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Research Article

From Best to Pest: changing perspectives on the impact of exotic salmonids in the southern hemisphere

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Exotic salmonids were deliberately introduced to the southern hemisphere during the last part of the 20th century, initially to boost sport fishing and later to develop an aquaculture industry. Early introductions were justified by governments on purely utilitarian arguments as it was felt that translocated salmonids would capitalize on otherwise 'underutilized' aquatic niches. A century later, exotic salmonids are established in nearly all places where they were originally introduced and beyond, and constitute one of the main threats to endemic fish fauna, amongst which galaxiid fishes have perhaps been impacted the most. We screened the literature to document the changing perspectives on exotic salmonids in the southern hemisphere, and employed SWOT analysis to assess the conservation prognosis of native galaxiids in the face of salmonid invasions. Our analysis indicates that opinions differ and contradictions abound as to how to prevent further salmonid encroachment. This is largely due to lack of information on the impact of exotics but, more importantly, because the problem is often approached merely from a socio-economic perspective. Sport fishermen, for example, actively support the stocking of rivers to enhance sport fisheries and argue in favour of considering established salmonids as part of the native biodiversity, but also want to see an end to salmonids escaping from fish farms. The salmon industry tends to stress the social and economic benefits brought about by aquaculture, but continues to demand the right to expand and self-regulate. Governments, on the other hand, have not always had consistent or clear policies on exotic salmonids, and have tended to favour some stakeholders and penalized others. Our analysis emphasizes the need to consider biologically meaningful time scales when assessing impacts on biodiversity, and stresses the need to anticipate shifts in public opinion and stakeholder support in conservation.

Key words: aquaculture, conservation, Convention on Biological Diversity, galaxiids, impacts, invasive species, salmonids, sport fishing, stocking, SWOT

Introduction

Exotic salmonids have brought – through sport fishing – wealth to many rural areas of the southern hemisphere where alternative sources of income are sometimes limited (Arismendi & Nahuelhual, 2007; Pascual *et al.*, 2009; du Preez & Hosking, 2010), and have made countries like Chile world leaders in aquaculture (Gajardo & Laikre, 2003). However, exotic salmonids have also caused widespread ecological damage, particularly to native fish fauna (Cambray, 2003*a*; Jackson *et al.*, 2004; McDowall, 2006; Hardie *et al.*, 2006), and the long-term socio-economic impacts of salmonid introductions have yet to be established (Soto *et al.*, 2006).

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Salmonids were first introduced into the southern hemisphere through acclimatization societies, who sought to 'enrich' the local fauna with species from around the world on the grounds that local fauna was deficient and impoverished (Lever, 1992). Nostalgic settlers desired to live with familiar species, while the nobility and the better-off introduced valuable game and trophy fish to boost hunting and fishing (Pears, 1982) in what has been termed 'Ecological Imperialism' (Crosby, 2004). In New Zealand, acclimatization societies were first established by British colonists at around the 1860s, and by 1867 the Trout and Salmon Protection Act was passed to aid 'in the preservation and propagation of salmon and trout in this Colony' (Anon., 1997). Following the successful introduction of brown trout, rainbow trout were introduced by the Auckland Acclimatisation Society in 1893, despite protests by local Maori

Table 1. Dates of successful introductions of exotic salmonids in the temperate waters of the southern hemisphere. Only self-sustaining species are shown (data sources: Chile: Basulto, 2003; Correa & Gross, 2007; Crawford & Muir, 2008; Argentina: Pascual *et al.* 2002; Falklands Islands: McDowall, 2001; South Africa: Cambray, 2003*a*, 2003*b*; Crawford & Muir, 2008; Australia–Tasmania: Jackson *et al.*, 2004; Koehn & MacKenzie, 2004; Lintermans, 2004; New Zealand: Anon., 2007; Pascual & Ciancio, 2007; Correa & Gross, 2008; Kerguelen Islands: Davaine & Beall, 1997; E. Beall, pers. comm.).

Species	Chile	Argentina	Falklands Is.	S. Africa	Australia–Tasmania	New Zealand	Kerguelen Is.
Brown trout	1905	1909	1940s	1876	1864	1867	1958
Atlantic salmon	–	1904	–	–	–	1864	1977[1]
Rainbow trout	1905	1904	–	1890s	1894	1893	–
Chinook salmon	1924	1904	–	–	–	1904	–
Coho salmon	1900s	–	–	–	–	–	1978
Brook trout	–	1904	–	–	1883	–	1962
Masu salmon	–	1987	–	–	–	–	–
Sockeye salmon	–	–	–	–	–	1901	–
Lake trout	–	1904	–	–	–	–	–
Arctic charr	–	–	–	–	–	–	1991

[1]relict, declining population.

people about the impact of exotic trout on native fisheries (Anon., 1997). At around the same time, rainbow trout and brown trout were introduced into Tasmania, Western Australia and South Africa, and then into Chile and Argentina, and more recently into the Falkland and Kerguelen Islands (Table 1). In Chile, the absence of salmonids was seen by some as one of the most 'negative' aspects of local fish fauna, something that called for swift remediation, initially by private entrepreneurs and then by Government itself; concerns about potential salmonid predation on local fish were raised as early as 1903 but were simply ignored (Basulto, 2003).

There is little information regarding the state of native fishes in the southern hemisphere before the introduction of salmonids (Morgan *et al.*, 2004; Pascual *et al.*, 2007) which makes a global salmonid impact assessment difficult, but two of the most widely introduced salmonids (rainbow rout and brown trout) are included in the '100 of the World's Worst Invasive Alien Species' (ISSG, 2008). Today conservation officers in New Zealand and other places in the southern hemisphere such as Tasmania (Morgan *et al*., 2004) or South Africa (Woodford & Impson, 2004) are charged with the seemingly impossible task of protecting 'indigenous species as well as the habitat of trout and salmon' (Anon., 1997), a conservation oxymoron. And while the deliberate stocking of exotic salmonids continues to be common practice in virtually all the southern hemisphere (Limson, 2002*a*; Basulto, 2003; Lintermans, 2004; Pascual *et al.*, 2007), accidental escapes from salmon farms are frowned upon and are regarded as major threats to native biodiversity (Sepúlveda *et al.*, 2009). Moreover, the same salmonid species are considered harmful or beneficial depending simply on the water body where they are found (Chadderton, 2003; Rowe, 2003; Pascual *et al.*, 2009), and are regarded as alien or naturalized depending on when they were first introduced (Cambray, 2003*a*; Gajardo & Laikre, 2003). For example, exotic trout in New Zealand are considered 'pest' in small lakes and ponds of the South Island, but are desirable species in Auckland reservoirs (Rowe, 2003), and in Chile brown trout and rainbow trout are considered 'naturalized' but Atlantic salmon is regarded as alien, despite the fact that the former has probably caused much more ecological damage than the latter (Young *et al.*, 2009, 2010). Thus, salmonids in the southern hemisphere are considered 'best' or 'pest' depending on how they are introduced, where they are found, for how long they have been around or what economic benefit they might provide.

Few anglers would regard salmonids as pests (Chadderton, 2003; Townsend, 2003), but exotic salmonids have had in many places 'negative economic or ecological impacts' and meet, therefore, pest criteria (Koehn & MacKenzie, 2004; but see Falk-Petersen *et al.*, 2006 for other, more stringent pest definitions). Although there are few, if any, global assessments of the net economic benefits and impacts of exotic salmonids in the southern hemisphere, there is no doubt that benefits and impacts have both been substantial (Pascual *et al.*, 2009; du Preez & Hosking, 2010). Today we know that seemingly harmless fish can, given the right conditions, easily turn into pests (Museth *et al.*, 2007; Borgstrøm *et al.*, 2010).

Here we compared the life-history traits of invasive salmonids and invaded galaxiids and undertook a bibliographical search of the literature on exotic salmonids in the southern hemisphere in order to identify the main challenges in the conservation of native galaxiid fishes in the face of salmonid invasions. Our specific objectives were threefold: (1) to identify those salmonid and galaxiid traits most likely to affect the impact of salmonid invasions; (2) to evaluate the changing perspectives on salmonid impacts and identify those areas in most need of research; and (3) to evaluate the main challenges underpinning the conservation of native fish fauna in the face of salmonid invasions.

Materials and methods

We employed three complementary methods to identify the main challenges in the conservation of native galaxiid fishes in the face of salmonid invasions: (1) a comparative study of life-history traits of invasive salmonids and invaded galaxiids; (2) a bibliographic search of studies on salmonids in the southern hemisphere; and (3) a SWOT (strengths, weaknesses, opportunities and threats) analysis.

Life-history variation of invasive salmonids and invaded galaxiids

We first looked at variation in life-history traits of six of the most widespread invasive salmonids (Atlantic salmon, *Salmo salar*; brown trout, *Salmo trutta*; rainbow trout, *Oncorhynchus mykiss*; coho salmon, *Oncorhynchus kisutch*; chinook salmon, *Oncorhynchus tshawytscha*; and brook trout, *Salvelinus fontinalis*) and six galaxiids that have been impacted by the presence of salmonids (peladilla or zebra trout *Aplochiton zebra*; *Aplochiton taeniatus*; puye chico, Falklands minnow or inanga, *Galaxias maculatus*; puye grande, *Galaxias platei*; *Galaxias argenteus*; and *Galaxias brevipinnis*). For these we compiled data from FishBase on maximum body size (cm), trophic level, resilience (calculated as minimum population doubling time, in years), vulnerability to fishing (as a proxy for intrinsic extinction vulnerabilities to other stressors, in percentage), and latitudinal range in their native range (degrees) to give an indication of plasticity and invasiveness. These were the traits available for all the study species. We then carried out PCA using PRIMER (v. 5) to visualize similarities and differences between invading salmonids and invaded galaxiids.

Extent and nature of research effort on exotic salmonids

We searched for papers listed in the ISI Web of Science for all years with 'salmon*' or 'trout' and countries in the southern hemisphere as wild terms in either the title or the topic of the paper. We then classified each paper by country(ies) of study and under one or more of the following (non-exclusive) seven categories based mostly on information gathered from the abstract: ecology, galaxiids, impacts, genetics, fisheries, aquaculture and diseases (including pathogens and parasites). We also employed PCA using PRIMER (v 5.0) to examine differences among countries in their research effort on invasive salmonids.

SWOT analysis

Based on our experience, the literature search and data on comparative life-history strategies outlined above we then carried out an analysis of strengths, weaknesses, opportunities and threats (SWOT) in relation to the protection of native galaxiids in the face of salmonid invasions. SWOT analysis is a strategic planning method traditionally used in business and marketing (Piercy & Giles, 1989), but also increasingly being used in environmental sciences (Paliwal, 2006) and conservation (Jenkins *et al.*, 2009; García-Arberas *et al.*, 2010). SWOT analysis attempts to identify the internal and external factors that are can either facilitate or impede the conservation of native galaxiid fishes threatened by salmonid invasions. Although SWOT analysis has been criticized because it can sometimes be of little practical value (Hill & Westbrook, 1997), it has proved useful in participatory conservation planning because it can identify constraints, highlight uncertainties and help to generate conservation strategies (Verfaillie *et al.*, 2009; Celiktas & Kocar, 2010), making information available to stakeholders.

Results

Expected salmonid impacts resulting from differences in life-history variation

Principal component analysis reveals large differences in life-history traits between invasive salmonids and invaded galaxiids, which form two distinctive groups (Fig. 1). Most of the separation occurs along the second principal component (PC2) which measures mostly variation in range, body size and vulnerability to overfishing. Compared with native galaxiids, invasive salmonids occupy a much larger latitudinal range in their native distribution (indicative perhaps of

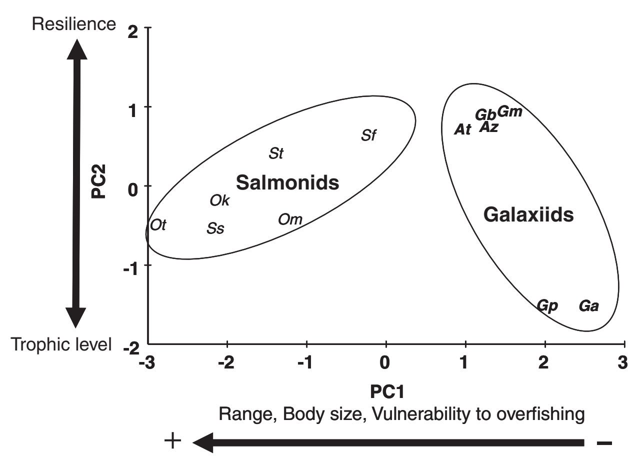

Fig. 1. PCA of the first two principal components accounting for 86% of variation in life history traits of invasive salmonids (in normal typeface) and native galaxiid fishes (in bold). Salmonid species shown are *Salmo salar* (*Ss*), *Salmo trutta* (*St*) *Oncorhynchus mykiss* (*Om*), *Oncorhynchus kisutch* (*Ok*), chinook salmon (*Ot*), *Oncorhynchus tshawytscha* (*Ot*), and *Salvelinus fontinalis* (*Sf*). Galaxiid fishes shown are *Aplochiton zebra* (*Az*), *Aplochiton taeniatus* (*At*), *Galaxias maculatus* (*Gm*), *Galaxias platei* (*Gp*), *Galaxias argenteus* (*Ga*), and *Galaxias brevipinnis* (*Gb*). Axes were labelled according to the two largest eigenvectors (PC1: range −0.500, body size −0.500, vulnerability to overfishing −0.474; PC2: resilience +0.882, trophic level −0.408).

Table 2. Range of direct impacts (+ increase; − decrease, 0 no effect) of exotic salmonids upon native galaxiids in the southern hemisphere (reviewed by Cadwallader, 1996; Morgan *et al.*, 2004; Hardie *et al.*, 2006; McDowall, 2003, 2006; Pascual *et al.*, 2007; Hannon, 2008).

Exotic salmonid	Impacted galaxiid	Trait examined	Observed effect	Location	Reference
Ss, Om	Az	growth	−	Chile	Young *et al.*, 2009
St	Az/At	distribution	−	Chile	Young *et al.*, 2010
Om	Az/At	distribution	0	Chile	Young *et al.*, 2010
St	Az	distribution	−	Falklands Is.	McDowall *et al.*, 2001
St	Gv	distribution	−/0	New Zealand	McIntosh *et al.*, 1994
St	Gv, Gan	distribution	−	New Zealand	Townsend, 1996
St, Om	Gv, Gpau	abundance	−	New Zealand	Jellyman & McIntosh, 2008
St, Om	Gv	abundance	−	New Zealand	Woodford & McIntosh, 2010
St, Om, Ss, Sf	Gm	predation	+	Argentina	Macchi *et al.*, 1999
Om	Gm	predation	+	Australia	Cadwallader & Eden, 1982
Om	Gb	predation	+	New Zealand	Kusabs & Swales, 1991
St	Gm	predation	+	New Zealand	Glova, 2003
St, Om, Sf	Gm	predation	+	Argentina	Macchi *et al.*, 2007
St	Gau	predation	+	Tasmania	Stuart-Smith *et al.*, 2007
Ss, Om, Ok, Ot	Gm, Gp, Az	predation	+	Chile	Arismendi *et al.*, 2009
St	Gm	habitat use	−	New Zealand	Glova, 2003
St	Gm	habitat use	0	New Zealand	Bonnett & McIntosh, 2004
St, Om	Gm	habitat use	−	Chile	Penaluna *et al.*, 2009
St	Gv	habitat use	−	New Zealand	McIntosh *et al.*, 1992
St	Gde, Gel, Gan	foraging	−	New Zealand	Edge *et al.*, 1993
St	Gau	refuge use	+	Tasmania	Stuart-Smith *et al.*, 2008
St	Gan	parasite loads	−	New Zealand	Kelly *et al.*, 2009
Om	Az	morphology	0	Argentina	Lattuca *et al.*, 2007

Ss = *Salmo salar*, St = *Salmo trutta*, Sf = *Salvelinus fontinalis*, Om = *Oncorhynchus mykiss*, Ok = *Oncorhynchus kisutch*, Ot = *Oncorhynchus tshawytscha*, Az = *Aplochiton zebra*, At = *Aplochiton taeniatus*, Gv = *Galaxias vulgaris*, Gm = *Galaxias maculatus*, Gan = *Galaxias anomalus*, Gde = *Galaxias depressiceps*, Gel = *Galaxias eldoni*, Gau = *Galaxias auratus*, Gp = *Galaxias platei*, Gpau = *Galaxias paucispondylu*, Gb = *Galaxias brevipinnis*.

a greater degree of phenotypic plasticity), are much larger (and since have similar age structure, have higher capacity for growth) and tend to be more vulnerable to overfishing. In contrast, there is considerable overlap along the first principal component indicating that – with few exceptions – salmonids and galaxiids tend to occupy similar trophic levels and show similar resilience. The salmonids that show the highest overlap in trophic level and resilience with galaxiids, and thus greatest scope for resource competition, are brown trout, brook trout and rainbow trout. In contrast, chinook salmon, Atlantic salmon and coho salmon are the salmonids that differ the most from galaxiids in terms of range and body size, and can thus be expected to disperse more easily and have greatest potential for predation resulting from a size advantage.

The results also suggest that while salmonid impacts upon *Aplochiton zebra*, *Aplochiton taeniatus*, *Galaxias brevipinnis* and *Galaxias maculatus* will likely result from trophic overlap and salmonid size advantage, impacts upon *Galaxias plateii* and *Galaxias argenteus* are likely to result from size advantage alone, as the scope for overlap in trophic resources appears more limited. Across the southern hemisphere, exotic salmonids directly impact on native galaxiids by reducing their foraging efficiency, limiting their growth, restricting their range, forcing them to seek cover or to use suboptimal habitats, and also by preying upon them (Table 2). On the other hand, exotic salmonids may act as sinks for parasites due to dilution effects and this could be beneficial for native galaxiids (Kelly *et al.*, 2009). Despite the presence of exotic salmonids for over a century in some systems, no evidence of predator-induced morphological changes in galaxiids has so far been documented that could be attributed to salmonid predation (Lattuca *et al.*, 2007).

Variation in research effort on invasive salmonids

Interest in salmonids in the southern hemisphere, although always present and at the heart of some classic studies on fish ecology (Allen, 1951) has increased exponentially since the mid 1990s (Fig. 2), coinciding with the development of salmonid aquaculture in open net cages in Chile. Although consideration of salmonids as invasive species and explicit recognition of salmonid impacts has long been acknowledged (Archey, 1915; Fish, 1966;

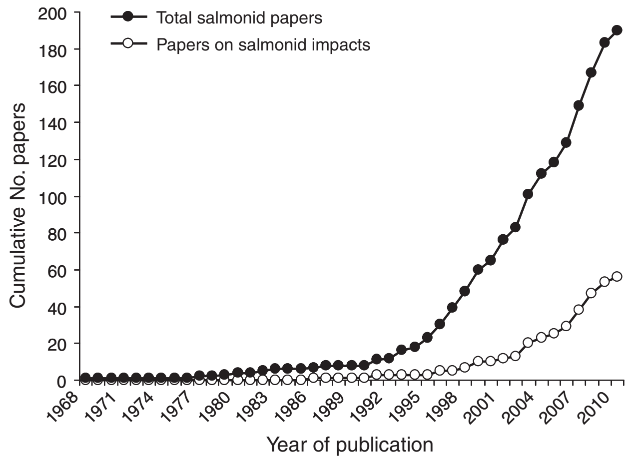

Fig. 2. Trends in the total number of publications on exotic salmonids in the southern hemisphere (no.: 190) and those that deal specifically with salmonid impacts (no.: 56), according to ISI Web of Science. Research effort on exotic salmonids has grown exponentially over the last two decades, but relatively little of it has been directed towards addressing salmonid impacts, despite the fact that native fish are becoming increasingly imperilled by salmonid encroachment.

McDowall, 1968), it was only at the beginning of the 21st century that studies addressing salmonid impacts became common place, currently representing about 30% of all salmonid studies carried out in the southern hemisphere (Fig. 2).

However, countries vary considerably on their research effort on exotic salmonids, as well as on their research emphasis (Table 3). Of the 190 papers examined, almost half (48%) correspond to studies carried out in Chile, and almost one third (28%) correspond to studies in New Zealand. The main driver of salmonid research in Chile is aquaculture or aquaculture-related topics such as salmonid diseases or genetics in salmonid aquaculture, while comparatively little effort has been invested on understanding salmonid impacts (Young *et al.*, 2010; Darwin Initiative www.biodiversity.cl) despite the fact that this is the country where free-ranging salmonids are most abundant, and where they have probably done most damage (Soto *et al.*, 2006; Arismendi *et al.*, 2009). In contrast, research emphasis in New Zealand is placed mostly on salmonid fisheries, salmonid ecology and impact upon native galaxiids. PCA indicates that the position of other countries is intermediate between these two extremes.

SWOT analysis of galaxiid conservation in the face of salmonid invasions

We used SWOT analysis to reveal the main challenges and constraints underpinning the conservation of native galaxiids threatened by the presence of exotic salmonids in the southern hemisphere. The analysis is summarized in Table 4.

Discussion

Our study has revealed several internal traits that can make native galaxiids able to cope, or at least withstand, the impact of salmonid invasions (strengths), as well as some traits that appear to make them particularly vulnerable to predation and competition from salmonids (weaknesses). SWOT analysis has also enabled us to identify external circumstances and policies that can either facilitate (opportunities) or hamper (threats) the recovery of native galaxiid fishes invaded by exotic salmonids. These are discussed below.

Strengths

The advantage conferred by prior residency must rank amongst the highest strengths of galaxiids being invaded by salmonids, as native galaxiids may be expected to show adaptations to local conditions (Crow *et al.*, 2009), and this

Table 3. Distribution of scientific papers (used as a proxy for research effort) on exotic salmonids in the southern hemisphere according to country of study and main topic area (keywords) listed in the ISI Web of Science from 1968 to 2010.

		Keywords							
Country	No. papers	Ecology	Galaxiids	Impacts	Genetics	Fisheries	Aquaculture	Diseases	Total
Argentina	24	10	6	16	4	5	1	3	45
Australia	3	1	2	2	1	0	1	0	7
Chile	91	13	5	17	16	5	73	49	178
Falklands Is.	1	0	1	1	0	0	0	0	2
Kerguelen Is.	7	3	0	0	4	3	1	0	11
New Zealand	54	32	12	17	5	16	10	6	98
Various	10	1	2	4	1	1	4	6	19
Total	190	60	28	57	31	30	90	64	360
	% of total	16.7	7.8	15.8	8.6	8.3	25.0	17.8	100.0

Table 4. SWOT analysis underpinning the conservation of native galaxiid fishes in the face of salmonid invasions.

	Beneficial	Harmful
	Strengths	**Weaknesses**
Internal	1. Galaxiids are local, will benefit from resident advantage	1. Smaller body size and slower growth rate than salmonids
	2. Flexible life strategies	2. Predation by salmonids very likely
	3. Widespread	3. Resource overlap with salmonids
	4. High larval dispersal	4. Smaller distributional range than salmonids
	5. Many are migratory, amphidromous, diadromous	5. Lack iconic/economic value
	6. Inhabit relatively pristine habitats, often free from other stressors	
	Opportunities	**Threats**
External	1. Competition between salmonids may ease impact on galaxiids	1. Most galaxiids are poorly known, data deficient
	2. Better regulations, moratorium on salmonid introductions	2. Expansion of salmon farming
	3. Education, increasing awareness and research	3. Salmonid sport fishing, colonization
	4. *In situ* conservation: salmonid eradication, exclusion devices	4. Synergy with other environmental stressors
	5. *Ex situ* conservation: captive breeding, reintroductions	5. New diseases, pathogens
		6. Most galaxiids lack legal protection, while salmonids are in most places protected

would be advantageous when confronted with salmonid invasions. Such local advantage may come in many forms, from morphologies that appear well matched to local environmental conditions (Crow *et al.*, 2009), to having a superior ability to forage efficiently on local prey or to escape from predators. For example, the burrowing behaviour shown by many Galaxiidae is thought to enable them to seek refuge from predators and to withstand extreme flow conditions (Hay, 2009), while the climbing behaviour of species such as *Galaxias brevipinnis* may allow them to have access to habitats that would be inaccessible to salmonids, as well as to escape from them (McDowall, 2006). Several nocturnal galaxiids in Australia and New Zealand possess accessory lateral lines that are thought to help them forage and avoid predators under low visibility conditions (McDowall, 1997), something salmonids lack. Other galaxiids, such as *Galaxias platei*, are specialized lake benthic feeders and this is thought to enable them to endure harsh winter conditions (Cussac *et al.*, 2004) and to withstand salmonid invasions (Habit *et al.*, 2010). In New Zealand, Leprieur *et al.* (2006) have shown that hydrological disturbances can benefit local galaxiids at the expense of the invading brown trout. Galaxiids in Chile appear to have been able to find thermal refugia from salmonids in some locations, and there is also some evidence that they may be able to better withstand salmonid invasions in lakes than in rivers (Habit *et al.*, 2010).

Many galaxiids show flexible life-history strategies and a high degree of phenotypic plasticity (Barriga *et al.*, 2007), being capable of living in freshwater, brackish and marine waters which should buffer populations against a variety of stressors, including salmonid invasions. For many galaxiids, gene flow appears to be substantial and is mediated through marine larval dispersal (Allibone & Wallis, 1993; Waters & Wallis, 2001; Zemlak *et al.*, 2010), which will tend to facilitate recolonization and prevent local extinctions. Some galaxiids such as *Galaxias maculatus* and *Galaxias platei* are extremely widespread (Baigún & Ferriz, 2003; Habit *et al.*, 2010) and populations may be expected to harbour high levels of genetic diversity (Waters & Burridge, 1999; Zemlak *et al.*, 2010), which may mitigate the impact of salmonids and other stressors. Finally, in many places galaxiids still inhabit relatively pristine habitats which are comparatively free from other stressors, and this would make them better able to withstand pressure from salmonids (but see Leprieur *et al.*, 2006 for the beneficial effect of hydrological disturbance).

Weaknesses

Several attributes of native galaxiids make them particularly vulnerable to invasive salmonids, making their conservation difficult. A small body size is perhaps the greatest problem faced by galaxiids being invaded by much larger salmonids (McIntosh, 2000; McIntosh *et al.*, 2010). Body size is the trait that separates galaxiids from salmonids the most (Fig. 1), as galaxiids tend to attain a much smaller body size than salmonids and grow at a much slower rate in fresh water (Young *et al.*, 2009). Invasion success in fish appears to depend on invader body size (Schröder *et al.*, 2009) and as prey–predator interactions in freshwater are strongly mediated by size differences (Lundvall *et al.*, 1999), galaxiids may be expected to be outcompeted by salmonids. In many places salmonids and galaxiids compete for similar habitats

(Penaluna *et al.*, 2009) and may feed on similar food items (Fig. 1). Absence of evolutionary segregation makes resource overlap, and therefore potential competition, likely.

Salmonids become piscivorous at a relatively small size in the southern hemisphere (Arismendi, 2009; Penaluna *et al.*, 2009; McIntosh *et al.*, 2010) and this, coupled with a size advantage, puts sympatric galaxiids at a risk of predation early in development and makes salmonid predation likely. In addition, galaxiids do not seem to innately recognize invasive salmonids as predators (McLean *et al.*, 2007) and may therefore be unable to mount an efficient antipredatory response other than through learning.

Most galaxiids tend to have a smaller distributional range than salmonids, and although species such as *Galaxias platei* may have been able to expand, recent evidence from Chile suggests that many galaxiid ranges have contracted following invasions by salmonids (Habit *et al.*, 2010). For species with already restricted native ranges such as *Brachygalaxias bullocki* in Chile (Habit *et al.*, 2010) or *Galaxias auratus* in New Zealand (Hardie *et al.*, 2004) further range contractions may put them at a greater risk of extinction.

Unlike exotic salmonids which support important fisheries and aquaculture industries in the southern hemisphere, most galaxiids are not fished and have little economic, cultural or iconic value. Thus, while the economic value of most of the salmonid species introduced into the southern hemisphere is 'Very high', the economic value of the 51 species of native galaxiids is either 'Not marketed' or 'Unknown' (Froese & Pauly, 2010). There are exceptions and some species such as *Galaxias maculatus* (puye, whitebait or inanga) that support small local fisheries hold socioeconomic values (Rowe *et al.*, 1992; Haggerty, 2007) as well as aquaculture potential (Mitchell, 1989; Rodríguez & Hernán, 2006; Mardones *et al.*, 2008). Nevertheless, in Chile and probably elsewhere, exotic salmonids, not the native galaxiids, are the freshwater fishes which are most readily identified by local people (Soto *et al.*, 2006). Such lack of utilitarian value makes galaxiid conservation difficult, particularly in places such as Chile where exotic salmonids are perceived to have brought considerable wealth to the country while native galaxiids contribute little or nothing to the economy. Public attitudes to invasive salmonids are thus strongly coloured by perceived economic benefits. For example, in Australia, public awareness of the impact of exotic fishes on aquatic ecosystems is highly positive for trout but mostly negative for carp simply depending on their different economic value. Thus, carp are regarded as a pest while salmonids have traditionally been revered as game fish and are deliberately stocked (Wilson, 2005).

Opportunities

A number of external conditions can facilitate the protection of galaxiids threatened by salmonid invasions, and constitute opportunities within the framework of a SWOT analysis. These include the development of specific management action plans for the protection of galaxiids, the implementation of education programmes aimed at increasing public awareness about the biodiversity value of native galaxiids, as well as *in situ* and *ex situ* conservation programmes.

It is a conservation paradox – 'crying foul' as McDowall (2006) termed it – that while endangered galaxiids lack specific legal protection in Chile (Soto *et al.*, 2006; Penaluna *et al.*, 2009), Argentina (Pascual *et al.*, 2007) or New Zealand (McDowall, 2006), invasive salmonids in these countries are in some cases fully protected. Giving galaxiids statutory protection as in Tasmania (Hardie *et al.*, 2006) or the Falkland Islands (McDowall *et al.*, 2001) would, therefore, appear to be an essential prerequisite for counteracting the threat posed by invasive salmonids. Public awareness of the plight of galaxiids and their conservation needs is increasing (McDowall, 2006; McIntosh *et al.*, 2010), and as more research is carried out, the threat posed by salmonids is better understood.

It has been suggested that to secure effective galaxiid protection, there should be a ban on the stocking of exotic salmonids (Cadwallader, 1996; Cambray, 2003*a*; Hardie *et al.*, 2006), particularly when such deliberate introductions are carried out by Government Agencies tasked with the protection of local biodiversity in countries which are signatories of the Convention on Biological Diversity. In places where exotic salmonids are farmed in open systems, such as in Chile or Tasmania, issues such as limiting the accidental escape of farmed fish from aquaculture facilities (Sepúlveda *et al.*, 2009) – and identifying salmonid escapees when these occur (Schröder & Garcia de Leaniz, 2010) – also need to be addressed. Farmed salmonids tend to be selected for fast growth, and therefore predation by large, voracious fish escaping from fish farms may pose a particularly insidious threat to galaxiids, both in coastal and freshwater habitats (Soto *et al.*, 2001). On the other hand, and perhaps paradoxically, the spread of farmed salmonids could conceivably benefit galaxiids if competition between farmed and wild (naturalized) salmonids helps to ease salmonid pressures on local galaxiids, or if maladapted genes from farmed populations introgress into naturalized salmonids and decrease their fitness through gene swamping (Thorstad *et al.*, 2008). To date there is no evidence to suggest that the presence of some salmonid species may facilitate further salmonid invasions or that galaxiids may suffer from salmonid invasion meltdown (Young *et al.*, 2009).

In situ conservation of galaxiids has tended to focus on the deliberate exclusion of invasive salmonids, and in some cases, also on salmonid eradication programmes. Salmonid-free areas have been proposed to serve as galaxiid refuges or sanctuaries (Baigún & Ferriz, 2003), and these can have positive impacts on galaxiid conservation (Lintermans, 2000; Jackson *et al.*, 2004). In their native range, migratory salmonids are commonly prevented from accessing upstream areas by a means of barriers and exclusion devices, including picket barriers, velocity barriers, vertical drops, as well as electric and acoustic fields (NMFS, 2008; Fausch *et al.*, 2009), and such a body of knowledge could also be applied to galaxiid conservation. In Australia and Tasmania, exclusion barriers have been moderately successful in preventing upstream movement of brown trout and this has had a positive impact in galaxiid conservation, while in New Zealand v-notched weirs have been designed that allow the passage of climbing galaxiids but exclude migratory salmonids (McDowall, 2006).

Salmonid eradication programmes have been implemented or are being considered in a number of places where salmonids are not native, including Australia (Lintermans, 2000; Lintermans & Raadik, 2003; Rayner & Cresse, 2006), Tasmania (Hardie *et al.*, 2006), South Africa (Limson 2002*a*, 2002*b*; Cambray, 2003*b*) and New Zealand (Chadderton, 2003). In New Zealand, widespread pest management of salmonids is 'neither practical nor fiscally or socially acceptable' (Chadderton, 2003), while in Tasmania opposition by anglers to salmonid eradication from waters inhabited by threatened galaxiids is decidedly stiff (Hardie *et al.*, 2006). In South Africa, it has been suggested that the cost of trout eradication should be partially borne by trout anglers (Cambray, 2003*b*), but no firm programmes appear to have been implemented. The high utilitarian value of salmonids has led some authors to question the wisdom of salmonid eradication programmes, even when salmonid impacts are evident (Townsend, 1996). It is also doubtful that salmonid eradication can be totally successful other than at small spatial scales (Welcomme & Bartley, 1998; Meyer *et al.*, 2006). Small, closed lakes and ponds, as well as headwaters, are the places where salmonid eradication is most likely to be effective (Moore *et al.*, 1986; Lintermans, 2000), and these are also the zones where threatened galaxiids can benefit the most (Lintermans, 2000; McDowall *et al.*, 2001; Baigún & Ferriz, 2003). Nevertheless, experience in managing salmonid invasions in North America indicates that it is usually better to target the early stages of invasions, namely introduction, establishment and spread than trying to reverse or mitigate subsequent impacts (Dunham *et al.*, 2002; Bisson, 2006). It must also be remembered that even when salmonid eradication programmes are successful, these may have unforeseen negative impacts upon native species (Dunham *et al.*, 2002; Rayner & Creese, 2006). *Ex situ* conservation offers opportunities for reversing, or at least mitigating, the impact of salmonids upon threatened galaxiids, but there seem to have been few, if any, successful captive breeding programmes of galaxiids for reintroduction (McDowall, 2006; McIntosh *et al.*, 2010). Recent interest in developing protocols for the commercial rearing of galaxiids (Mitchell, 1989; Rodríguez & Hernán, 2006; Mardones *et al.*, 2008) could perhaps be adapted for live gene banking and reintroduction purposes (McDonald, 2007). The reintroduction of artificially reared galaxiids could help halt their decline and reverse impacts caused by salmonid encroachment, especially if reintroductions are carried out in combination with salmonid eradication and exclusion programmes to prevent subsequent recolonization (Rayner & Creese, 2006). This is certainly an area where research is badly needed (McIntosh *et al.*, 2010), especially for highly imperilled and rare galaxiids (McDowall, 2006), though given their taxonomic uncertainty and difficulty of identification, DNA barcoding may be needed for galaxiid broodstock selection and captive breeding (Ward *et al.*, 2005; Swartz *et al.*, 2008).

Threats

Several external conditions can hinder the conservation of galaxiids in the face of salmonid invasions and these can be regarded as threats within a SWOT framework. Notwithstanding a substantial increase in galaxiid research effort in recent years (Fig. 1), most galaxiids are still poorly known (Pascual *et al.*, 2002; McDowall, 2006) and this possibly constitutes one of the most important obstacles to their conservation. Indeed, almost 20% of the 51 listed species of galaxiids have only been identified in the last 25 years, and their conservation status has either not been evaluated (NE – 55%) or suffers from data deficiency (DD – 14%; Froese & Pauly, 2010). Given that most of the remaining galaxiids are listed by the IUCN Red List as being critically endangered (CR, 8%), or vulnerable (VU, 18%), it seems clear that invading salmonids are impacting upon species about which very little is known, making it difficult to develop sound conservation strategies.

As with many other conservation challenges, two sources of scientific uncertainty may hamper galaxiid conservation: epistemic and aleatory uncertainties (Brown *et al.*, 2010). Epistemological uncertainty results from lack of knowledge and represents a property of the observer and therefore extrinsic to the scientific problem being addressed. Many aspects of the ecology and life history of galaxiids, as well as of the ways salmonids may impact upon them, are seriously data deficient and this may compromise their conservation. For example, the reproduction of *Aplochiton zebra*, a species listed as threatened in parts of its range (McDowall, 2006), has only been described recently (Lattuca *et al.*, 2008) and very little is still known about it. Aleatory or random uncertainty, on the other hand, is an inherent property of the system, and cannot be reduced by an improvement in knowledge (Brown *et al.*, 2010). Many galaxiids are widespread and have complex life histories, and as population differences are likely to be significant, there will always be uncertainty over the extent to which knowledge gained in parts of their range can be transposed to other situations. For example, it is not clear whether resident galaxiids are more or less threatened than migratory galaxiids, or require different conservation strategies (McDowall *et al.*, 2001; Habit *et al.*, 2010; McIntosh *et al.*, 2010). Salmonid impacts on galaxiids are also likely to differ substantially between species (Young *et al.*, 2010), between rivers and lakes (Pascual *et al.*, 2009; McIntosh *et al.*, 2010), as well as between freshwater and marine environments (Correa & Gross, 2008). Scientific uncertainty, it seems, will always characterize the management of risks imposed by non-native salmonids (Leprieur *et al.*, 2009).

The continuing stocking of exotic salmonids for sport fishing, along with the expansion of salmon farming, constitute additional threats to the protection of native galaxiids, not only in salmon farming nations such as Chile or Australia (Tasmania), but also in neighbouring countries which may be invaded by migratory salmonids, as has occurred recently in Argentina (Ciancio *et al.*, 2005; Becker *et al.*, 2007; Correa & Gross, 2008). Cultured salmonids can add pressure to native galaxiids already threatened by the spread of established (naturalized) salmonids, although experience in the Kerguelen Islands suggests that it is difficult to predict the evolution of salmonid invasions (Ayllon *et al.*, 2006). Invading salmonids can introduce new pathogens and alter diseases patterns of native galaxiids (Torres *et al.*, 2004; Kelly *et al.*, 2009), and can also act synergistically to augment the impact of other stressors (Nyström & McIntosh, 2003; Habit *et al.*, 2010; Woodford & McIntosh, 2010). Finally, as exotic salmonids are now the most abundant freshwater fishes in many parts of the southern hemisphere (Soto *et al.*, 2001; McIntosh *et al.*, 2010), benefitting from widespread public support and legal protection (Chadderton, 2003; McDowall, 2006), it may be difficult to curtail, let alone reverse, salmonid impacts without changes in legislation.

Conclusions

Since their original introduction over a century ago, exotic salmonids have been favoured over native fishes in much of the southern hemisphere. To this date salmonids continue to be revered and benefit from legal protection in many areas of Chile, Argentina, South Africa, Australia and New Zealand while native galaxiid fishes remain largely unprotected and few, if any, concerted efforts have been made towards their conservation. Government agencies tasked with the protection of native galaxiids continue in many cases to live under a conservation oxymoron: they protect and propagate the very same species which have caused much of the galaxiid's demise. And although research effort on exotic salmonids in the southern hemisphere has in recent years increased significantly, relatively little of it has been directed towards understanding, let alone reversing, salmonid impacts. To a large extent, in galaxiid conservation, science has merely provided what Coblentz (1990) termed 'information only for the eulogy'.

Managing for co-existence between exotic salmonids and native galaxiids is possibly the best management option that can realistically be achieved in many situations. But it is difficult to imagine how the restoration of the most threatened galaxiids can be accomplished without controlling the spread of invasive salmonids, and in some cases culling them. History has shown that salmonids can evolve and spread surprisingly rapidly and that they will likely continue to spread if left unchecked. We failed to find evidence to suggest that trout angling has resulted in the protection of native fishes, or that statutory protection of salmonid habitats has always been beneficial for galaxiid conservation. On the contrary, it can be argued that trout fishing possibly represents one of the greatest obstacles for long-term galaxiid conservation because it serves to perpetuate the very same utilitarian view of biodiversity that acclimatization societies had over a century ago. Galaxiids do not have, and will likely never have, any significant appeal for sport fishing. It is also doubtful they will fulfil an important aquaculture niche, or that galaxiid fisheries will ever acquire the same high value that salmonid fisheries have. But it is indefensible to treat exotic salmonids as 'best' or 'pest' depending simply on whether they accidentally escape from fish farms, are deliberately introduced by anglers or bring short-term revenue. Ultimately, and as with many other dilemmas in biological invasions (Gozlan & Newton, 2009), societies will need to decide what risks are worth taking, and what the trade-offs in the salmonid–galaxiid conflict should be. To this end, the Convention on Biological Diversity represents probably the best hope for finding a common ground for galaxiid conservation in the face of salmonid invasions.

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