Not all lineages are equally invasive: genetic origin and life-history in Atlantic salmon and brown trout acclimated to the Southern Hemisphere

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Abstract Salmonids are fish from the Northern Hemisphere which have been introduced and acclimated to many regions in the Southern Hemisphere for commercial (aquaculture) and recreational (sport fishing) purposes. In some cases a species like brown trout *Salmo trutta* rapidly spread across the host ecosystem and became invasive, threatening local fauna, and even outcompeting other exotic fish. We have analyzed life-history traits in combination with genetic variation of Atlantic salmon and brown trout adapted to the lake systems of the Argentinean Patagonia (South America). We have identified two main characteristics that conferred invasive capacity to those exotic species: undomesticated status and lifelong growth. Stocks originated from wild populations adapted better than long-term domestic lineages, and their geographic origin seems to be less important for adaptation to exotic environments. We propose that considering these characteristics in future planning of commercial aquaculture projects by selecting non-invasive lineages will minimise the impact of accidental escapes.

Keywords Domestication · Introduced species · Life-history traits · Patagonia · *Salmo*

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Introduction

Biological invasions are to a great extent a consequence of human activity. Organisms are often inadvertently transported by humans (Carlton and Geller 1993; Vitousek et al. 1997; Smith et al. 1999; Fofonoff et al. 2003; Perez et al. 2007), and new ways for spontaneous dissemination of many species like roads and channels (Ruiz et al. 2006; Gollasch 2006) are constructed every year. In addition, deliberate releases of exotic species have been carried out with purposes of acclimation to new habitats for further exploitation. Salmonids fall within the last category. Native to the Northern Hemisphere, millions of eggs of many Salmonidae species have been transplanted to different regions of the Southern Hemisphere (Davaine and Beall 1982, 1997; Pascual et al. 2002; McDowall 2003; Baigún and Ferriz 2003; Becker et al. 2007; Aigo et al. 2008; Correa and Gross 2008; Inoue et al. 2009). In the new habitats their fate has

been quite diverse, depending on various factors that are not yet well understood. In some cases they have displaced local native species and have become a pest, like brown trout in New Zealand (Townsend 2003), where the cost of their adaptation has been the loss of some native Galaxiidae species (McDowall 1990, 2006; Townsend 1996; McIntosh 2000). In other cases they have adapted to coexist with local organisms and can be considered naturalized, like various salmon and trout species in South America (Ciancio et al. 2005; Astorga et al. 2008). Finally, in some cases they have been unable to show successful adaptation –or may have been outcompeted by other exotic salmonids- and are extinct, like in some systems of the Kerguelen Islands (Ayllon et al. 2004a).

One of the key questions for understanding what makes a salmonid species invasive is: what are the traits which confer invasive capacity? Is it genetics, that is, animals from some genetic lineages possess an inherent tendency to explore and colonize other habitats? Or is it associated with one or various life-history traits, like growth (Kinnison et al. 1998; Macchi et al. 2007; Pascual et al. 2007), migratory behaviour (Valiente et al. 2010) and/or others? Although the role of genetic variability per se has not been confirmed in conferring invasiveness in Salmonids (Valiente et al. 2007), the answer is likely a combination of different environmental and genetic factors.

Even when a species exhibits colonizer capacity and can theoretically become a pest, not all their lineages are equally invasive. Domestication may interfere with invasive capacity. An example is brown trout. Domestic stocks are able to adapt to new environments and advantageously compete with wild ones of the same species (Lura and Saegrov 1991; Naylor et al. 2005; Braithwaite and Salvanes 2005), substituting wild populations in some environments, such as in areas of low water flow (e.g. Moran et al. 1991; Ford and Myers 2008). However, in other cases domestic trout failed to colonize new habitats (e.g. Moran et al. 1991; Ayllon et al. 2006). It is crucial to determine what are the main factors involved in invasiveness in order to set up control mechanisms of invasive species.

New stock transfers or common garden experiments have inherent risks because total containment of experimental animals is difficult to ensure, particularly in aquatic environments. However, one possibility is to study the outcome of old transplants, when more than one species and population have been transferred to the same exotic habitat. Such situations could be considered a sort of non-deliberate common garden experiment. In this study we have identified a region where Atlantic salmon *Salmo salar* and brown trout *S. trutta* of different origins and domestication status have been released: the Argentine province of Neuquen (Patagonia) in South America. We have analyzed growth and genetic diversity of the extant naturalized populations and compared them with founder stocks (or stocks inhabiting their regions of origin). The results allowed us to identify some key factors that determined adaptation and –by extension- invasiveness in these two species.

Materials and methods

Study sites

In Patagonia we have studied two river systems where the two salmonid species considered have been introduced: Río Blanco (Curruhué system) and Río Traful, within the province of Neuquén (Argentina) (Fig. 1). The watersheds of the two systems are derived from Andean glacial lakes. There is no evidence that Salmonids established sea migrating stocks in the region (Riva Rossi 2008), and native and introduced species coexist (Table 1).

Salmonids introductions to North Patagonia have been described in detail by Macchi et al. (2008). Atlantic salmon was introduced first in the Neuquén region (Table 2). Landlocked salmon from lakes Sebago and Grand (Maine, USA) were probably the first consignment and arrived successfully in Patagonia in 1904 (Tulian 1908; MacCrimmon and Gots 1979). They were likely wild or recently domesticated, as Atlantic salmon domestication first occurred around those years (Jensen 2002). That first introduction was followed by successive releases of eggs and alevins imported from domestic European stocks (Germany, British Isles). Brown trout was introduced later (Table 2), principally imported from Chile (Macchi et al. 2008) where it was naturalized, and to a minor extent from other European countries (Baigún and Quirós 1985). The origin of brown trout introduced to Chile is not totally well known. Of

Fig. 1 Map showing the location of the studied rivers in Neuquén (Patagonia, Argentina)

Atlantic origin as opposed to Mediterranean (Colihueque et al. 2003), they had been imported from different European countries to establish populations in Chilean rivers (Faundez et al. 1997), principally from Germany and some introductions from other European countries. It can be supposed that at least some of them were imported from Spain, given the historical commercial and cultural relationships between this country and South America. The German stocks were likely domestic and those native from South European regions were probably wild or recently domesticated, as little domestication activity of native brown trout exists in this area (Perez-Rubin 2006).

Measures of abundance

For the Patagonian systems there are no published systematic inventories of fish abundance, therefore the proportion of sport catches for each *Salmo* species (their relative mass in the total number of sport catches) was roughly considered as a proxy of their relative abundance.

Table 1 Hydrographic, topographic and geographic characteristics of the Patagonian (Neuquén) systems

Configuration	Cordilleran valleys, lakes
Valley length (maximum)	13–25 km
Total area of lakes	10–79 km^2
Mean river width	4–18 m
Latitude	39°–40°30′ S
Longitude	71°25′ W
Altitude	800–1,000 m
Geology	Sedimentary, volcanic and pyroclastic rocks
Ecosystem type	Glacial lakes–rivers
Average annual rainfall (mm)	1,500
Mean annual temperature	5.5–8°C
Type of vegetation	*Nothofagus antarctica*, *N. dombeyi* and *Lomatia hirsute*
Aquatic vegetation	Grassy plants; submersed aquatic plants; floating aquatic fern; mosses
Available prey	Planktonic Plecoptera; Diptera; Ephemeroptera; Coleoptera; Hymenoptera; Tricoptera; Amphipoda
	Terrestrial invertebrates; larvae of native fish species
Native fish	*Hatcheria macraei*, *Galaxias platei*, *G. maculates*, *Diplomystes viedmensis*, *Percichthys trucha*, *Odontesthes hatcheri*
Other introduced salmonids	*Salvelinus fontinalis*; *Oncorhynchus mykiss*

Table 2 Introduction of *Salmo* species in the considered Patagonian region (Neuquen)

Species	Introduction year	Status		Number of fish introduced
		D	W	
S. salar	1904	–	Great Lakes[a]; Maine; USA	844543
	1906	British Isles[b]	–	Unknown
	1931–1973	Germany[c]	–	Unknown
S. trutta	1931	Germany (via Chile)[d]	–	431398
	1931–1981	–	Different European countries[b] (some via Chile)	Unknown

D, domestic; W, likely wild

[a] MacCrimmon and Gots (1979); [b] Baigún and Quirós (1985); [c] de Buen (1959); [d] Macchi et al. (2008)

Samples analyzed

A summary of the samples analysed and the type of analysis carried out is shown in Table 3. Representatives of Maine Atlantic salmon founders (Sebago Lake and Grand Lake) were analyzed. Detailed genetic data can be found in Valiente et al. (2007). For European founders, because Atlantic salmon is now extinct in Germany, the comparison with present German stocks is not possible. However, there are wild Atlantic salmon populations and domestic stocks in the British Isles; genetic data of hatchery stocks from these islands were taken from Säisä et al. (2005).

Brown trout samples from the Elbe and Rhine rivers were chosen as representative of founder German brown trout. Detailed data are published in Valiente et al. (2010). We have chosen a mixture of wild Spanish brown trout samples ($n = 1284$) as representative of South European imports. Genetic data from most of these samples have been published in Izquierdo et al. (2006).

Naturalized Atlantic salmon inhabiting the Blanco and Traful rivers systems were analyzed for both genetic variability ($n = 100$) and morphological traits ($n = 308$) (Table 3). Naturalized brown trout inhabiting the same systems were also genetically ($n = 50$) and morphologically ($n = 226$) analyzed (Table 3). Samples were obtained in 1994 and 1995.

Life-history traits analysis

Fork length and weight were obtained (directly measured) from salmonids caught by electrofishing in field surveys (March and July 1994 and 1995). To determine the cohort or brood year of the analyzed individuals, age determination of scales was performed according to Busacker et al. (1990).

Genetic analysis

The DNA source tissue was scales (donated by anglers). Theses scales (2–5 per specimen) were dried and preserved in paper envelopes for DNA extraction.

DNA was extracted based on Chelex methodology (Estoup et al. 1996). Five non-coding hypervariable microsatellite loci were analyzed. Microsatellite

Table 3 Samples analyzed

		Patagonia B		Patagonia T	
		n	Caught	*n*	Caught
Genetic analysis	*S. trutta*	50	2004[a]	–	–
	S. salar	50	2004[a]	50	2004[a]
Morphological characteristics	*S. trutta*	126	March[b] and July 1994 and 1995	100 Juvenile (age 1+)	April[b] and May 1995
	S. salar	208	April[b] and May 1995	100 Juvenile (age 1+)	April[b] and May 1995

B, Río Blanco; T, Río Traful n = sample size. Caught = time of sample collection

Obtained from: [a] angling catches; [b] Electrofishing

typing at loci SSOSL85, SSOSL311 and SSOSL417 (Slettan et al. 1995), BF002 (Sušnik et al. 1997), and SS4 (Martinez et al. 1999), was based on standard PCR-fragment size determination methodology by capillary electrophoresis in an ABI Prism 3100 DNA Sequencer and the GENSCAN V. 3.7 software (Burge and Karlin 1997) at the DNA Sequencing Unit of the University of Oviedo. Annealing temperatures in PCR cycles were the following: locus SSOSL85 and SSOSL311, 55°C (Slettan et al. 1995); SSOSL417, 52°C (Slettan et al. 1995), BF002, 50°C (Sušnik et al. 1997) and SS4, 58°C (Martinez et al. 1999); Reaction mixtures and cycle conditions followed standard protocols (for example Ayllon et al. 2004b). One protein-coding locus ($LDH-C1*$) was also analyzed. $LDH-C1*$ genotypes were determined by restriction digestion of the gene DNA sequence (McMeel et al. 2001).

Statistical analyses

Life-history traits

Statistical analyses were performed with the program SSPS 8.0 to assess differences between mean length and weight of age 1 + juvenile salmonids (Atlantic salmon and brown trout). Homocedasticity (equality of variances) was checked employing Levene's test. Means were compared employing t-tests for independent samples. The curve that best fitted the evolution of each morphological parameter (length, weight) through time was estimated employing the same program, which gives significance to each model curve. Comparison of linear growth slopes (when a linear model was the best-fit) of Atlantic salmon and brown trout inhabiting the same systems was made based on t-tests.

Genetic variation

Variation at the loci considered was quantified for two different purposes. Genetic variability at all loci was assessed in donor and derivative stocks for evaluating its possible role in adaptation. The parameters of genetic variability considered were the number of alleles per locus and heterozygosity observed and expected. They were estimated with the GENETIX (2000) computer package, which was also employed for calculating allele frequencies.

Genetic variation can also serve for determining the origin stock of naturalized Salmonids, when more than one donor type has been stocked in or has colonized a system. There are some stock-specific alleles, for example the locus SSOSL311 is continent-specific for *Salmo salar* (Säisä et al. 2005) and can be employed for differentiating naturalized salmon of American and European lineages. The microsatellite locus BF002 and the coding locus LDH-C1* are useful markers for differentiating domestic and wild stocks of brown trout in Southern Europe (Izquierdo et al. 2006). Allele variation at those loci was employed for identification of the proportion of each donor stock in naturalized individuals. When assignment was not direct (exclusive alleles), the program GENECLASS was employed for self- assignment of naturalized individuals to each donor stock based on all the loci analysed. Self-assignment tests (Bayesian method) were done using the program GENECLASS 1.0.02 (Cornuet et al. 1999). This is a likelihood-based method in which individuals are assigned to the population in which the likelihood of their genotype is highest. The following settings were used: 10,000 simulated individuals, threshold = 0.01 and Bayesian estimation of frequencies.

Results

Both Atlantic salmon and brown trout acclimated and constituted naturalized populations in the studied systems. Temperature was relatively low due to the altitude of the considered Patagonian systems (above 800 m). Accompanying fauna included many invertebrate and other native fish species.

Interspecific differences were found for morphological traits in juvenile stages (Fig. 2). Extant 1 + Atlantic salmon were shorter and lighter than brown trout in the River Traful ($P < 0.001$ for both traits), but in the River Blanco the initial growth was the opposite: Atlantic salmon were longer and heavier than brown trout ($t = 4.214$, 63 df, and 2.543, 118 df with $P = 0.000$ and $P = 0.012$ for length and weight respectively, after testing equality of variances with Levene's test). However, when extending the analysis to the entire lifespan of salmon and trout the results were different. The coefficients of the logarithmic curve that best fitted growth were higher for brown trout than for Atlantic salmon

(Fig. 3) indicating higher long-term growth of the former species. Adjusting size data to linear growth, the values b_0 (intercepts) of the regression line were significantly higher for brown trout than for Atlantic salmon: 4.3 for brown trout versus 0.8 for Atlantic salmon ($t = 6.8571$, 7 df, $P < 0.005$).

Adaptation of Atlantic salmon and brown trout to the new environments was not identical for all the lineages of each species introduced in the Blanco and Traful rivers. Genetic markers (Table 4a) evidenced that in these Patagonian systems the extant naturalized Atlantic salmon was of North American origin, because they were fixed for one SSOSL311 allele exclusive of North America (allele 114) that was not present in European salmon (Table 4; Säisä et al. 2005). It seems that the European domestic salmon introduced in Patagonia failed.

With respect to brown trout, absolute markers of donor stocks were not found (Table 4). For BF002 allele variation, in the Patagonian systems most naturalized individuals exhibited the less frequent allele of domestic German populations (allele 122), which was in turn the most frequent in South European wild populations. Variation at the LDH-C1* locus revealed a frequency of 0.23 for the *100 allele in Patagonian trout (Table 4). LDH-C1*100 is the most frequent allele in South European populations and very infrequent in domestic German ones (less than 0.05), therefore the trout adapted to Patagonia is likely a mixture of donor stocks. The program GENECLASS assigned 16 and 22% of individuals to German and South European stocks respectively in the studied systems when all the loci analyzed were included. The rest of the individuals were not significantly assigned to any putative donor
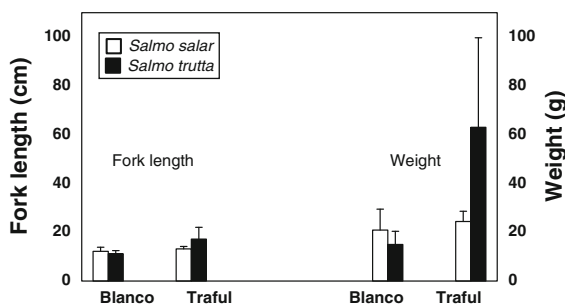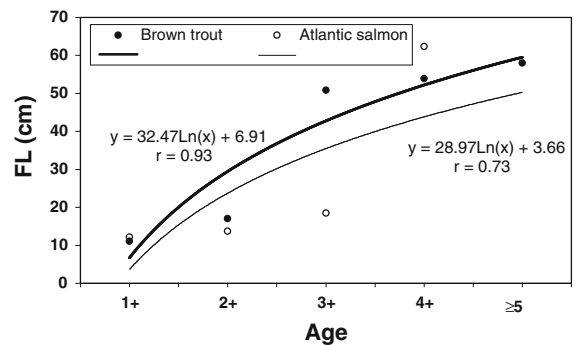

Fig. 3 Mean size at age (length in cm) for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) in the River Blanco

stock. South European alleles would be overrepresented, considering that releases of south European individuals were minor in comparison with the much more abundant domestic German imports (Table 5).

With respect to the levels of genetic variation at microsatellite loci found for these naturalized Salmonids, Atlantic salmon and brown trout exhibited similar values for the three parameters considered (Fig. 4). The differences between species in allelic richness, mean Ho and He were not significant ($P > 0.1$ for all cases).

Although the measures of species abundance were not precise in Patagonia because they were based on angling catches, increasing abundance of brown trout in parallel with Atlantic salmon declines seems to be clear. In the Patagonian Traful system sport catches were primarily of Atlantic salmon in the 1980s but the dominant species is brown trout only 20 years later (Fig. 5).

Discussion

In the Traful and Blanco river systems, brown trout adapted better than Atlantic salmon (e.g. Macchi et al. 2008; Valiente et al. 2010), as was also demonstrated in other even more remote ecosystems like the virgin Subantarctic French territory of the Kerguelen Islands (Ayllon et al. 2004a, b). Decline of *Salmo salar* in Northern Patagonia is a well known phenomenon (Macchi et al. 2008; Vigliano and Alonso 2007), and has been attributed to difficulties in adaptation to landlocked situations, dam construction, and generalized habitat change in the Traful system. Brown trout, however, overcome those

Fig. 2 Morphological characteristics of 1 + juvenile salmonids in Patagonia (Blanco and Traful rivers). Mean (and standard deviation) weight and fork length

Table 4 Genetic markers of origin of the studied Salmonids

Atlantic salmon				Brown trout			
Marker	Founder-D (British Isles)	Founder-W? (Maine)	Naturalized	Marker	Founder-D (Germany)	Founder-W (S. Europe)	Naturalized
SSOSL311 alleles				BF002 alleles			
114	–	0.90	1.00	118	0.98	–	–
116	–	0.10	–	120	–	–	–
Other	1.00	–	–	122	0.02	0.70	0.99
				124	–	0.13	–
				126	–	0.17	0.01
				LDHC–1* alleles			
				*100	0.05	0.83	0.23
				*90	0.95	0.17	0.77

Allele frequencies of donor (representative of ancient donors) and derivative (naturalized in Patagonia) stocks at different coding (LDH-C1*) and noncoding (microsatellites SSOSL311 and BF002 for Atlantic salmon and brown trout, respectively) markers. D, domestic; W, wild. Naturalized Atlantic salmon: Río Blanco and Traful, pooled together. Naturalized brown trout: Río Blanco

Table 5 Proportion of each type of *Salmo* stock introduced (donors) and successfully adapted in Patagonia

Atlantic salmon (Starting 1904)			Brown trout (Starting 1931)		
Origin	Status	Proportion	Origin	Status	Proportion
Donors					
NA (Maine)	W	>50%	CE (Germany)	D	>90%
CE (British Isles)	D	<50%	SE (probably Spain)	W	<10%
Adapted					
NA	N	100%	CE	N	16%
			SE	N	22%

D, domestic; W, wild; N, naturalised; NA, North America; CE, Central Europe; SE, South Europe
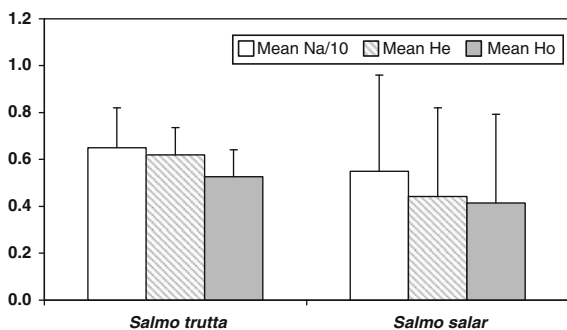

Fig. 4 Parameters of genetic variability at four microsatellite loci (SSOSL85, SSOSL311, SSOSL417 and SS4) for Blanco River (Patagonia) populations of Atlantic salmon and brown trout. Mean number of alleles (Na); expected (He) and observed (Ho) heterozygosities
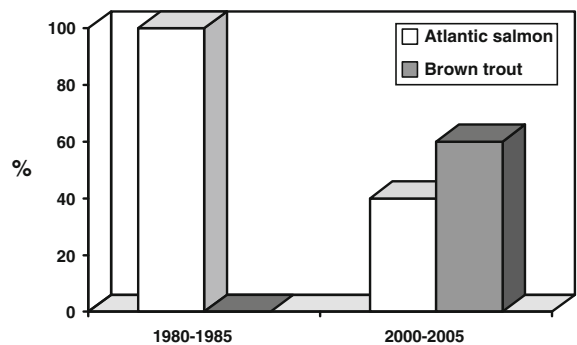

Fig. 5 Relative abundance (in percent) of Atlantic salmon and brown trout in River Traful (Patagonia) for the last few decades

disadvantageous circumstances and seem to be well adapted to the new ecosystems. The better adaptation of brown trout over Atlantic salmon in the Andean Argentine Patagonia and its higher invasiveness is highly evident from the existing bibliography on distribution and abundance of these two species (Pascual et al. 2002, 2007; Macchi et al. 2008; Aigo et al. 2008). This bibliography covers a geographic range extending from Northern Neuquen Province to Tierra del Fuego. Our results confirm it in the two systems studied.

Other lessons can also be learned from this study. Our results point out that the degree of domestication is important for adaptation and eventual invasiveness in wild habitats. The outcome of introductions of domestic and wild stocks into this exotic system was a final colonization by a majority or exclusiveness of undomesticated individuals belonging to wild populations, even if domestic releases were initially more abundant (Table 5). In the wild, domestic salmon exhibit lower fitness than wild salmon and aquaculture escapes can endanger natural populations compromising their viability (Clifford et al. 1998; McGinnity et al. 1998, 2003, 2009). Domestication encompasses genetic changes in life-history traits, which can be subjected to directional selection in farm conditions (Fleming and Einum 1997; Hindar et al. 2006) and also in behavioral components such as aggressiveness, mate choice and others (Fleming and Gross 1993; Fleming et al. 2000, 2002; Mignon-Grasteau et al. 2005; Orlov et al. 2006; Castillo et al. 2008). As an indicator of such altered behavior, individuals of domestic origin provide most hybrid crosses between Atlantic salmon and brown trout in southern Europe (Castillo et al. 2008).

As the whole history of salmonid introductions in South America over the past 100 years is incomplete, it is possible that the number and origin of real founders deviates somewhat from the published information and the geographic lineages of the donors are more complex than presented here. From the available information, it seems that the geographic origin of the donor stocks was not relevant for adaptation, at least in comparison with the effect of domestication status. Wild (or recently domesticated) southern European stocks adapted to Patagonian systems better than domestic central European trout. However, successful adaptation of brown trout to different exotic regions has occurred irrespective of

their geographic origin; for example, although in this study we demonstrated that German brown trout did not perform well in the studied systems within the Argentinean Patagonia, they adapted perfectly to and colonized varied systems in different latitudes, from Chile to North America (Fausch et al. 2001; Pascual et al. 2002; Macchi et al. 2007; Soto et al. 2006). The explanation for their low success in Patagonia was probably the presence of conspecific competitors (other donors) of wild origin.

Life-history traits likely contribute to explain adaptation to new environments much better than genetics (Valiente et al. 2007, 2010). Growth is crucial for adaptation. Early growth and therefore capacity of a fast biomass increase has been cited as key for invasiveness (Townsend 2003, Valiente et al. 2010). Our results are relatively concordant with that hypothesis: trout grew faster than salmon during the first year of life in the River Traful, but in the River Blanco salmon grew faster (Fig. 2). But, Not only growth during the first year is important. Higher growth rate during the entire lifespan (Fig. 3) is likely the decisive factor that determines invasiveness. The habitat requirements of year classes of salmon and trout overlap in all their freshwater life stages (Heggenes et al. 1999; Armstrong et al. 2003), including spawning. Exhibiting a bigger size is advantageous when competing for space, food and spawning sites, and brown trout tend to out-compete Atlantic salmon in most situations (e.g. Armstrong et al. 2003).

These results may have important implications for management. Aquaculture is an activity in expansion worldwide (Reilly and Kaeferstein 1999; Naylor et al. 2000; Vergara 2003; James 2009), but encompasses risks like potential invasions from accidental escapes (e.g. Linde et al. 2008; Krishnakumar et al. 2009). Total containment of cultured fish is not possible or is very difficult and total sterilization of all farm fish may not be feasible at this point (Piferrer et al. 2009). In this situation, some recommendations for brown trout and Atlantic salmon producers and managers can be suggested. The first and most logical is to avoid farming of these species in exotic regions, as it encompasses a risk of escapes. But in some cases economic reasons are prevalent and these fish species, of high commercial value, are cultivated for enhancing the economy of regions in development. In such cases, selection of long-term domesticated individuals can be

a possibility of some value for conservation. Total prevention of invasions if escapes are produced can not be guaranteed, but their capacity of naturalization and therefore invasiveness is likely lower than that of recently domesticated farm stocks.

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