettenmaier, *Bull. Amer. Meteor. Soc.* 86, 39 (2005).
3. S. U. Islam, S. J. Déry, A. T. Werner, *J. Hydrometeorol.* 18, 473 (2017).
4. T. L. Frölicher, C. Laufkötter, *Nat. Commun.* 9, 650 (2018).
5. S. T. Lindley et al., "What caused the Sacramento River fall Chinook stock collapse?" (Tech. Memo NMFS-SWFSC-447, National Oceanic and Atmospheric Administration, 2009).
6. K. I. Ashley, in *Salmon 2100: The Future of Wild Pacific Salmon*, R. T. Lackey, D. H. Lach, S. L. Duncan, Eds. (AFS, 2006), chap. 4.
7. D. E. Schindler et al., *Fisheries* 33, 502 (2008).
8. U.S. Army Corps of Engineers (USACE), "Pebble Project EIS" (USACE, 2019); www.pebbleprojecteis.com/.
9. G. Knapp, M. Guettabi, S. Goldsmith, "The economic importance of the Bristol Bay salmon industry" (Institute of Social and Economic Research, 2013; <https://iseralaska.org/publications/?id=1410>).
10. S. Bronstein, C. Devine, D. Griffin, A. Hackett, "EPA dropped salmon protection after Trump met with Alaska governor" *CNN* (2019); www.cnn.com/2019/08/09/us/epa-alaska-pebble-mine-salmon-invs/index.html.
11. T. Gresh, J. Lichatowish, P. Schoonmaker, *Fisheries* 25, 15 (2000).
12. N. J. Muñoz, A. P. Farrell, J. W. Heath, B. D. Neff, *Nat. Clim. Change* 5, 163 (2015).

Appendix E.

Upholding Science-Based Risk Assessment Under a Weakened *Endangered Species Act*⁵

Background

Since the United States enacted its first species-at-risk legislation in 1966, many jurisdictions have similarly adopted legislation aimed at conserving biodiversity through the identification of species at risk of extinction, the protection of these species from harm, and the establishment of recovery programs (Ray and Ginsberg 1999; Waples et al. 2013). Although these statutes have successfully thwarted extinction for hundreds of species, they have also failed to recover many at-risk species (Schwartz 2008; Mooers et al. 2010; Evans et al. 2016). As global extinction rates approach those observed during the five mass extinction events in Earth’s history (Barnosky et al. 2011), robust, well-implemented conservation laws are critically needed to slow the loss of biodiversity (Westwood et al. 2019; Leclère et al. 2020).

In Canada, the federal species-at-risk legislation (Species at Risk Act 2002, S.C. 2002, c. 29) generally applies only to land under federal jurisdiction and thus relies on provincial or territorial governments to adopt and implement their own legislation. Ontario’s Endangered Species Act (henceforth “OESA” or “the Act”) passed in 2007 and has been considered the strongest species-at-risk legislation among the provinces and territories with such legislation (Nixon et al. 2012; Olive and Penton 2018). The implementation of OESA begins with the Committee on the Status of Species at Risk in Ontario (COSSARO), which is an independent panel of scientists and other experts that is responsible for developing criteria for assessing the status of species and using these criteria to classify species as endangered, threatened, special concern, or not at risk. The assessment criteria used by COSSARO largely follow those used by COSSARO’s federal counterpart (COSEWIC) and consider risk factors such as declining abundance, declining geographic range, small population size, and extinction risk estimates based

⁵ A version of this appendix appears as Muñoz, N.J.*, Obrist, D.S.*, 2020. Upholding science-based risk assessment under a weakened Endangered Species Act. FACETS 5, 980–988.*co-first authors

on life history traits (COSSARO 2014a). After COSSARO classifies a species, the Minister of Environment, Conservation, and Parks either accepts the classification (thereby “listing” the species), rejects the classification (if listing would entail significant social or economic impacts), or requires a re-classification from COSSARO (if of the opinion that the classification is inappropriate). After a classification is accepted, endangered and threatened species (and their habitat) receive legal protection from harm, and programs aimed at recovering at-risk species are developed.

In July 2019, the government of Ontario made five fundamental changes to OESA with the stated aim of improving species protections, streamlining the Act’s implementation, and maintaining support for economic development (MECP 2019). These five changes involve (i) requiring risk classifications to reflect the status of species throughout their geographic range inside and outside of Ontario (instead of focusing on status inside of Ontario), (ii) opening up COSSARO membership to individuals with “community knowledge” (instead of membership being limited to scientists and traditional knowledge holders), (iii) increasing the timelines between classification, listing, and protection, (iv) allowing permit holders to engage in activities harmful to listed species across large geographic areas via “landscape agreements”, and (v) allowing parties to engage in harmful activities and avoid conservation action by paying into a fund (Ogden 2019; Bergman et al. 2020).

In a review of these amendments, Bergman et al. (2020) argue that they collectively weaken the ability of OESA to conserve biodiversity and recommend that they should be reversed or modified in the future. Although we agree with these conclusions, there remain interpretations of the amended legislation that must be made imminently by those who implement OESA (e.g. COSSARO). These interpretations will determine some of the consequences of the amendments for species at risk in Ontario and will occur far sooner than any legislative changes to OESA. As biologists, we describe here possible interpretations of the clauses relevant to change (i) and discuss their implications for species at risk. We focus on change (i) because it concerns which species are to be listed under OESA, and listing determinations are the step “from which all other consequences” of species-at-risk legislation come (Bean and Rowland 1997).

Interpreting ambiguity

When assessing the status of a species, COSSARO must now consider “[...] the condition of the species across the broader biologically relevant geographic range in which it exists both inside and outside of Ontario” (Endangered Species Act 2007, S.O. 2007, c. 6, s. 5 (4)). If consideration of a species’ condition both inside and outside of Ontario would result in a lower-risk classification than if only condition inside of Ontario was considered, OESA now requires that the classification must reflect the lower level of risk that the species faces across its “biologically relevant” range (Endangered Species Act 2007, S.O. 2007, c. 6, s. 5 (5)).

For these clauses to be implemented by COSSARO, ambiguities in the amended language will require interpretation. What makes a given part of a species’ geographic range “biologically relevant”? To what or to whom is it relevant? How does one evaluate the “condition” of a species? Guiding any interpretation is the fact that COSSARO is mandated in the Act to carry out status classifications using the best available science. Indeed, one of the purposes of OESA is to “identify species at risk based on the best available scientific information” (Endangered Species Act 2007, S.O. 2007, c. 6, s. 1). The purpose of OESA was not amended in 2019, meaning COSSARO must translate the new language in the Act into assessment criteria while ensuring that status assessments remain scientifically derived.

If “biologically relevant geographic range” is interpreted as the range that is relevant to the entire species, a simple approach would be to consider the entire geographic range of the species. However, this approach is problematic for wide-ranging species. For example, the gypsy cuckoo bumble bee (*Bombus bohemicus*) is distributed throughout the northern hemisphere and is stable in Europe but has sharply declined in North America (COSSARO 2014b). On what scientific grounds could it be argued that its status in Europe is “biologically relevant” to its status in North America? A different approach would be to borrow from interpretations of the U.S. Endangered Species Act. There, the status of a species across a “significant portion of its range” is considered in status assessments. After being the subject of much controversy and litigation (reviewed in Wilhere 2016), this phrase has been defined as the range without which the entire species would become endangered or threatened (FWS and NMFS 2014). Robust quantification of such a “significant portion” is highly limited by data availability, requires

substantial assumptions, and is more difficult for species with complex life histories (Earl et al. 2017).

Instead of considering a range that is relevant to the entire species, one could argue that the considered range should be “biologically relevant” to the species’ subpopulations in Ontario. In this case, the relevant range outside of Ontario would be that to which Ontario subpopulations are biologically connected in the form of migration and metapopulation dynamics. Such connectivity to extra-regional subpopulations is already considered in COSSARO status assessments to evaluate the potential for rescue effects (i.e. the mitigation of local extinction risk due to the immigration of gametes or individuals into Ontario). If there is evidence for rescue effects, the species’ status classification is downgraded by one category. For example, the gray fox (*Urocyon cinereoargenteus*) meets the COSSARO criteria for endangered due to its population size in Ontario being fewer than 110 mature individuals; however, its status was downgraded to threatened because there is immigration of individuals from adjacent U.S. jurisdictions (COSSARO 2016).

Another interpretation that must be made is the term “condition”. Condition outside of Ontario could be described by considering whether extra-regional subpopulations are stable, increasing, or decreasing and whether there are any significant threats facing these subpopulations. Such information is already used in COSSARO status assessments. Specifically, condition outside of Ontario is described using the rankings provided by the non-profit organization NatureServe (www.natureserve.org). These rankings convey the extinction risk of a species at global, national, and subnational (i.e. state, provincial) levels and are derived from shared, standardized methods. When these rankings are available, they are used to inform the potential for rescue effects. For example, the gray fox is ranked as “apparently secure” or “secure” (i.e. fairly low or very low risk of extinction) in the U.S. states from which individuals migrate to Ontario (Table E1), causing COSSARO to downgrade the status of gray fox from endangered to threatened (COSSARO 2016).

As described above, the potential for rescue effects is currently used by COSSARO to downgrade risk categories, and this potential is evaluated by considering the extent of immigration into Ontario subpopulations as well as the status of source populations. If “biologically relevant geographic range” is interpreted as the range to

which Ontario subpopulations are biologically connected, the criteria for evaluating rescue effects sufficiently encapsulate the language in the amendment. If, instead, this phrase is interpreted as the range that is relevant to the entire species, intra-regional status would often be devalued in favour of extra-regional status for species that have a geographic range outside of Ontario.

Table E1. NatureServe conservation ranks of the gray fox (*Urocyon cinereoargenteus*), including ranks in Ontario and in adjacent U.S. jurisdictions (from COSSARO 2016).

Jurisdiction	Level	Rank
Canada	National	1 (critically imperiled)
Ontario	Subnational	1 (critically imperiled)
United States	National	5 (secure)
Michigan	Subnational	4 (apparently secure)
Minnesota	Subnational	NR (not ranked)
New York	Subnational	5 (secure)
Ohio	Subnational	NR (not ranked)
Pennsylvania	Subnational	5 (secure)

Implications for species at risk

If risk classifications are determined more by extra-regional status than by intra-regional status, many species could be arbitrarily precluded from listing due to the biogeography of Ontario. Southern Ontario represents the northern range limit for a myriad of species distributed throughout eastern North America (Ricketts et al. 1999), particularly those native to the Eastern Temperate Forest ecoregion (henceforth ETFE), which extends from southern Canada to Florida and from the Atlantic coast to Texas (CEC 1997; Figure E1). Populations living at the periphery of their species' geographic range are often less abundant than those at the core of their range (Brown et al. 1995), meaning many species that are native to the ETFE may be common outside of Ontario relative to inside. For example, the spotted turtle (*Clemmys guttata*; Figure E2a) has a geographic range that typifies that of many species from the ETFE and is locally common at the core of its range in eastern U.S. but is endangered in Ontario

(COSSARO 2015; NatureServe 2016; Figure E2b). This pattern is pervasive: of the 152 species listed as endangered or threatened under OESA, 80% of species ($n = 121$) reach their northern range limit in Ontario and have a broader geographic range that spans multiple other jurisdictions in eastern United States.

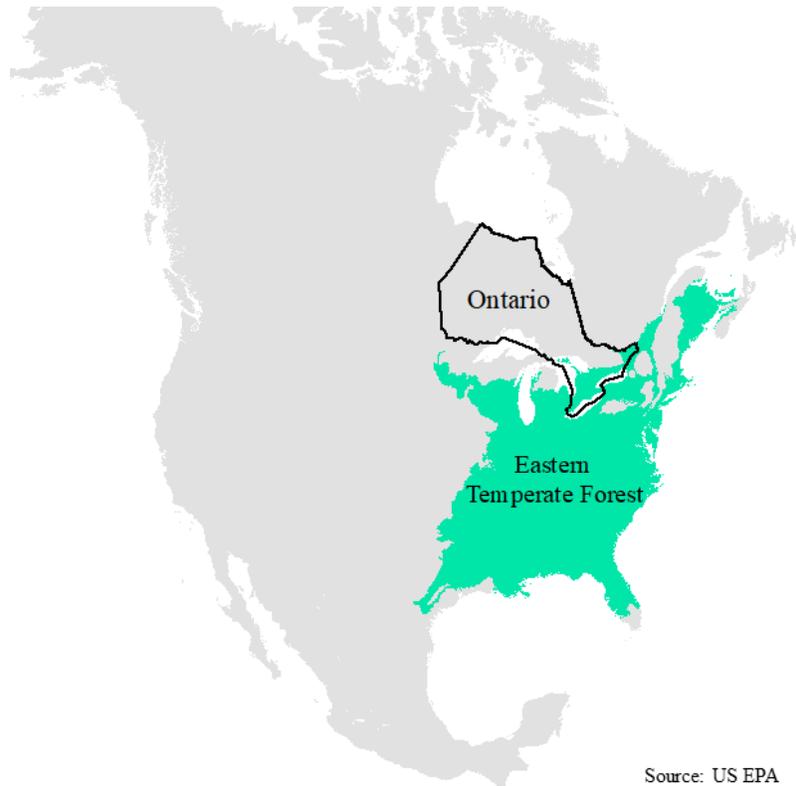


Figure E1. Map of North America showing the boundaries of the Eastern Temperate Forest ecoregion (CEC 1997) and the province of Ontario, Canada

The portion of southern Ontario that overlaps with the ETFE is the most densely populated region in Canada. Upwards of 88% of habitat here has been lost to agriculture or urban development (Kerr and Deguise 2004), and this habitat loss has caused this region to have one of the highest densities of species at risk in Canada (Kerr and Cihlar 2004; Cristine et al. 2017). Removing or failing to provide protection for species based on extra-regional status would leave many species from the ETFE unprotected in a region where recovery potential is already limited by extensive habitat loss (Kerr and Deguise 2004). Thus, such a policy would likely lead to the extirpation (i.e. local extinction) of many ETFE species from Ontario.

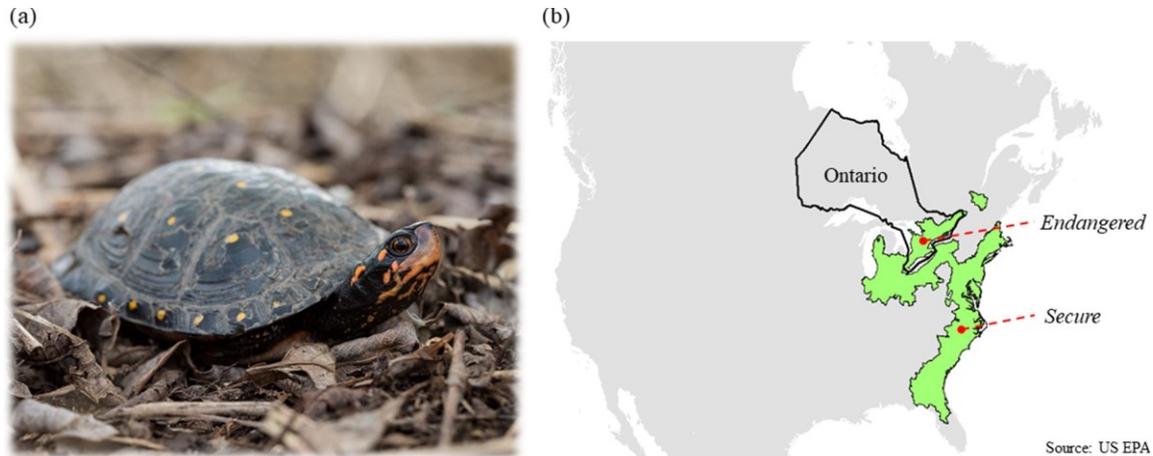


Figure E2. (a) The spotted turtle (*Clemmys guttata*) is among the species that could be left unprotected in Ontario due to its biogeography. (b) Map of North America showing the geographic range of the spotted turtle (highlighted in green) and the boundaries of Ontario, Canada.

The spotted turtle is classified as endangered in Ontario and as secure in the core of its range (COSSARO 2015; NatureServe 2016). Photo by Patrick Randall.

Populations at the periphery of a species' geographic range are key to the overall survival of the species for several reasons (Steen and Barrett 2015). Firstly, species often persist at the edges of their historical ranges following human-induced range contraction (Channell and Lomolino 2000; Calkins et al. 2012). Across the eastern U.S., land-use demands have caused a net loss of forest habitat in recent years (Drummond and Loveland 2010), increasing the importance of peripheral habitat such as in southern Ontario. Secondly, peripheral populations are on the front lines of the poleward range expansion being driven by climate change (Sunday et al. 2012). Indeed, shifting northward in tandem with suitable climatic conditions has already been documented for species at risk in Ontario (e.g. Melles et al. 2011). Lastly, peripheral populations are often genetically distinct from their core counterparts. For example, the Ontario population of the branched bartonia (*Bartonia paniculata* subsp. *paniculata*) – listed as threatened in Ontario – has high genetic distinctiveness from core populations in the U.S. (Ciotir et al. 2013). The conservation of genetically-distinct, leading-edge populations is vital for facilitating persistence under anthropogenic stressors such as climate change (Gibson et al. 2009); allowing the extirpation of species from Ontario would therefore directly increase the global extinction risk of affected species.

Conclusion

There is overwhelming scientific evidence indicating that devaluing intra-regional status in favour of extra-regional status would undermine OESA's goal of biological conservation. COSSARO's mandate to identify species at risk based on the best available science should compel COSSARO to ensure that the implementation of the new clauses in OESA does not lead to the de facto preclusion of peripheral populations from listing. To that end, "biologically relevant geographic range" should be interpreted as the range that is relevant to species' subpopulations in Ontario. This interpretation would avoid the scientific issues inherent in considering a range that is relevant to the entire species (e.g. Earl et al. 2017) while recognizing that extirpation from Ontario can have global consequences for many species. This interpretation could also avoid any litigation that might arise from scientifically-flawed interpretations of this phrase, as occurred with a similar phrase in the U.S. Endangered Species Act (Wilhere 2016). Indeed, legal experts should be consulted to inform the validity of possible interpretations of the new clauses in OESA.

Species-at-risk legislation is an imperfect tool that can be regarded as the "last line of defence" (ECO 2013) for species faced with extinction. Ontario has an important role in North American conservation given its biogeography and its 1.08 million km² of land and water; a weakening of Ontario's species-at-risk legislation is a weakening of region-wide conservation prospects. Although we recognize that fulfilling commitments to biological conservation while minimizing impediments to economic development is a daunting task for any government, amending species-at-risk legislation such that it tacitly permits extirpation is egregiously regressive. We hope that this editorial helps COSSARO uphold the integrity of evidence-based risk assessment in Ontario at a time when effective conservation is needed most.

Supplementary References for Appendix E

Barnosky AD, Matzke N, Tomiva S, Wogan GOU, Swartz B, Quental TB, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336): 51–57. DOI: 10.1038/nature09678

Bean MJ, and Rowland MJ. 1997. *The evolution of national wildlife law*, 3rd ed. Praeger, Connecticut.

- Bergman JN, Binleya AD, Murphy RE, Proctor CA, Nguyen TT, Urness ES, et al. 2020. How to rescue Ontario's Endangered Species Act: a biologist's perspective. *FACETS*, 5: 423–431. DOI: 10.1139/facets-2019-0050
- Brown JH, Mehlman DW, and Stevens GC. 1995. Spatial variation in abundance. *Ecology*, 76(7): 2028–2043. DOI: 10.2307/1941678
- Calkins MT, Beever EA, Boykin KG, Frey JK, and Andersen MC. 2012. Not-so splendid isolation: modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography*, 35(9): 780–791. DOI: 10.1111/j.1600-0587.2011.07227.x
- CEC (Commission for Environmental Cooperation). 1997. Ecological regions of North America: toward a common perspective [online]: Available from www3.cec.org/islandora/en/item/1701-ecological-regions-north-america-toward-common-perspective-en.pdf
- Channell R, and Lomolino MV. 2000. Dynamic biogeography and conservation of endangered species. *Nature*, 403(6765): 84–86. DOI: 10.1038/47487
- Ciotir C, Yesson C, and Freeland J. 2013. The evolutionary history and conservation value of disjunct *Bartonia paniculata* subsp. *paniculata* (branched bartonia) populations in Canada. *Botany*, 91(9): 605–613. DOI: 10.1139/cjb-2013-0063
- Coristine LE, Jacob AL, Schuster R, Otto SP, Baron NE, Bennett NJ, et al. 2018. Informing Canada's commitment to biodiversity conservation: a science-based framework to help guide protected areas designation through Target 1 and beyond. *FACETS*, 3: 531–562. doi:10.1139/facets-2017-0102
- COSSARO. 2014a. Categories and criteria for status assessment used by the Committee on the Status of Species at Risk in Ontario (COSSARO) [online]: Available from cossaroagency.ca/wp-content/uploads/2017/06/Accessible_COSSAROCriteria201403En.pdf
- COSSARO. 2014b. Ontario species at risk evaluation report for gypsy cuckoo bumble bee (*Bombus bohemicus*) [online]: Available from cossaroagency.ca/wp-content/uploads/2017/12/AccessibleCOSSAROEvalGypsyCuckooBumbleBee.pdf
- COSSARO. 2015. Ontario species at risk evaluation report for spotted turtle (*Clemmys guttata*) [online]: Available from cossaroagency.ca/wp-content/uploads/2017/06/Accessible_COSSARO-evaluation-Spotted-Turtle.pdf
- COSSARO. 2016. Ontario species at risk evaluation report for gray fox (*Urocyon cinereoargenteus*) [online]: Available from cossaroagency.ca/wp-content/uploads/2017/06/Accessible_Final_COSSAROEvaluation_Gray-Fox_June2016.pdf.

- Drummond MA, and Loveland TR. 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. *BioScience*, 60(4): 286–298. DOI: 10.1525/bio.2010.60.4.7
- Earl JE, Nicol S, Wiederholt R, Diffendorfer JE, Semmens D, Flockhart DTT, et al. 2017. Quantitative tools for implementing the new definition of significant portion of the range in the U.S. Endangered Species Act. *Conservation Biology*, 32(1): 35–49. DOI: 10.1111/cobi.12963
- ECO (Environmental Commissioner of Ontario). 2013. Laying siege to the last line of defence: a review of Ontario’s weakened protections for species at risk [online]: Available from docs.assets.eco.on.ca/reports/special-reports/2013/2013-Laying-Siege-to-ESA.pdf.
- Endangered Species Act. 2007. c. 9 [online]: Available from ontario.ca/laws/statute/07e06.
- Evans DM, Che-Castaldo JP, Crouse C, Davis FW, Epanchin-Niell R, Flather CH, et al. 2016. Species recovery in the United States: increasing the effectiveness of the Endangered Species Act. *Issues in Ecology*. Report No. 20. Ecological Society of America, Washington, D.C. 27 p. [online]: Available from fs.fed.us/rm/pubs_journals/2016/rmrs_2016_evans_d001.pdf.
- FWS and NMFS (U.S. Fish and Wildlife Service and National Marine Fisheries Service). 2014. Final policy on interpretation of the phrase “significant portion of its range” in the Endangered Species Act’s definitions of “endangered species” and “threatened species”. *Federal Register* 79: 37578–37612.
- Gibson SY, Van der Marel RC, and Starzomski BM. 2009. Climate change and conservation of leading-edge peripheral populations. *Conservation Biology*, 23(6): 1369–1373. DOI: 10.1111/j.1523-1739.2009.01375.x
- Kerr JT, and Cihlar J. 2004. Patterns and causes of species endangerment in Canada. *Ecological Applications*, 14(3): 743–753. DOI: 10.1890/02-5117
- Kerr JT, and Deguise I. 2004. Habitat loss and the limits to endangered species recovery. *Ecology Letters*, 7(12): 1163–1169. DOI: 10.1111/j.1461-0248.2004.00676.x
- Leclère D, Obersteiner M, Barrett M, Butchart SHM, Chaudhary A, De Palma A, et al. 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, DOI: 10.1038/s41586-020-2705-y
- MECP (Ministry of the Environment, Conservation, and Parks). 2019. 10th year review of Ontario’s Endangered Species Act: discussion paper. Environmental Registry of Ontario [online]: Available from ero.ontario.ca/notice/013-4143.

- Melles SJ, Fortin M-J, Lindsay K, and Badzinski D. 2011. Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Global Change Biology*, 17(1): 17–31. DOI: 10.1111/j.1365-2486.2010.02214.x
- Mooers AO, Doak DF, Findlay CS, Green DM, Grouios C, Manne LL, et al. 2010. Species, policy, and species at risk in Canada. *BioScience*, 60(10): 843–849. DOI: 10.1525/bio.2010.60.10.11
- NatureServe. 2016. Spotted turtle (*Clemmys guttata*) [online]: Available from explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.100580/Clemmys_guttata
- Nixon S, Page D, Pinkus S, Podolsky L, and Russell S. 2012. Failure to protect: grading Canada's species at risk laws. Ecojustice Canada, Vancouver, BC, Canada [online]: Available from ecojustice.ca/wp-content/uploads/2014/08/Failure-to-protect_Grading-Canadas-Species-at-Risk-Laws.pdf.
- Ogden LE. 2019. Ontario weakens species at risk act. *Frontiers in Ecology and the Environment*, 17(5): 248. DOI: 10.1002/fee.2051
- Olive A, and Penton G. 2018. Species at risk in Ontario: an examination of environmental non-governmental organizations. *The Canadian Geographer/Le Géographe canadien*, 62(4): 562–574. DOI: 10.1111/cag.12483
- Ray JC, and Ginsberg JR. 1999. Endangered species legislation beyond the borders of the United States. *Conservation Biology*, 13(5): 956–958. DOI: 10.1046/j.1523-1739.1999.099i1.x
- Ricketts TH, Dinerstein E, Olson DM, Loucks CJ, Eichbaum W, DellaSala DA, et al. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington DC.
- Schwartz MW. 2008. The performance of the Endangered Species Act. *Annual Review of Ecology, Evolution, and Systematics*, 39(1): 279–299. DOI: 10.1146/annurev.ecolsys.39.110707.173538
- Species at Risk Act. 2002. c. 29 [online]: Available from laws-lois.justice.gc.ca/eng/acts/S-15.3/index.html.
- Steen DA, and Barrett K. 2015. Should states in the USA value species at the edge of their geographic range? *Journal of Wildlife Management*, 79(6): 872–876. DOI: 10.1002/jwmg.897
- Sunday JM, Bates AE, and Dulvy NK. 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2(9): 686–690. DOI: 10.1038/nclimate1539

- Waples RS, Nammack M, Cochrane JF, and Hutchings JA. 2013. A tale of two acts: endangered species listing practices in Canada and the United States. *BioScience*, 63(9): 723–734. DOI: 10.1525/bio.2013.63.9.8
- Westwood AR, Otto SP, Mooers A, Darimont C, Hodges KE, Johnson C, et al. 2019. Protecting biodiversity in British Columbia: recommendations for developing species at risk legislation. *FACETS*, 4: 136–160. DOI: 10.1139/facets-2018-0042
- Wilhere GF. 2016. The role of scientists in statutory interpretation of the U.S. Endangered Species Act. *Conservation Biology*, 31(2): 252–260. DOI: 10.1111/cobi.12833