

Differential invasion success of salmonids in southern Chile: patterns and hypotheses

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Abstract Biological invasions create complex ecological and societal issues worldwide. Most of the knowledge about invasions comes only from successful invaders, but less is known about which processes determine the differential success of invasions. In this review, we develop a framework to identify the main dimensions driving the success and failure of invaders, including human influences, characteristics of the invader, and biotic interactions. We apply this framework by contrasting hypotheses and available evidence to explain variability in invasion success for 12 salmonids introduced to Chile. The success of *Onchorhynchus mykiss* and *Salmo trutta* seems to be

influenced by a context-specific combination of their phenotypic plasticity, low ecosystem resistance, and propagule pressure. These well-established invaders may limit the success of subsequently introduced salmonids, with the possible exception of *O. tshawytscha*, which has a short freshwater residency and limited spatial overlap with trout. Although propagule pressure is high for *O. kisutch* and *S. salar* due to their intensive use in aquaculture, their lack of success in Chile may be explained by environmental resistance, including earlier spawning times than in their native ranges, and interactions with previously established and resident Rainbow Trout. Other salmonids have also failed to establish, and they exhibit a suite of ecological traits, environmental resistance, and limited propagule pressure that are variably associated with their lack of success. Collectively, understanding

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how the various drivers of invasion success interact may explain the differential success of invaders and provide key guidance for managing both positive and negative outcomes associated with their presence.

Keywords Salmonids · Biological invasions · Propagule pressure · Environmental resistance · Biotic resistance · Non-native species · Chile

Introduction

Biological invasions represent one of the greatest threats to freshwater ecosystems, yet many of the most successful invaders were introduced intentionally because they have a high value to humans (García-Berthou 2007; Leprieur et al. 2009; Marr et al. 2010; Ehrenfeld 2010). Several lines of evidence have been developed to explain the success and failure of species introductions, including biotic (Elton 1958) and environmental resistance of invaded systems (Moyle and Light 1996; Ricciardi and Atkinson 2004), the frequency and intensity of propagule pressure (Lockwood et al. 2005; Colautti 2005), and the plasticity and evolutionary history of invaders (Collyer et al. 2007; Yonekura et al. 2007; Westley 2011). Due to the complex and dynamic forces operating simultaneously in the ‘invasion pathway’ (i.e., transport, establishment, and spread), generalizations and predictions about successful introductions are limited (García-Berthou 2007; Hayes and Barry 2008; Leprieur et al. 2009). Although much more is known about the ecological consequences or impacts of biological invasions, this knowledge often exists only after the introduced species have become well established (Crowl et al. 1992; Moyle and Light 1996; Sakai et al. 2001; Dunham et al. 2002) and the ecological impacts are difficult to reverse (Kaufman 1992;

Vander-Zanden et al. 1999; Simon and Townsend 2003; Vitule et al. 2009). Unsuccessful invaders are even more poorly known, as are the reasons underlying their failures to establish. Trade-offs between undesirable effects and perceived societal benefits add complexity to the understanding of biological invasions (Kaufman 1992; Dunham et al. 2004; Gozlan 2008; Arismendi and Nahuelhual 2007) and the ability to control invasions through management (Sakai et al. 2001; Dunham et al. 2002; Fausch et al. 2006).

In this review, we adapt and expand a conceptual framework for understanding biological invasions that considers dimensions related to the human influence, the invader itself, and biotic interactions (e.g., Sakai et al. 2001; Heger and Trepl 2003; García-Berthou 2007; Hayes and Barry 2008; Fig. 1). We apply this framework to evaluate invasions of Pacific salmon and trout (*Oncorhynchus* spp.), Atlantic salmon and trout (*Salmo* spp.), and char (*Salvelinus* spp.) in southern Chile in an attempt to understand their markedly different rates of invasion success. Salmonid introductions represent an ideal case-study to illustrate biological invasions in aquatic ecosystems because trout and salmon (hereafter salmonids) rank among the most widely introduced fish species around the globe (MacCrimmon and Marshall 1968; MacCrimmon and Gots 1979; Casal 2006; Crawford and Muir 2008). In their native distributions in the Northern Hemisphere, salmonid introductions have been motivated by conservation issues, restoration concerns, and their societal value as a fishery resource (i.e., subsistence, commercial, and recreational purposes; Crawford 2001; Dunham et al. 2004; Fausch et al. 2006). Outside of their native distributions, salmonids have been introduced since the late 1800s for sport-fishing purposes (Crawford and Muir 2008; Marr et al. 2010; García de Leaniz et al. 2010), and more recently for aquaculture (Basulto 2003; Thorstad et al. 2008; Jensen et al. 2010). Consequently, species such as Rainbow Trout (*Oncorhynchus mykiss* Walbaum, Salmonidae) and Brown Trout (*Salmo trutta* L., Salmonidae) have established self-sustaining populations around the globe, and proved to be highly successful invaders in many cases (MacCrimmon and Marshall 1968; Casal 2006; Crawford and Muir 2008). Other salmonids, including Pacific salmon (*O. tshawytscha*, *O. kisutch*, *O. keta*, *O. gorbuscha*, *O. nerka* Walbaum, Salmonidae; *O. masou* Brevoort Salmonidae), Atlantic Salmon (*S. salar* L., Salmonidae), and chars (e.g., *Salvelinus fontinalis* Mitchill Salmonidae and *Salvelinus namaycush*

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Fig. 1 Conceptual framework of biological invasion processes, including the three core dimensions (invader, biotic interactions, and human influences). *Arrows* represent links between main drivers

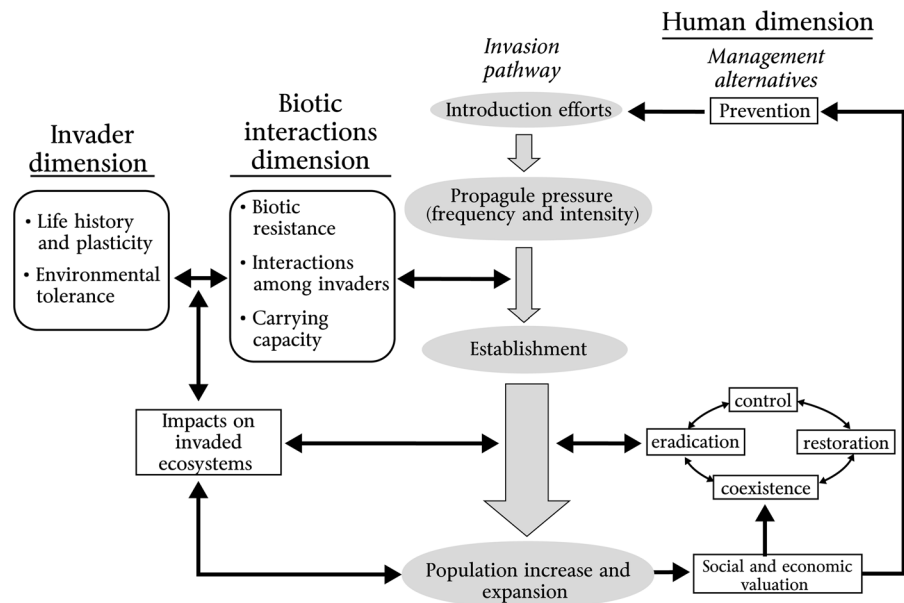


Table 1 Percentage of examined streams and lakes in Chile occupied by salmonids (number of sites sampled in final row)

Standard English name	Scientific name (Table 3 abbreviation)	Database		
		Authors' generated data ^a	Darwin Initiative ^b	Literature review ^c
Brown Trout	<i>Salmo trutta</i> (Str)	76	63(0)	87
Atlantic Salmon	<i>Salmo salar</i> (Ssa)	15	11(40)	34
Rainbow Trout	<i>Oncorhynchus mykiss</i> (Omy)	73	73(5)	86
Chinook Salmon	<i>Oncorhynchus tshawytscha</i> (Ots)	17	10(0)	37
Coho Salmon	<i>Oncorhynchus kisutch</i> (Oki)	11	8(0.5)	32
Cherry Salmon	<i>Oncorhynchus masou</i> (Oma)	0	0	1
Chum Salmon	<i>Oncorhynchus keta</i> (Oke)	0	0	0
Pink Salmon	<i>Oncorhynchus gorbuscha</i> (Ogo)	0	0	6
Sockeye Salmon	<i>Oncorhynchus nerka</i> (One)	0	0	0
Brook Trout	<i>Salvelinus fontinalis</i> (Sfo)	0	0	22
Lake Trout	<i>Salvelinus namaycush</i> (Sna)	0	0	4
Arctic Char	<i>Salvelinus alpinus</i> (Sal)	0	0	0
Number of sites examined		142	204	201

Database sources are indicated by each column. The percentage of sites with fish identified as escapees from aquaculture facilities are indicated in parentheses

^a Database originated by authors during the period 1996–2006 and published previously. Most of the sites have been repeatedly sampled including streams and lakes (37–44°S and 50–54°S; Soto et al. 2006, 2007; Arismendi 2009; Arismendi et al. 2009)

^b Darwin initiative: database from the UK DEFRA-funded Darwin Initiative during 2007–2011 (www.biodiversity.cl). Includes streams and lakes in southern Chile (38–46°S)

^c Literature review: database from intensive literature review (approximately 260 documents) throughout the entire country (18–55°S; Vargas unpublished data)

Walbaum Salmonidae) have shown mixed success (MacCrimmon and Gots 1979; Quinn and Unwin 1993; Cadwallader 1996; Pascual et al. 2002; Basulto 2003; Soto et al. 2006). Paradoxically, while enormous efforts are made to restore and expand salmonid populations in their native range in the Northern Hemisphere (see other studies in this special issue), the emphasis in research into invaded systems in the southern Hemisphere has been only recently directed toward minimizing negative impacts (Cadwallader 1996; Soto et al. 2006; McDowall 2006; Arismendi et al. 2009; García de Leaniz et al. 2010; Marr et al. 2010, 2013).

Salmonid invasion success in southern Chile varies widely (Table 1). Brown Trout, Rainbow Trout, and more recently, Chinook Salmon have become widely established throughout this region (Soto et al. 2006, 2007; Correa and Gross 2008; Arismendi et al. 2009; Young et al. 2010; Habit et al. 2012; Correa and Hendry 2012). In contrast, Coho Salmon, Atlantic Salmon, and other salmonids appear to have failed to establish self-sustaining populations or have had only limited success (Soto et al. 2001a, 2006; Basulto 2003). To evaluate these observations in more detail, we consider a series of hypotheses nested within a conceptual framework for predicting the success of invasions based on human influences, characteristics of the invader, and biotic interactions.

Framework for predicting the success of invasions

The framework we apply here (Fig. 1) is adapted and expanded from ideas first developed by Elton (1958) that were subsequently ordered into a structure of sequential steps that result in the establishment, population increase, and consequent range expansion of the invader (Moyle and Light 1996; Kolar and Lodge 2001; Sakai et al. 2001; Dunham et al. 2002). We argue that to predict future invasions, a better understanding is needed of the underlying processes influencing the success of species introductions, which we have laid out in this framework. This framework can be applied to any species in any system as a first step in trying to understand and ultimately predict successful invaders. We consider three main dimensions: (1) the influences of human activities, including propagule pressure and management alternatives; (2) the characteristics or traits of the invader, including

environmental requirements (based on the Grinnellian view of an ecological niche; Grinnell 1917); and (3) biotic interactions with native biota and other invaders, and carrying capacity (based on Eltonian and Hutchinsonian views of the ecological niche; Soberón and Nakamura 2009). Although these suites of processes are not strictly independent, we consider each dimension in turn to evaluate the evidence in support of alternative hypotheses explaining the differential success of salmonid invasions in southern Chile.

The human dimension

The largest dimension affecting initial invasion—introduction efforts—along with propagule pressure and management alternatives, are considered part of the human dimension of invasions. All of these factors are shaped by social and economic valuation and hence should always be considered as part of the invasion process (Fig. 1).

Introduction efforts

Introduction efforts refer to the capture, transportation, and subsequent release of the invader in the receiving ecosystem (Kolar and Lodge 2001, 2002; Dunham et al. 2002; Moyle and Marchetti 2006). Historically, these influences have been considered the main drivers of invasions, although additional influences (see invader dimension) have been more recently recognized.

Salmonids in Chile

In Chile, as well as in other Mediterranean-climate regions, understanding fish invasions requires an understanding of human values and interests (Marr et al. 2010, 2013). The history of salmonids in Chile may be separated into three time periods, with recreational fisheries, commercial fisheries, and aquaculture being the main motivations for salmonid introductions (Golusda 1907; Basulto 2003). Basulto (2003) compiled the most complete record of attempts to introduce salmonids to Chile, with information by species, origin in the Northern Hemisphere, and release location (Supplementary material 1). The first attempts to introduce salmonids in Chile for

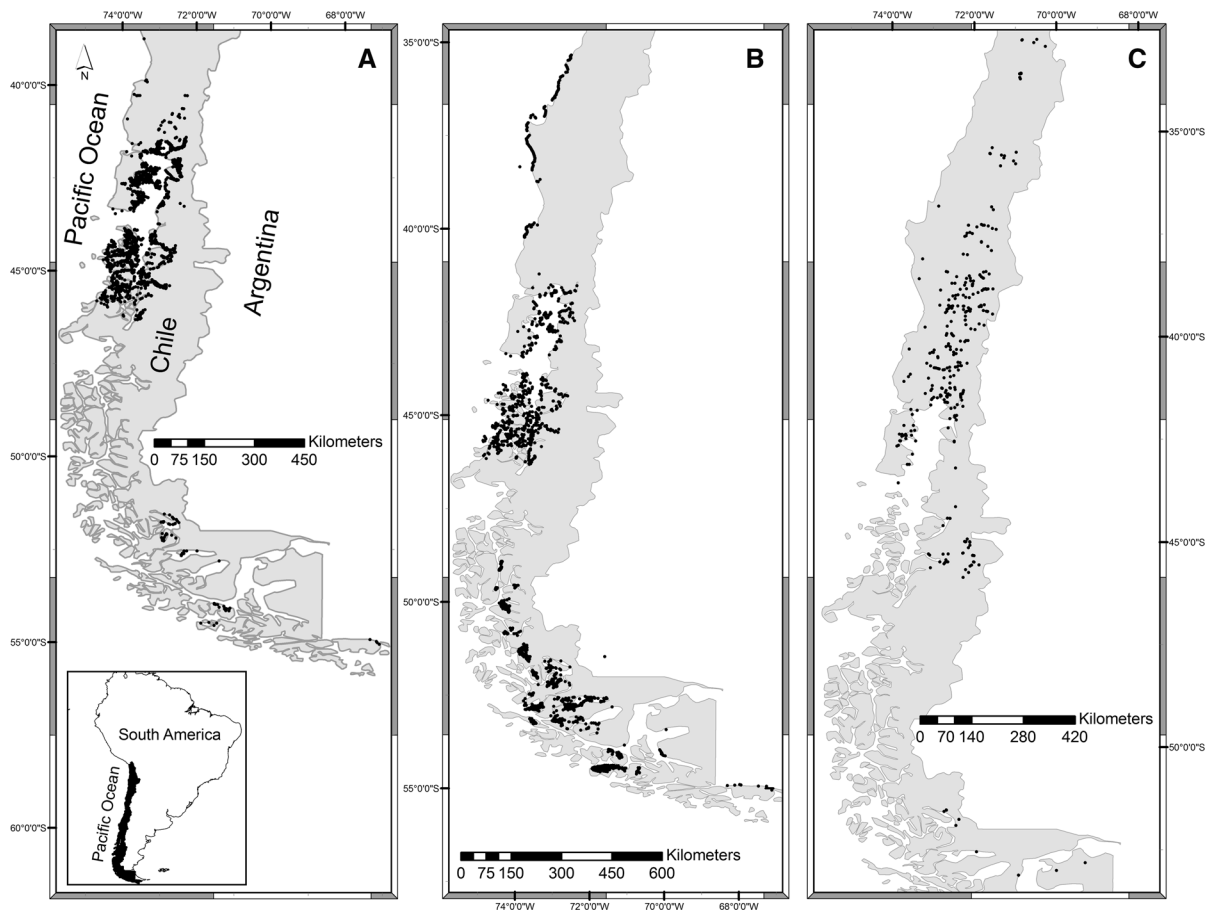


Fig. 2 Location of salmonid aquaculture facilities in Chile up to April 2012. The map includes **a** existing facilities ($N = 1,311$) and **b** pending applications in saltwater ($N = 1,776$), and

c existing facilities in freshwater ($N = 338$). Source SERNAP-ESCA and SUBPESCA unpublished information

recreational fishing purposes occurred from 1890 to 1930 (by transplanting eggs of mainly Brown Trout, Rainbow Trout, Atlantic Salmon and Chinook Salmon). Subsequent introductions occurred during 1960–1980, motivated by the increasing popularity of recreational fisheries (Rainbow and Brown Trout), and the introductions of new Pacific salmon species, driven by the expansion of the salmon canning industry from the Northern Hemisphere. During this second period, advances in transportation, improved technology, and human expertise gained from earlier introductions resulted in an increase in the magnitude of salmonid releases. The most recent period (1980 to present) has been marked by the promotion of a free-market economy in Chile that allowed for explosive development of the aquaculture industry, beginning in the 1970s. The salmonid aquaculture industry makes

both extensive and intensive use of lakes and estuarine areas for the farming of Atlantic Salmon, Coho Salmon and Rainbow Trout (Fig. 2). As the fish are farmed in open-net cages, escapes are common and likely inevitable (Soto et al. 2001a; Arismendi et al. 2009; Sepúlveda et al. 2013). Moreover, stocking practices for Brown and Rainbow Trout to maintain and promote their recreational fisheries have occurred from the 1980s to present (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010).

Propagule pressure

Propagule pressure is defined as the frequency and intensity of releases and the associated likelihood of establishment and spread (Lockwood et al. 2005). Propagule pressure has received much attention

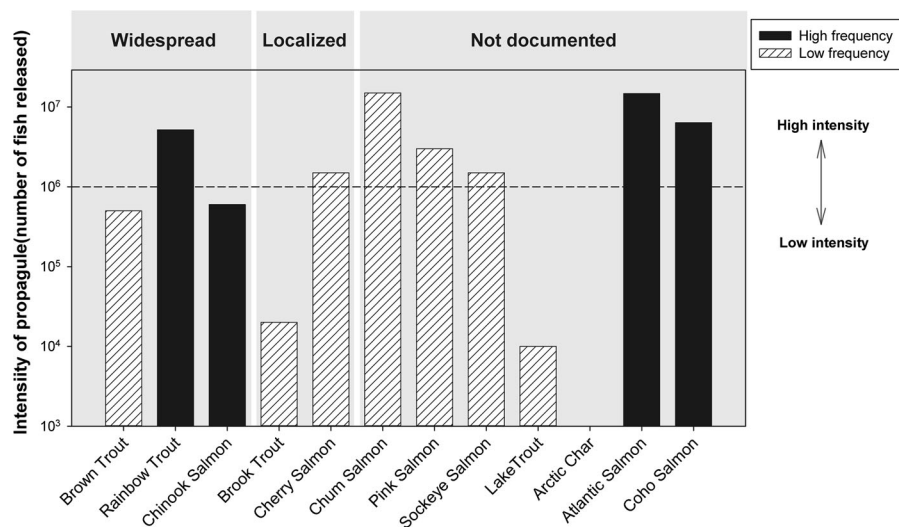


Fig. 3 Hypothesized propagule pressure (frequency and intensity) for the invasion of salmonids in Chile. Values were estimated based on historical information of stocking for recreational purposes (Supplementary material 1) and aquaculture escapees. For aquaculture escapees we assumed an escape of 0.19 % for salmon and 0.40 % for trout from the cumulative production between 1994 and 2011, with an individual fish weighing 3 kg

(Jensen et al. 2010). The frequency of propagule releases from aquaculture escapees is likely under represented because it has been a continuous process occurring over time beginning in the 1980s (Supplementary material 2). The success of each invader is referred to as “widespread”, “localized”, and “not documented” (definitions of these terms are provided in Table 2)

recently, and is seen as one of the fundamental predictors of establishment success (Wonham et al. 2005; Colautti 2005; Roman and Darling 2007; Hayes and Barry 2008).

Salmonids in Chile

As with nearly all introductions, the ability to comprehensively account for absolute numbers of individuals is limited, but examination of relative patterns is instructive. Propagule pressure has differed among salmonids over time, measured either as the scale of intentional releases (Basulto 2003) or as number of escapees from aquaculture facilities (Soto et al. 2001a; Arismendi et al. 2009; Sepúlveda et al. 2013), contributing to different degrees of success for each species. Successful establishments (Table 1; Fig. 3) have been confirmed for widespread and localized invasions having: (1) low frequency and low intensity (Brown Trout, and more locally Brook Trout, *S. fontinalis*); (2) high frequency and low intensity (Chinook Salmon); (3) high frequency and high intensity (Rainbow Trout); or (4) low frequency and high intensity (Cherry Salmon *O. masou*). Introduction failures have been characterized by propagule pressures of low frequency and low intensity (Lake

Trout, *S. namaycush*); low frequency and high intensity (other Pacific salmon species including Chum Salmon *O. keta*, Pink Salmon *O. gorbuscha*, and Sockeye Salmon *O. nerka*); and high frequency and high intensity (Atlantic Salmon and Coho Salmon). However, a time lag in the potential establishment of these unsuccessful salmonids remains unknown, as does the role of domestication (intentional releases of naturalized fish versus fish farm escapees) in impeding the likelihood of establishment. For example, domesticated fish that escape from aquaculture facilities may be less likely to establish than those deliberately released for stocking purposes into habitats potentially more suitable for establishment.

The answer to the question of how often intentional stocking efforts result in a successful establishment of a species is complicated by the fact that fish introductions may include illegal, amateur, and sophisticated/professional efforts. We used publicly available information on the frequency and intensity of stocking regimes to illustrate the difficulty of identifying a successful invader using only the propagule pressure as predictor (Fig. 3). For example, the survival at early stages before individuals were released to the new environment is important to consider, as is the density and spatial aggregation of stocking efforts. Detailed

information for each release event is scarce, however, and in this review we do not attempt to exhaustively examine all of this information. Overall, comprehensive information on stocking efforts once local hatcheries developed capabilities to produce fish on their own is limited (i.e., without the need to import brood stocks). Stocking in transboundary watersheds shared with Argentina, where fish release programs have existed for more than a century (Macchi et al. 2008), may further complicate patterns. This is particularly relevant for both Brown and Rainbow Trout, as they are most often propagated in local hatcheries. We acknowledge that a more complete and up-to-date database containing information about introduction events would be useful. Toward this end, Correa and Gross (2008) compiled the history of Chinook Salmon introductions in Chile, and Sepúlveda et al. (2013) have assembled an updated account of salmonid escapes from aquaculture facilities. Propagule pressure also likely works in synergy with characteristics and factors related to both the invader and biotic interaction dimensions.

Management alternatives: prevention, control, eradication, restoration, and coexistence

Management alternatives include multiple options during different phases of the invasion process, and depend on the social and economic valuation at that stage of the process. Invader prevention is an anticipatory strategy aimed at preventing the introduction of non-natives, often through public education and awareness. This pre-emptive management strategy can occur only before a species has been introduced to a new area, and is aimed at blocking its arrival. Prevention is generally considered the most effective means of management because: (1) it is the only safe way to avoid impacts (García-Berthou 2007); (2) it is the only option available prior to invasion; and (3) it offers the opportunity to shift the costs of reducing impacts to industries that run the risk of unintentional introductions (Keller et al. 2011).

Other management alternatives can be considered after the invasion process has already begun. They include invader control, invader eradication, ecological restoration (Myers et al. 2000; Sakai et al. 2001), and co-existence (Dunham et al. 2002). Invader control encompasses managing invader abundances or distributions to desired levels in a particular area.

Invader eradication is the complete removal of an invader from a designated area, and restoration focuses on restoring habitat or environmental conditions to encourage the presence of native species. Coexistence involves managing native and non-native species so that they can both exist within a designated area. However, by the time these management alternatives are considered, the costs involved with implementing them are most often externalized, becoming a public responsibility rather than being paid for by the initial parties responsible for the species introductions. In general, many of these management alternatives often involve extensive efforts and high costs (Myers et al. 2000).

Salmonids in Chile

Eradication as a management alternative for biological invasions is not always possible, particularly when the invader provides major economic benefits (MacIsaac et al. 2001; Arismendi and Nahuelhual 2007; García de Leaniz et al. 2010), and thus alternative strategies can be considered for management. In Chile, direct control and eradication of salmonids is difficult due to the large cost and logistical difficulties of removing salmonids and the socio-economic importance of salmonid-based recreational (Arismendi and Nahuelhual 2007, Núñez and Niklitschek 2010) and artisanal (Soto et al. 2001a) fisheries, as well as that of the aquaculture industry (Fig. 2 and Supplementary material 2; Buschmann et al. 2006). Due to poor efforts at, and the ineffectiveness of, recapture approaches for aquaculture escapees, escape prevention has been suggested for incorporation into current and future policy and regulation (Sepúlveda et al. 2013). In addition, restoration and control efforts (by decreasing densities of free-living salmonids) have been suggested for invaded streams to enhance the performance of native fish into the future (Soto et al. 2006). Moreover, understanding the potential for coexistence between native fishes and introduced salmonids may help in designing effective management strategies that protect both native fishes and important economic activities provided by introduced salmonids in this region.

Coexistence may be facilitated by understanding more about the aquatic ecosystem that supports salmonids and native fishes, the ecological relationships among species, and the dynamics of both recreational and artisanal fisheries. For example, it

has been proposed that an increase in salmonid fishing pressure in areas where the protection of native fishes is a priority could help to alleviate predation by salmonids on native fishes (Soto et al. 2001a, 2006; Arismendi and Nahuelhual 2007; Correa et al. 2012). In such cases, managers could extend the recreational fishing season and capture quota for less desirable salmonid species and implement a catch-and-release fishery for the most desired fish species and sizes (Arismendi and Nahuelhual 2007). In some cases, salmonid escapees from aquaculture facilities may also provide resources to develop properly regulated artisanal fisheries at a local scale (see Soto et al. 2001a). While additional work is relevant to understand patterns and processes underlying the invasion by salmonids in southern Chile, more empirical data could improve management alternatives in areas where salmonids have negatively affected native fishes (see conservation status for native fishes in Campos et al. 1998; Habit et al. 2006).

Social and economic valuation

The management strategy for dealing with species introductions depends on the results from the societal valuation of the invasion impacts. Damage caused by invasive species amounts to several billions of dollars every year (Pimentel et al. 2001). In some cases, however, the control and eradication of invaders is not strictly desired, especially when society empathizes with them or when there are associated economic benefits to the species (Kaufman 1992; MacIsaac et al. 2001). This trade-off between positive and negative impacts of invasions is complex, but can be considered when adopting a suitable management strategy for introduced species (Van Wilgen 2012).

Salmonids in Chile

In addition to the economic benefits from aquaculture (Buschmann et al. 2006), salmonid introductions support local economies through recreational (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010) and artisanal fisheries (Soto et al. 2001a). Moreover, many people have begun to feel connected to salmonids because some species have been present in local rivers for over a century, and thus stories about them have been passed down for generations. Local economies surrounding lakes and streams have

benefited indirectly from both historical and current intentional and accidental salmonid introductions. In the Lakes District (40.3–43.2°S), where most of the salmonid farming production is concentrated (Fig. 2), rapid improvement in infrastructure and employment opportunities have occurred as a consequence of these operations. Simultaneously, recreational fisheries of southern Chile (Arismendi and Nahuelhual 2007; Núñez and Niklitschek 2010) have grown and regulations have been put in place to protect and stock both Brown and Rainbow Trout. Conversely, native fishes seem to have less social and monetary value, but greater ecological and evolutionary value (Campos et al. 1998; Soto and Arismendi 2005; Habit et al. 2006; García de Leaniz et al. 2010). Social and economic valuation of this trade-off between positive economic benefits and negative impacts on native ecosystems is fundamental to: (1) estimating the real societal value of salmonid introductions; (2) understanding the value of retaining ecosystem services provided by the native biodiversity of the aquatic systems; and (3) manage future fish invasions. As an example, these concepts might be useful for managing potential invasion of the Arctic Char (*Salvelinus alpinus* L.; Supplementary material 2).

The invader dimension

Characteristics of an invader can dramatically influence the success of invasions (Hayes and Barry 2008; Martin et al. 2009; Collyer et al. 2007; Yonekura et al. 2007; Westley 2011; Sol et al. 2012). This dimension includes traits linked to species demography, migratory life history, phenotypic plasticity, and tolerance of environmental conditions in receiving ecosystems that may limit invasion success (Fig. 1). Perhaps the simplest and most straightforward way to view invader characteristics is in terms of an ecological niche, as originally offered by Grinnell (1917). The Grinnellian niche is typically defined as the limits to the distribution of a species in nature imposed by environmental factors (habitat requirements) that are unaffected by intra- or interspecific interactions (Soberón and Nakamura 2009). This perspective assumes that niche requirements of the invader are unaffected by the invasion itself. It is possible, however, that a species may change via selection in response to an invasion (Facon et al. 2006; Sax et al. 2007) including the

degree to which niches are “conserved” in the face of an invasion, although the latter has proven difficult to demonstrate (Soberón and Nakamura 2009).

Life history and plasticity of the invader

Often the ability of the introduced species to tolerate the invaded ecosystem conditions depends on its plasticity (e.g., in life-history tactics; Sloat et al. 2014). In some cases, species-specific traits have been suggested as being more important than human-mediated dispersal in determining invasion success (Chizinski et al. 2006). In general, adaptation to novel conditions will depend on trait plasticity, degree of environmental mismatch, and standing levels of genetic variation, both neutral and adaptive (Roman and Darling 2007; Bell and Gonzalez 2009). While the role of adaptive (and thus functional) variation is key to explaining successful invasions (Keller and Taylor 2008; Lucek et al. 2010), the role of neutral variation has been more contentious (Roman and Darling 2007). Neutral variation, as measured using molecular markers, may be poorly correlated with adaptive variation (Lee 2002); also, small and bottlenecked populations of invaders that successfully colonize and spread beyond their points of introduction appear to be the exception rather than the rule (Dlugosch and Parker 2008; Roman and Darling 2007). Indeed, some invasive populations originate from multiple geographic sources and exhibit higher neutral variation than their native counterparts (Kolbe et al. 2004).

Salmonids in Chile

Brown and Rainbow Trout had become established in Chile before other salmonids were introduced (Basulto 2003; Gajardo and Laikre 2003). The general success of both Rainbow and Brown Trout has been associated with their high phenotypic plasticity (Table 2; Jonsson and Jonsson 2011; Westley et al. 2013a, b), and evidence from their invasions in Chile supports this explanation for their success. For example, the diverse migratory and reproductive life history exhibited by these two trout species includes documented cases of populations that are resident (Soto et al. 2006), adfluvial (Sakai and Espinos 1994; Arismendi et al. 2011b), and anadromous (Zama 1987; Pascual et al. 2001; O’Neal and Stanford 2011). In Chile, both

species have also been shown to be ecologically plastic with respect to feeding behavior (Arenas 1978; Zama 1987; Villalobos et al. 2003; Figueroa et al. 2010; Arismendi et al. 2012) and habitat use (Penaluna et al. 2009).

Although both Rainbow and Brown Trout have created self-sustaining populations in many regions of southern South America (Soto et al. 2006; Pascual et al. 2007), they have done so despite having limited genetic variability in the wild (Faundez et al. 1997; Gajardo 1997; Gajardo et al. 1998; Colihueque et al. 2003; Valiente et al. 2007, 2010). In the case of Rainbow Trout, large numbers of fish escape each year from aquaculture facilities (Sepúlveda et al. 2013), and these escapees interbreed with some existing naturalized populations, bringing in new genetic variants and potentially contributing to their establishment (Consuegra et al. 2011). Functional genetic diversity (but not neutral diversity) appears to decrease with time at liberty among Rainbow Trout escapees in Chile, suggesting that there is selection against farmed fish (Monzón-Argüello et al. 2013). Thus, although high genetic diversity may initially enhance fitness among Rainbow Trout escapees, adaptation to novel conditions may subsequently result in loss of functional diversity. Brown Trout, on the other hand, are not used for intensive aquaculture in Chile, and thus their variability comes only from earlier introductions for recreational fishery purposes.

Chinook Salmon from Chile and Argentina are composed of genetically diverse populations, possibly from multiple introductions and subsequent hybridization among these sources, which may have contributed to their rapid establishment (Astorga et al. 2008; Becker et al. 2007; Riva Rossi et al. 2012). More broadly, diverse life histories for naturalized Chinook Salmon in invaded ecosystems have been reported in Patagonia (Correa and Gross 2008; Di Prinzio and Pascual 2008) and previously in New Zealand (Quinn and Unwin 1993). These may include differences in age-related (stream- versus ocean-type juveniles; years spent at sea prior to maturity), size-related (length at age, weight at length, and fecundity at length), and behavioral traits such as spawn timing (Quinn et al. 2001). A genetic basis for these traits suggests that not only phenotypic plasticity, but rapid evolution that occurred in tens of generations, facilitated the spread of Chinook Salmon in New Zealand (Quinn et al. 2001; Kinnison et al. 2008, 2011).

Table 2 Overview of key traits of salmonids introduced to Chile

Standard English name	Freshwater residency	Potential lifespan	Iteroparity	Spawning	Egg burial depth (cm)	Thermal tolerance (UILT)	Established?
Brook Trout	Long	Long	Yes	Autumn	5	29.8 ^c	Localized
Brown Trout	Long	Long	Yes	Autumn	8	29.9 ^c	Widespread
Chinook Salmon	Variable	Moderate	No	Autumn	15	25.0	Widespread
Rainbow Trout	Long	Long	Yes	Spring	10	29.4 ^e	Widespread
Arctic Char	Long	Long	Yes	Autumn	?	21.5^c	Not documented
Lake Trout	Long	Long	Yes	Autumn	–	24.5	Not documented
Atlantic Salmon	Long	Moderate/long	Yes	Autumn/winter ^b	15	27.8 ^d	Not documented
Cherry Salmon	Variable	Moderate	Yes	Autumn	?	?	Localized
Sockeye Salmon	Variable	Short	No	Summer/autumn	10	24.8	Not documented
Coho Salmon	Short^a	Short	No	Autumn/winter ^b	15	25.0	Not documented
Chum Salmon	None	Short	No	Summer/autumn	15	23.8	Not documented
Pink Salmon	None	Short	No	Summer/autumn	15	23.9	Not documented

Freshwater residency is classified as “long” if a species typically spends at least 2 years in freshwater, “short” if freshwater residency is <2 years, or “none” if the species immediately migrates to sea. Potential lifespan is classified as “long” (>10 years), moderate (5–9 years), or short (<5 years). Iteroparity is classified as possible or not. The season of spawning is indicated, along with egg burial depths based on DeVries (1997). Egg burial depth also depends on female size (numbers are crude estimations). Temperature tolerances are expressed in terms of upper incipient lethal limits (UILT) and are taken from a review by McCullough (1999) unless otherwise noted. Trait values in bold face correspond to those only exhibited by species that failed to establish in Chile. Establishment is classified into three broad categories: widespread (established in many locations), localized (established only in one or a few locations), and not documented (indicating not established or established at a very low level at present)

^a Based on sites around 45° north latitude in North America

^b These species can spawn well into February (even March) in some populations of Norway and British Columbia respectively (Fleming 1998)

^c Baroudy and Elliott (1994)

^d Elliott (1991)

^e Lee and Rinne (1980)

Other salmonids, including Atlantic and Coho Salmon in southern Chile, have failed to establish, with no evidence of existing naturalized populations (Soto et al. 2006). To our knowledge, the only established populations of Atlantic Salmon in South America are in Argentina, and they are found only in lakes and rivers as resident (non-migratory) populations (MacCrimmon and Gots 1979; Stewart 1980; Pascual and Ciancio 2007). While there are no reports of Coho Salmon having established self-sustaining populations in South America, the source of their presence in some freshwater environments in Chile is unclear. Where they have

been reported informally, it is unclear whether they derive from escapes from local hatcheries or represent instances of local establishment. Is important to consider more detailed surveys, particularly in the southern part of the country, to clarify the origin of these individuals (Fig. 2). In general, early studies of farmed Atlantic and Coho Salmon in Chile report low genetic variability, a pattern also seen among escapees in the wild (Torres et al. 1996; Gajardo 1997; Winkler et al. 1999; Perez et al. 2001). It is possible that low genetic variability within these species may also limit phenotypic expression or plasticity, and thus invasion success.

Environmental tolerance

The ability of an introduced species to cope with a new environment comes from the innate tolerances of the invader itself. Environmental tolerance encompasses the abiotic properties of the invaded ecosystem that the invaders encounter once they are released (Moyle and Light 1996; Dunham et al. 2002; Hayes and Barry 2008). Among these properties are the characteristics of environmental regimes (e.g., climatic, physical, chemical), including the influence of extreme events. It has been hypothesized that environmental conditions may be more important in explaining the success of an invasion than the composition of biota already present in the invaded system (Moyle and Light 1996; Moyle and Marchetti 2006). For example, Rainbow Trout have been the most successful invader in areas with flood regimes similar to those of their native distribution, including winter floods and summer low flows, but they apparently fail in areas with harsh summer flooding (Fausch 2007).

Salmonids in Chile

Although the relationship between specific environmental conditions and particular salmonid species has not been studied in depth in Chile, it has been suggested that the environmental conditions of central and southern Chile were particularly suitable for salmonids and may explain the success of their invasions (Golusda 1907; Vila et al. 1978; Campos et al. 1986; Basulto 2003; Correa and Gross 2008; Correa and Hendry 2012; Habit et al. 2012). Most environmental conditions in these areas of Chile are similar to those present in the native range of salmonids in the Northern Hemisphere. For example, streamflow regimes (e.g., rain-dominated, snow-dominated, mixture of rain and snow, lake-regulated) appear to mimic regimes in the native range (Thomasson 1963; Niemeyer and Cereceda 1984; Campos 1984, 1985). Specifically, the hydrological regime of a significant portion of the streams in southern Chile is comparable to those of western North America where Rainbow Trout are naturally found, with winter flooding and summer low flows (Niemeyer and Cereceda 1984). In addition, the optimal thermal regime for Brown Trout growth (Elliott 1994) and that of other salmonids (e.g., Coho, Chinook and Atlantic Salmon) coincides with the thermal regime of most

streams and lakes of southern Chile (Thomasson 1963; Vila et al. 1978; Campos 1984, 1985; Campos et al. 1986). Vila et al. (1978) found that the frequency and duration of spring-summer flooding, and the lack of suitable gravel for spawning, may limit the survival of juvenile salmonids in some areas (e.g., Coho, Chinook and Atlantic Salmon). Recently, Habit et al. (2012) have suggested that there is a potential thermal barrier to the presence of salmonids in lakes of southern Patagonia, although they often occur in streams at those latitudes (Vila et al. 1999; Niklitschek and Aedo 2002).

Environmental tolerance may affect several factors that drive spawning success, especially for Atlantic and Coho Salmon. Rainbow and Brown Trout successfully spawn in Chile during the Austral fall to early spring (May–September; Soto et al. 2002; Arismendi et al. 2011b). Chinook Salmon also successfully reproduce in Chile during a shorter period from late summer through fall (March–May; Soto et al. 2006, 2007). In contrast, to the best of our knowledge, evidence of successful reproduction of Coho and Atlantic Salmon in Chile is scarce (e.g., presence of offspring or early life-stage individuals in streams), though juveniles have been found in some locations, often near aquaculture facilities and occasionally in remote locations (C. Correa *pers. comm.*). Coho and Atlantic Salmon would be expected to spawn during the same time period as Chinook, as estimated from gonadosomatic index values (Soto et al. 2002). Although the spawn timing for Coho and Atlantic Salmon appears to be out of phase (from late summer to mid-fall) with what is observed in their native range in the Northern Hemisphere (from mid-fall through mid-winter; Table 2), such mismatches did not pose problems for establishment of other species (Chinook Salmon, Rainbow Trout, and Brown Trout). An important consideration is that reproductive timing may vary with latitude and that the gonadosomatic index may be an imprecise measure of spawn timing. It is also possible that unsuccessful invaders are unable to survive in the environmental conditions found where they have been introduced in Chile (Table 2; Supplementary material 1). For example, some species may not find cool enough temperatures in many freshwater habitats available in Chile (Table 2).

The apparent failure of other Pacific salmonids (Cherry, Chum, Pink, and Sockeye Salmon) and

Atlantic Salmon may be related to their inability to find suitable ocean currents to allow them to find their way back to their natal streams in Chile, though this is merely speculative. Information on the suitability of the marine environment for anadromous salmonids in Chile is lacking, and the question of whether factors operating in the southern Pacific Ocean influence the lower invasion success of more obligatorily anadromous fish is highly interesting and deserves more attention. Early work by Davidson and Hutchinson (1938) indicates a high similarity of environmental conditions in the marine and fresh waters of the southern coast of Chile and the North Pacific coast of North America, in particular the directional drifts in ocean currents during the spawning migration period of salmon (i.e., Japan or Kuroshio Current and West Wind Drift versus South Pacific Current and Antarctic Drift and Humboldt Current). Accordingly, Nash (1976) suggests that the ocean migration success of Pacific salmon in Chile would improve if salmon were released below the divergence of the South Pacific Current and Antarctic Drift and Humboldt Current (45°S). This could avoid potential migrations further north into warmer waters. Contrasting with this prediction, Chinook Salmon have established self-sustaining populations as far north as 39°S (Soto et al. 2007; Correa and Gross 2008).

The biotic interactions dimension

Since Grinnell's original formulation (Grinnell 1917), niche concepts have evolved considerably. The idea of the niche described by Elton (1927), later renamed the realized niche by Hutchinson (1957), has more recently been elaborated on by others to include the influences of biotic interactions (see Soberón 2007; Soberón and Nakamura 2009). We interpret the realized niche to relate to biotic constraints on the probability of success for a given invader. In the context of biological invasions considered here, establishment of successful invaders can be facilitated or inhibited by biotic interactions (Elton 1958; Ricciardi and Atkinson 2004; Mitchell et al. 2006). We adopt a broad view of biotic interactions to encompass not only competition, but other possible ecological interactions (e.g., predators or parasites; Chase and Leibold 2003) that may constrain invasion success. Among these interactions, we consider how the

invader itself may modify the receiving environment and how this may influence invasion success beyond the initial phase of establishment, including the possibility that carrying capacity or population size may be limited, or the species actually drives itself to extinction (niche destruction; Holt 2009). In reference to the framework presented here and the differential success of salmonid invaders in southern Chile (Fig. 1), we follow these ideas to consider three classes of interactions: 1) interactions between invaders and native biota (biotic resistance); 2) interactions among invaders; and 3) carrying capacity.

Interactions between invaders and native biota (biotic resistance)

The opposition posed by biota to new invaders in the receiving ecosystem includes native competitors, predators, parasites, and pathogens (Elton 1958). Although biotic resistance from competitors, predators, or diseases is an important factor limiting or preventing invasions, demonstrating these mechanisms is difficult (Peterson and Fausch 2003). Several hypotheses have been proposed to explain the success of invaders based on their relationship with native species. Based on the island hypothesis, young or species-poor communities should be more vulnerable to invasions (Elton 1958; Ricciardi and Atkinson 2004) compared to those composed of relatively rich species assemblages that are more competitive, and thus able to resist invasions (Fausch 2007). The enemy release hypothesis states that introduced species experience less regulation by natural predators and enemies, which facilitates their invasion (Keane and Crawley 2002). Accordingly, the most successful invaders are likely to belong to genera not already present in the invaded system (Ricciardi and Atkinson 2004). In addition, episodic biotic events such as disease outbreaks, predator aggregations, demographic stochasticity, and population fluctuations among competitors may also play a role.

Salmonids in Chile

Several studies have suggested that biotic resistance from native species does not explain the limited success of some salmonids in Chile (Soto et al. 2006, 2007; Young et al. 2010; Habit et al. 2012). Native freshwater fishes in this region have evolved in very

isolated conditions bounded by the Atacama Desert, the Andean range, and the Pacific Ocean, resulting in a high proportion of endemism (Dyer 2000; Vila et al. 2006). Consequently, most native fishes have retained ancestral characteristics, including small body size and restricted locomotive ability (Campos 1985; Dyer 2000; Vila et al. 2006). In southern Chile, however, some fishes from the Galaxiidae family are able to move longer distances between fresh and salt waters, and are classified as anadromous and catadromous fishes (McDowall 1997). Regardless of this, experimental and field evidence has shown reduced performance (i.e., growth and habitat use) of native fishes in sympatry with introduced salmonids (Glova 2003; Penaluna et al. 2009; Young et al. 2009; Vargas et al. 2010; Correa et al. 2012). Moreover, native fishes in Chile may already be depressed due to legacy effects from early invasions of Rainbow and Brown Trout (Soto et al. 2006; Penaluna et al. 2009; Arismendi et al. 2009, 2012). Thus, biotic resistance against future invasions may be compromised.

Biotic resistance from other sources such as terrestrial or avian predators is a possibility, although it may not be capable of preventing an invasion. Some authors have reported the presence of fishes in stomach contents of Southern River Otter (*Lontra provocax* Thomas; Medina-Vogel 2005) and South American Gray Fox (*Lycalopex [Pseudalopex] griseus* Gray; Rau et al. 2005). Although it is likely patchy, bird predation may occur (Steinmetz et al. 2003), especially by Ringed Kingfisher (*Megaceryle [Ceryle] torquata* Darwin), Cooi Heron (*Ardea cooi* Linnaeus) and Neotropic Cormorant (*Phalacrocorax brasilianus* Hartlaub), among others (González and Victoriano 2005; Alarcón et al. 2012). Although this review is focused on fresh water, evidence from aquaculture activities in inner seas of southern Chile suggests some degree of predation pressure on salmonids from South American Sealions (*Otaria flavescens* Shaw; Vilata et al. 2010). Overall, it seems unlikely that predators are important in providing resistance to salmonid invasions because there are few predators on fish in Chile, and those present have not co-evolved with salmonids.

With reference to episodic biotic events, the transfer of pathogens by salmonid escapees from aquaculture facilities (Naylor et al. 2005) is likely to be particularly important in Chile, given the size of the salmon-farming industry (Fig. 2 and Supplementary

material 2), and widespread occurrence of escapees (Sepúlveda et al. 2013). Many diseases and parasites, such as the parasitic sea lice (Krkošek et al. 2005), are favored by the conditions of confinement and close proximity among aquaculture facilities. In addition, once infected, salmonids have the ability to move long distances, and thus they are ideal vectors to spread parasites and diseases across lakes, streams, and estuarine areas. For example, the entire aquaculture production of Atlantic Salmon (Supplementary material 2) in Chile was affected by an extensive outbreak of the infectious salmon anemia (ISA) virus that was first reported in 2007 (Godoy et al. 2008) and quickly spread. Similarly, the sea lice copepod (*Caligus* spp.), which is a natural parasite found on estuarine-dwelling fishes, has affected aquaculture production (Carvajal et al. 1998), and is spreading southward (Bravo et al. 2013) in parallel with the expansion of aquaculture (Fig. 2). At present, the consequences of these pathogens for salmonids and other species in the natural environment are unknown (Torres et al. 2002; Cabello 2007).

Interactions among invaders

Given a worldwide increase in the number of species introductions over time (Lockwood et al. 2006), there is concern about the effects of multiple biological invasions (O'Dowd et al. 2003; Grosholz 2005; Johnson et al. 2009). The interactions among invaders may play an important role in the invasion process by potentially influencing one another. Although there are interactions among invaders that may result in neutral responses among them (Johnson et al. 2009), often introduced species act to either enhance or discourage new invasions. More generally, interactions can also be synergistic, from one-way facilitation to mutualism (Richardson et al. 2000; O'Dowd et al. 2003; Grosholz 2005). Synergistic interactions among invaders may also lead to 'invasional meltdown' by accelerating the rate of new invasions of the receiving ecosystem (Simberloff and Von Holle 1999; Simberloff 2006). In some cases, however, multiple invaders may bring about complex effects that are not obvious and do not result in additive effects, but rather cause effects that differ from the 'sum of their parts' (Crowder et al. 1997; Shurin 2001; Best and Arcese 2009). Interestingly, antagonistic interactions among invaders may alleviate some of the negative effects on invaded ecosystems

(Gruner 2005; Griffen et al. 2008). These interactions can be a result of predation, resource competition (Fausch and White 1986; Ross et al. 2004; Griffen et al. 2008), and prior establishment. Here, we propose that prior establishment of early invaders may reduce the probability of new invaders establishing. This proposition is based on the concept of prior residence (Maynard Smith and Parker 1976; Tobias 1997; Olsson and Shine 2000) that accounts for the location and time of arrival, giving first invaders an advantage over subsequent invaders. The prior residence effect is well known in salmonids (e.g., Huntingford and Garcia de Leaniz 1997; Cutts et al. 1999) and may influence interactions among invaders and their relative abundances.

Salmonids in Chile

Interactions among salmonids in Chile involve a potentially complex array of processes and a variety of competitive asymmetries. Here we develop our hypotheses that the outcomes of behavioral interactions among species may be driven by differences in species' phenologies (Table 2), body size, and timing of establishment. Alternatively, non-interactive, exploitative processes, namely pre-emptive consumption of food or acquisition of space (e.g., Grant et al. 1998) may be important as well. In the streams of southern Chile, indirect evidence suggests that inter-specific competition for resources occurs between Rainbow and Brown Trout (Young et al. 2010; Arismendi et al. 2012), especially among large-sized individuals (Arismendi et al. 2012), as well as between Atlantic Salmon and Rainbow Trout (Young et al. 2009). Overlap in resource use is likely among ecologically similar species introduced to Chile (Table 2), but competition requires resource limitation (Connell 1983). The potential for resource limitation or depletion of food resources is evidenced by declining condition indices for Rainbow Trout in large lakes of the Lakes District of Chile (Arismendi et al. 2009, 2011a). Because trout are less likely to migrate than species with obligate anadromous life histories, such as Atlantic and Chinook Salmon, they may have greater potential to deplete prey availability in fresh water. In circumstances where Rainbow Trout maintain a relatively high condition, they may be more likely to maintain a competitive advantage over other

salmonids, such as Coho and Atlantic Salmon (Soto et al. 2001b; Young et al. 2009).

A variety of behavioral processes may influence interactive segregation and competition among salmonids in Chile, including differential competitive abilities tied to body size or domestication selection. The importance of these processes is not well-studied in Chilean systems, but there is some circumstantial evidence to suggest that Atlantic Salmon do not compete well against other established salmonids (Soto et al. 2001b). Although massive numbers of Atlantic Salmon have escaped from aquaculture facilities (see propagule pressure above; Sepúlveda et al. 2013), and are typically larger in size for a given age than resident trout, it is possible that domestication could reduce their competitive ability (e.g., Fleming et al. 2000; McGinnity et al. 2003; Metcalfe et al. 2003; Hill et al. 2006) relative to established trout. In parts of their native range, Atlantic Salmon and Brown Trout live in sympatry and overlap their habitats (Armstrong et al. 2003), but this has yet to occur in the invaded systems of Chile. In North America, evidence suggests that non-native Brown Trout have not displaced native Atlantic Salmon (Westley and Fleming 2011). Moreover, it is possible that prior establishment of Rainbow and Brown Trout may exert non-competitive biotic resistance to new salmonid invaders in Chile; for example, sea-run Brown Trout (sea trout) have been reported to feed on released juvenile Chum and Pink Salmon in estuarine areas (Zama 1987).

Among species commonly used in aquaculture, less is known about Coho Salmon in Chile, especially in freshwater systems. In other invaded systems, however, Coho Salmon have successfully colonized and competed for food and space with non-native Brown Trout (Great Lakes of North America; Crawford 2001), possibly due to the larger size of Coho Salmon (Fausch and White 1986). In their native systems in the Pacific Northwest of North America, juvenile Coho Salmon can maintain a natural size advantage over other competitors (e.g., Rainbow Trout) and are behaviorally dominant (Young 2004).

In contrast to Atlantic and Coho Salmon, Chinook Salmon may be more naturally segregated from established trout, due to their propensity to use larger rivers and associated substrates for spawning (DeVries 1997; Burnett et al. 2007). Such segregation could minimize interactions among juveniles of salmon and

trout, and at least partially explain the successful invasion of Chinook Salmon throughout southern South America (Di Prinzio and Pascual 2008).

Interactions among invaders in Chile have been shown to be primarily antagonistic, but in some cases introduced species may promote establishment, enhancing food resources in these systems. In Tierra del Fuego, introduced North American Beaver (*Castor canadensis* Kuhl) may indirectly provide improved food resources, facilitating the growth of introduced Brown Trout (Arismendi 2009). Also, in rivers of northern Patagonia, Chinook Salmon carcasses bring marine-derived nutrients to freshwater ecosystems, resulting in enriched food resources for established resident trout (Arismendi and Soto 2012).

Carrying capacity

Although initial colonization of introduced species can be hindered by either biotic or environmental limitations, if initial colonization is successful the probability of establishment may depend strongly on carrying capacity. In its simplest terms, carrying capacity is the maximum abundance of a given invader that a particular environment can sustain (Odum 1989). Carrying capacity may influence invasion success (probability of long-term persistence) and expansion via dispersal of individuals to potentially colonize new locations. In concept, the abundance of an invader may be considered in terms of the intrinsic potential of a given location to support a species (Burnett et al. 2007) and the realized potential, or actual observed level of abundance. The latter may be constrained by cycles of productivity of the environment (e.g., prey availability), episodic patterns of physical disturbance (fire, floods, or droughts) and connectivity or access to suitable habitats. Understanding the carrying capacity of receiving ecosystems not only provides insight into ecosystem thresholds during invasions, but it also allows natural resource managers to consider a suite of scenarios that might maximize societal benefits and minimize negative effects from species introductions.

Salmonids in Chile

Oligotrophic conditions prevail in the freshwaters of southern Chile, including low nutrient concentrations and limited primary production (Thomasson 1963;

Campos 1984, 1985; Soto 2002; Soto and Stockner 1996). Accordingly, it is reasonable to hypothesize that the carrying capacity of these systems with respect to salmonids is limited in part by environmental productivity (Soto and Stockner 1996). Recent evidence from lakes suggests that sites with multiple species of free-living salmonids and high aquaculture production could be at their maximum fish carrying capacity (Arismendi et al. 2009). Indeed, the increase in the relative abundances of free-living salmonids in these lakes has been associated with decreases in the well-being (multiple condition indices) of self-sustaining trout populations, suggesting a density-dependent effect from competition due to limited food availability (Arismendi et al. 2011a) and shifts in trophic position of trout under lower relative abundances of native *Galaxias platei* (Correa et al. 2012). Such associations between salmonid abundances and condition indices have not been observed in streams, however, suggesting the possibility that streams have not yet reached their salmonid carrying capacity (Soto et al. 2001b).

Summary of factors influencing the differential success of salmonids in Chile

In this review, we have summarized factors influencing the differential success of salmonid invasions in southern Chile, based on our assessment of the existing evidence (Table 3). Specifically, Rainbow and Brown Trout were initially introduced into salmonid-free habitats; both species exhibit broad phenotypic plasticity and environmental tolerance, all factors that would be expected to contribute to their success as invaders. High propagule pressure, especially from aquaculture escapees, also seems to have played a role in facilitating the establishment and dispersal of Rainbow Trout. Chinook Salmon are the only obligate migratory species known to have become established in the region, possibly due to their high phenotypic plasticity and ability to escape competition from other salmonids, owing to spatial segregation from established trout. Similarly to other invaded regions of the southern Hemisphere, such as New Zealand and Australia, Chinook Salmon, Rainbow Trout, and Brown Trout are species that have successfully established self-sustaining populations (Crown et al. 1992; Quinn

Table 3 Summary of factors hypothesized to influence the differential success of invasions in southern Chile, and our assessment of the existing evidence in support of them

Dimension	Component	Species											
		Str	Ssa	Omy	Ots	Oki	Oma	Oke	Ogo	One	Sfo	Sna	Sal
Invader	Life-history characteristics	+	0	+	+	–	0	–	–	0	+	0	0
	Environmental tolerance	+	+	+	+	+	+	–	–	–	+	–	–
Biotic interactions	Interactions among invaders	+	–	+	+	–	–	+	+	–	–	+	–
	Interactions with native species	+	+	+	+	+	+	+	+	+	+	+	+
	Carrying capacity	+	+	+	+	+	+	+	+	+	+	+	+
Human	Propagule pressure	High	High	High	Low	Low	Low	Low	Low	Low	Moderate	Low	Low
	Direct control	None	None	None	None	None	None	None	None	None	None	None	None
	Coexistence	Some	Some	Some	Some	Some	None	None	None	None	None	None	None

Three invader dimensions are identified, each with separate components that relate to invasion success (Fig. 1). Species abbreviations indicate the genus with a single uppercase letter followed by lowercase text indicating the first two letters of the species name, as shown in Table 1. Within the invader dimension, life-history characteristics are scored with a positive “+” sign if the species exhibits traits associated with successful invasion (e.g., longer lifespan, long freshwater residency), and with a negative “–” sign if traits are associated with unsuccessful invasion (shorter lifespan, shorter freshwater residency; Table 2). Environmental tolerance is scored as positive or negative based on whether or not the species is restricted to cold water (Table 2). Within the biotic interactions dimension, interactions among salmonids are scored as positive for species with a prior establishment advantage (Str, Omy, Sfo), or for species that use portions of the stream network or have short freshwater resident times that minimize interactions with established salmonid invaders (Ots, Oke, Ogo), or are lentic (lake-dwelling) specialists (Sna). Species that overlap spatially with previously established salmonids are scored as negative. Interactions with other species and carrying capacity are all scored as positive, as there is no strong evidence in support of natural biotic resistance or limitations on invasion success imposed by the natural carrying capacity of ecosystems. Human influences on invasion success are ranked qualitatively into relative categories of “high,” “moderate,” or “low” with respect to propagule pressure (Figs. 2, 3). In cases where a species was long established prior to documented human activities linked to propagule pressure, it is ranked as “high”, assuming that natural productivity leads to high propagule pressure. Human influences from direct control are universally ranked as “none” because we are not aware of any specific examples in southern Chile and for coexistence management influences of fishing pressure allow us to rank certain species as “some”

and Unwin 1993; Cadwallader 1996). Prior establishment of trout populations and environmental resistance (mismatch of spawning seasons) may have reduced the potential for subsequent invasions by Atlantic and Coho Salmon, although time lags in establishment and domestication in these species may also explain their lack of success in southern Chile. Biotic interactions, including diseases and predators, seem less likely to be important in impeding invader success, based on what we know thus far, but differential susceptibilities (e.g., to the ISA virus) could stall invasions by some species. Similar to Atlantic and Coho Salmon, propagule pressure does not explain the failure of other species of salmonids to establish self-sustaining populations.

For these fishes, species traits (e.g., short life-spans and low tolerance of warmer water; Table 2) or constraints on the ability to respond phenotypically to the invaded systems may help explain their lack of establishment. However, none of these traits explain why Atlantic Salmon have failed to establish. Interestingly, with respect to patterns of anadromy, “partial” or facultatively anadromous species seem to have had more success than species with more obligate anadromy (e.g., Utter 2001; Fleming and Petersson 2001). Thus, anadromy may hinder initial establishment to some degree; however, once established, it may facilitate expansion and colonization of a species (e.g., Chinook Salmon).

Overall conclusions

Salmonids are among the best-studied and most widely introduced fishes worldwide, yet there is much to learn about factors explaining the variable success of their invasions in Chile and elsewhere. Is important to consider salmonid invaders on a case-by-case basis due to the idiosyncratic differences in the processes that result in differential invasion success. Our review indicates that the success of salmonid invasions in Chile is best addressed within a framework that includes human influences, the invaders themselves, and the environmental and biotic interactions that the invaders encounter in their new habitats. A range of knowledge gaps that pose challenges for evaluating the full range of potential hypotheses are identified. For example, propagule pressure is only partially documented in terms of numbers of individuals introduced, general locations, and times. It is also known little about details of those introductions that could ultimately determine their success (e.g., condition of introduced fish, detailed information on sites of introduction). This is particularly relevant to establish the degree of invasiveness for species that have been continuously stocked even after they have resulted in naturalized populations. In other cases, there is little or no information that can provide a basis for evaluating alternative hypotheses to explain invasion success (e.g., carrying capacity, food web processes).

The framework laid out here provides relevant information leading to different management alternatives and recommendations. Most studies related to invasion ecology only consider single aspects related to the invader, biotic and environmental resistance, or propagule pressure. Here, we provide a more holistic perspective that considers the complexity of interactions and the role that humans play in invasions. Components from each dimension may exert a neutral, positive, or negative influence on the success of each species introduction. This approach will help to identify why certain invasions may fail while others succeed. It allows us to incorporate more educated predictions about the success of existing invasions and improve the process of risk assessment prior to the introduction of other exotic species (Bondad-Reantaso et al. 2008). In Chile, prevention may still be possible in places where salmonids are not yet present or have not yet invaded, such as high mountain streams and lakes located in remote areas. As a first step, it is

important to identify these salmonid-free waters and then generate a management plan to continue to prevent future invasions. This framework can also be applied to understand how fish adapt and recolonize habitats in their natural ecological ranges, for example, after the removal of stream barriers.

A consideration of a full range of hypotheses, as seen in our framework, should stimulate future work that not only documents the spread of biological invasions and their impacts, but allows us to better understand the role of multiple interacting drivers during the invasion process. As the understanding of these drivers increases, so too will the ability to predict and manage biological invasions more effectively. This should prove crucial to developing sustainable approaches for valuable fisheries and aquaculture operations, while ensuring the persistence of native species, along with intact freshwater and marine ecosystems upon which it depends.

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