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ORIGINAL PAPER

Conservation of endangered galaxiid fishes in the Falkland Islands requires urgent action on invasive brown trout

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Abstract Non-native salmonids are protected in the Southern hemisphere where they sustain aquaculture and lucrative sport fisheries, but also impact many native fishes, which poses a conservation conundrum. Legal protection and human-assisted secondary releases may have helped salmonids to spread, but this has seldom been tested. We reconstructed the introduction of brown trout (*Salmo trutta*) to the Falkland Islands using historical records and modelled its dispersal and probability of invasion using a generalized linear model and Leave One out Cross Validation. Our results indicate that establishment success was ~ 88%, and that dispersal was facilitated over land by proximity to invaded sites and density of stream-road crossings, suggesting it was human assisted. Brown trout have already invaded 54% of Falkland rivers, which are 2.9–4.5 times less likely to contain native galaxiids than uninvaded streams. Without strong containment we predict brown trout will invade nearly all suitable freshwater habitats in the Falklands within the next ~ 70 years, which might put native freshwater fishes at a high risk of extinction.

Keywords Invasive species · Translocations · Risk management · Invasion risk competitive exclusion

Introduction

Invasive species represent one of the major threats to freshwater biodiversity, and yet their introduction has in many cases been intentional. For example, salmonids have been deliberately translocated all over the world to provide fishing and aquaculture opportunities since the nineteenth century (McDowall 2006), despite being responsible for the demise of native fish fauna (Arndt et al. 2018; Cussac et al. 2020; Garcia de Leaniz et al. 2010; McIntosh et al. 2010).

Human activities have not only been responsible for the introduction of invasive species, but in many cases have also helped with their expansion (Hulme 2015). Yet, knowledge on the extent and speed of ongoing invasions is limited, due to lack of accurate introduction records and confounding environmental

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factors (Tabak et al. 2017). Islands provide ideal scenarios to examine the speed and impact of invasions because the date and location of introductions are typically well known, and there is often baseline information on the status of native species before the invasion (Ewel and Högberg 1995).

Brown trout (*Salmo trutta*) is one of the most successful freshwater invaders and has been included as one of the '100 of the world's worst invasive alien species' (Lowe et al. 2000) due to its widespread ecological damage. The species has been implicated in the decline of native galaxiid fishes in many parts of the Southern hemisphere (McDowall 2006), most notably in South America (Elgueta et al. 2013; Ortiz-Sandoval et al. 2017; Young et al. 2010), New Zealand (Jones and Closs 2015; McDowall 2003; McIntosh et al. 2010), South Africa (Weyl et al. 2017) and the Falkland Islands, where it has benefitted from protected status (Falkland Islands Government 1964; McDowall et al. 2001). This has created a conservation conundrum because protecting non-native salmonids to boost sport fishing contributes to putting native fishes at risk (Garcia de Leaniz et al. 2010; Weyl et al. 2017).

Three surveys of the freshwater fish of the Falkland Islands, conducted 10–20 years ago, concluded that brown trout had severely impacted both the resident and migratory ecotypes of two of the three native galaxiids, *Aplochiton zebra* and *Aplochiton taeniatus* (Fowler 2013; McDowall et al. 2001; Ross 2009). *Aplochiton* spp. appear to have contracted their range and are threatened by secondary releases, i.e., invasions following the initial introductions (McDowall 2006; McDowall et al. 2001), but without knowledge on the speed of invasions it is difficult to predict future impacts. In the Kerguelen Islands, also in the Southern hemisphere, the expansion of invasive brown trout was initially very rapid, and 17 watersheds were colonised within the first 30 years after the species was introduced, and then slowed down as more habitats became invaded (Labonne et al. 2013; Lecomte et al. 2013). Whether the same has happened in the Falkland Islands and other invaded islands is not clear.

Here we reconstructed the introduction and establishment of brown trout in the Falkland Islands using historical records and modelled its dispersal using anthropogenic and bioclimatic variables. We derived risk maps to help identify galaxiid populations at high risk of invasion and prioritise the establishment of freshwater refugia. We also estimated past and future rates of invasion under different management scenarios to help managers understand the urgency of the situation.

Methods

Reconstructing the introductions of brown trout

Historical records of the introduction of brown trout in the Falkland Islands (Table S1) were compiled and cross-referenced from Arrowsmith and Pentelow (1965) and Stewart (1973, 1980), supplemented with information from the media in the United Kingdom (Salmon and Trout 2012), and from Basulto (2003), Faundez et al. (1997) and Daciuk (1975) in South America. We also searched the Stirling University library for shipment records from the Howietoun hatchery (built in 1881) as this hatchery had dispatched salmonid eggs to North America (Westley and Fleming 2011).

Sampling of freshwater fish

A database of presence/absence records of the four species of freshwater fish present in the Falkland Islands (three native galaxiids, *A. zebra, A. taeniatus,* and *Galaxias maculatus;* and the non-native brown trout) was compiled by cross-checking records from McDowall et al. (2001) and Ross (2009), supplemented with information from anglers and our own sampling (Fowler 2013; Minett et al. 2021a, 2021b). The survey by McDowall et al. (2001) employed seine, gill and fyke netting, spotlighting at night, and electrofishing of ~ 50 m stream reaches. Ross (2009) employed electrofishing, seine netting and visual checks. We used single-pass electrofishing (Smith-Root ELBP2), seine netting and visual surveys during 2011–2013 to add 28 new sites to the database, bringing the total number of sites sampled for freshwater fish to 134 (Table S2). As the two *Aplochiton* species are morphologically similar and easily confused during sampling (Vanhaecke et al. 2012b), we combined them for analysis.

Species distribution modelling

We divided the Falkland Islands into 8,813 1×1 km^2 grid cells, and excluded cells that had more than 30% of their area in the sea and those that contained no rivers, as in a previous species distribution modelling (Rodriguez-Rey et al. 2019). We modelled brown trout presence/absence data from 134 sites (Table S2) using 12 anthropogenic and 9 bioclimatic predictors (Table S3) for which we extracted mean values or took the value from the centre of the grid cell using zonal statistics and sample raster value tools in QGIS 3.4. We calculated the Variance Inflation Factor (VIF) using the *corvif* function in R3.5.3 (R Core Team 2019), excluded three predictors with VIF > 3 to reduce collinearity (Dormann et al. 2013), and randomly divided equal numbers of presence and absence records into training and testing datasets.

Brown trout distribution was modelled via a generalized linear model using a binomial distribution with a logit-link function with the Leave One Out Cross Validation (LOOCV) following Hooten and Hobbs (2015); R code details are given in Table S5. We used the *drop1* function in R3.5.3 to test the significance of individual predictors and arrive at a minimal adequate model *sensu* Crawley (2007) based on changes in AIC (details of model terms and model selection are given in Table S4). Model performance was assessed using the *evaluate* function in the *dismo* R package to examine the area under the curve (AUC) (Fielding and Bell 1997). Statistical significance was determined via parametric bootstrapping (1,000 simulations) against a null model containing the same testing and training datasets as the most plausible model (Rodriguez-Rey et al. 2019), using the *PBmodcomp* function in the *pbkrtest* R package (Halekoh and Højsgaard 2014). Model assumptions were checked by inspection of residuals and diagnostic plots.

Establishment success and calculation of invasion risk

To calculate establishment success, we compared the proportion of introduction sites that still had brown trout ~ 50 years later against the random 50% expectation using a binomial test. We then assessed how the presence of brown trout influenced the presence of native galaxiids by calculating relative risks.

Risk maps

We used QGIS 3.4 to generate invasion risk maps based on the probability of brown trout occurrence, calculated using the LOOCV procedure across all valid grid cells, as explained above. For clarity, we classified each suitable grid cell into four risk categories: very high risk of invasion ($R \geq 0.75$), high risk ($R = 0.50$–0.75), moderate risk ($R = 0.25$–0.50) and low risk ($R < 0.25$).

Predictive modelling of brown trout invasions under different management scenarios

We modelled the occupancy of brown trout since 1950 and predicted future expansion over a 142-year period (~ 24 generations) considering three different management scenarios: (1) no containment, (2) moderate containment (a 10% reduction in the probability of invasion at each cell), and (3) strong containment (a 30% reduction in the probability of invasion at each cell). For cells with a high probability of invasion ($P \geq 0.8$) we assumed that containment would not be effective so we maintained the original invasion probabilities (i.e. no containment, scenario 1). Management scenarios were modelled using the most plausible species distribution model (Table S4) and the LOOCV invasion probabilities that we had calculated for each grid cell.

As grid cells were found to be more likely to become invaded if they were close to invaded sites (see Results), we calculated the Euclidean distance from each uninvaded site to the nearest invaded site. Invasion probabilities were then updated at each iteration under the three scenarios outlined above. Each scenario was run over 300 iterations, and from this a mean percentage occupancy and 95% confidence intervals were estimated. We used the observed rate of expansion (0.9% increase in occupancy/yr since 1950) to calibrate the model and convert the number of model iterations into calendar years (one iteration = ~ 24 years or ~ 4 generations; details and R code are given in Table S5).

Ethics & permits

Fish sampling was carried out under permit number R18/2018 (17/04/2018) issued by the Falkland Islands Government (Falkland Islands

Environmental Committee) and Swansea University Ethics Committee (Reference number SU-Ethics-Student-081217/307; SU-Ethics-Student-090118/299; SU-Ethics-Student-160118/463.

Results

Origin of brown trout

Approximately 113,000 brown trout eggs were shipped to the Falkland Islands on eight separate occasions over an 18-year period (1944–1962, Table S1). Although original records are missing, many consignments were described as arriving in 'excellent condition' (Stewart 1973). The first introductions (1944–1947) came from the Lautaro hatchery in Chile (Arrowsmith and Pentelow 1965; MacCrimmon and Marshall 1968), and were primarily sourced from resident (i.e. non-anadromous) broodstock of German origin (Faundez et al. 1997; Radcliffe 1922). Subsequent eggs came from three sources in England: Surrey, Pentlands and Lancashire. The Surrey and Pentlands fish were from resident parents, while the Lancashire trout were derived from 'sea run trout' caught in the River Lune (Arrowsmith and Pentelow 1965). The provenance of the Pentlands resident trout is unclear, but they may have originated from Cobbinshaw Loch (Arrowsmith and Pentelow 1965; Stewart 1973), Loch Leven (Fish Loch Leven 2019), or the Howietoun Hatchery (Ross Gardiner, pers. comm.). The Howietoun hatchery had reared trout from Loch Leven and many other sources, but we found no records of fish having ever been sent to the Falkland Islands. In total 28 different sites were stocked, but three rivers–all within a 25 km radius of the capital Stanley—received most of the introductions (Table S1).

Establishment success and rate of invasion

Of the 17 stocked sites for which there are fish survey data, 15 sites still had brown trout ~ 50 years later. Establishment success can therefore be estimated as 88% (95CI = 62–98%), which is significantly better than chance ($\chi^2 = 8.47$, df = 1, $P = 0.004$).

Following the initial introductions during 1947–1962, brown trout have invaded 34 new sites over a ~ 60 year period, which represents an invasion rate of 0.6 new sites/year or ~ 6 new sites/generation, using a generation time of 6 years (Fowler 2013).

Modelling of brown trout distribution

At the time of the last survey (2012), brown trout occupied 54% of all sampled 1km^2 grid cells, while *Aplochiton* spp. only occupied 18% of the area, confined to the South of the Islands (Fig. 1). More recent samples from Minett et al. (2021a) were not included as information was not available for all species. The most plausible model of brown trout occurrence contained only three predictors (Table S4): euclidean distance to the nearest invaded point (estimate = -0.238, SE = 0.067, t = -3.56, $P < 0.001$), absence of *Aplochiton* spp. (estimate = -1.57, SE = 0.769, t = -2.04, $P = 0.041$) and number of river road crossings in the drainage basin (estimate = 0.156, SE = 0.066, $t = 2.37$, $P = 0.018$). The model explained the occurrence of brown trout significantly better than chance (Likelihood Ratio Test, $\chi^2 = 52.17$, df = 3, $P < 0.001$, AUC = 0.85).

Impact of brown trout on native galaxiids

Native galaxiids were less likely to occur in streams invaded by brown trout than in uninvaded ones (Fig. 2), but the impact of invasive brown trout was more pronounced in the case of *Aplochiton spp* than in the case of *G. maculatus. Aplochiton spp.* was 4.5 times less likely to persist in streams invaded by brown trout than in uninvaded streams (95CI = 1.8–11.2, $P < 0.001$), whereas for *G. maculatus*, the presence of brown trout decreased the probability of co-existence 2.9 times (95CI = 2.0–4.2, $P < 0.001$).

Mapping invasion risk

A risk map generated from the LOOCV probabilities of new brown trout occurrence identified 21% of uninvaded cells with a very high risk of invasion ($R \geq 0.75$), 24% with a high risk ($R = 0.50$–0.75), 17% with moderate risk ($R = 0.25$–0.50) and 38% with low risk ($R < 0.25$). By overlaying the distribution of the endangered *Aplochiton* spp. we identified 10 uninvaded sites having a high or very high risk of brown trout invasions and where containment

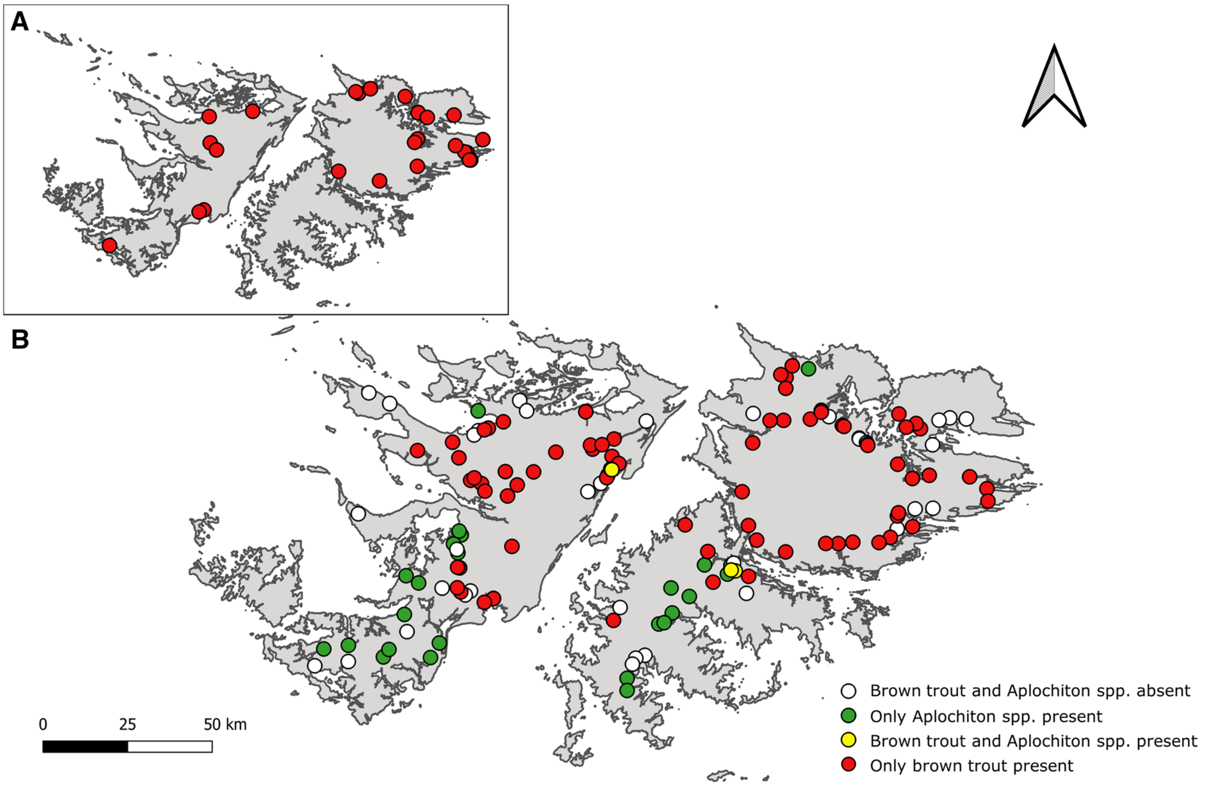

Fig. 1 Map of the Falkland Islands showing (A) sites of the historical introductions of brown trout during 1944–1962 (details given in Table S1) and (B) presence/absence of brown trout and native *Aplochiton* sp. based on 1999–2012 surveys (detailed in Table S2) with 6 additional sites sampled in 2018–2019

measures should be considered to exclude brown trout and protect native freshwater fish (Fig. 3).

Invasion under different management scenarios

Our simulations indicate that if nothing is done to contain the expansion of brown trout (scenario 1) the species is predicted to increase its occupancy from 54 to 93% within the next 70 years (95CI = 70–99%). Under scenario 2 (moderate containment) occupancy is predicted to increase to 86% (95CI = 59–94%), while under scenario 3 (strong containment) occupancy is predicted to be 69% (95CI = 47–81%; Fig. 4). Thus, occupancy is predicted to increase under all three scenarios, but only with strong containment can current *Aplochiton* refugia be afforded some protection from brown trout invasions.

Discussion

Our study indicates that brown trout have already invaded 54% of the streams in the Falkland Islands since they were introduced in 1944–1962 and are impacting native freshwater fish. Streams invaded by brown trout were significantly less likely to harbour native galaxiids than uninvaded streams, suggesting that the impacts are substantial. This finding is consistent with competitive exclusion of native galaxiids by invasive brown trout (Garcia de Leaniz et al. 2010; Young et al. 2009), exacerbated by predation and trophic interference (Arismendi et al. 2014; Elgueta et al. 2013) seen elsewhere in South America. Our simulations suggest that unless more stringent measures are put in place, brown trout will probably invade nearly all remaining suitable freshwater habitats in the Falkland Islands within the next ~ 70 years. Given that endangered *Aplochiton* sp. currently

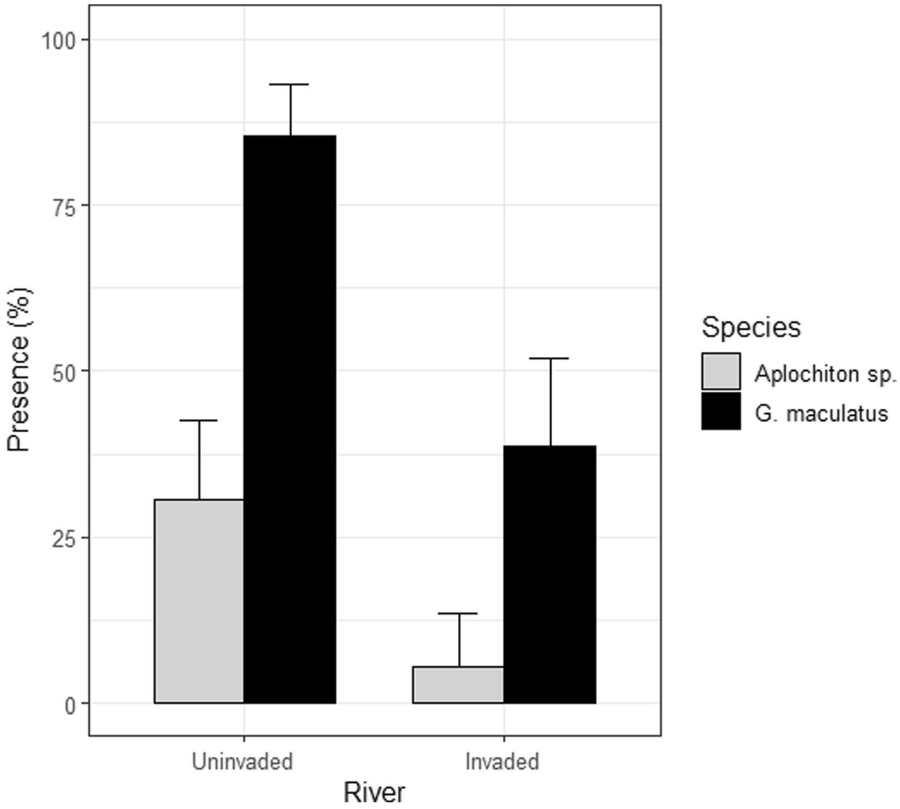

Fig. 2 Frequency of occurrence (% and binomial upper 95CI) of native galaxiids (*Galaxias maculatus* and *Aplochiton* spp.) in streams invaded by brown trout ($N=62$) and in uninvaded streams ($N=72$)

only occupy ~ 18% of the area, mostly confined to the southern part of the islands, brown trout may be expected to drive *Aplochiton* sp. to near extinction.

It is possible that some galaxiid refugia may persist in the headwaters if these are inaccessible to brown trout, but slope was not a significant predictor of brown trout presence in our study and even the steepest sites already contain brown trout. Some land-locked ponds had also been invaded. This suggests that without active measures and more stringent protection, few if any places in the Falklands should be considered safe from brown trout invasions. The recent construction of culverts at river-road crossings may make it more difficult for sea run trout to invade some areas in the future, but the same structures will also impact *Aplochiton* migrations (Fowler and Garcia de Leaniz 2012; Ross 2009). For this reason the use of artificial barriers and exclusion devices to limit the spread of brown trout will require careful consideration (Jones et al. 2021b).

The establishment success of brown trout in the Falkland Islands was very high (88%), as seen elsewhere in the Southern hemisphere (Arismendi et al. 2014; Davidsen et al. 2021; Lecomte et al. 2013; Young et al. 2010). Remarkably, no failed introduction of brown trout has ever been reported in Argentina (Baigún and Quirós 1985), which serves to highlight the extraordinary invasiveness of this species. Several factors may help explain this. Firstly, our study shows that brown trout introduced into the Falkland Islands originated from at least four different origins with two life history strategies (anadromous, non-anadromous), which resulted in genetic admixture (Minett et al. 2021b). It is known that multiple origins and genetic admixture can increase genetic diversity and facilitate adaptation to novel conditions (Consuegra et al. 2011), which along with repeated introductions may increase invasion success. Establishment success may have also been facilitated by phenotypic plasticity and marine dispersal, as demonstrated recently by acoustic tracking (Davidsen et al. 2021; Minett et al. 2021b).

However, marine dispersal alone cannot explain the current distribution of brown trout in the Falklands; secondary translocations must have also taken place because the species is now found in at least two

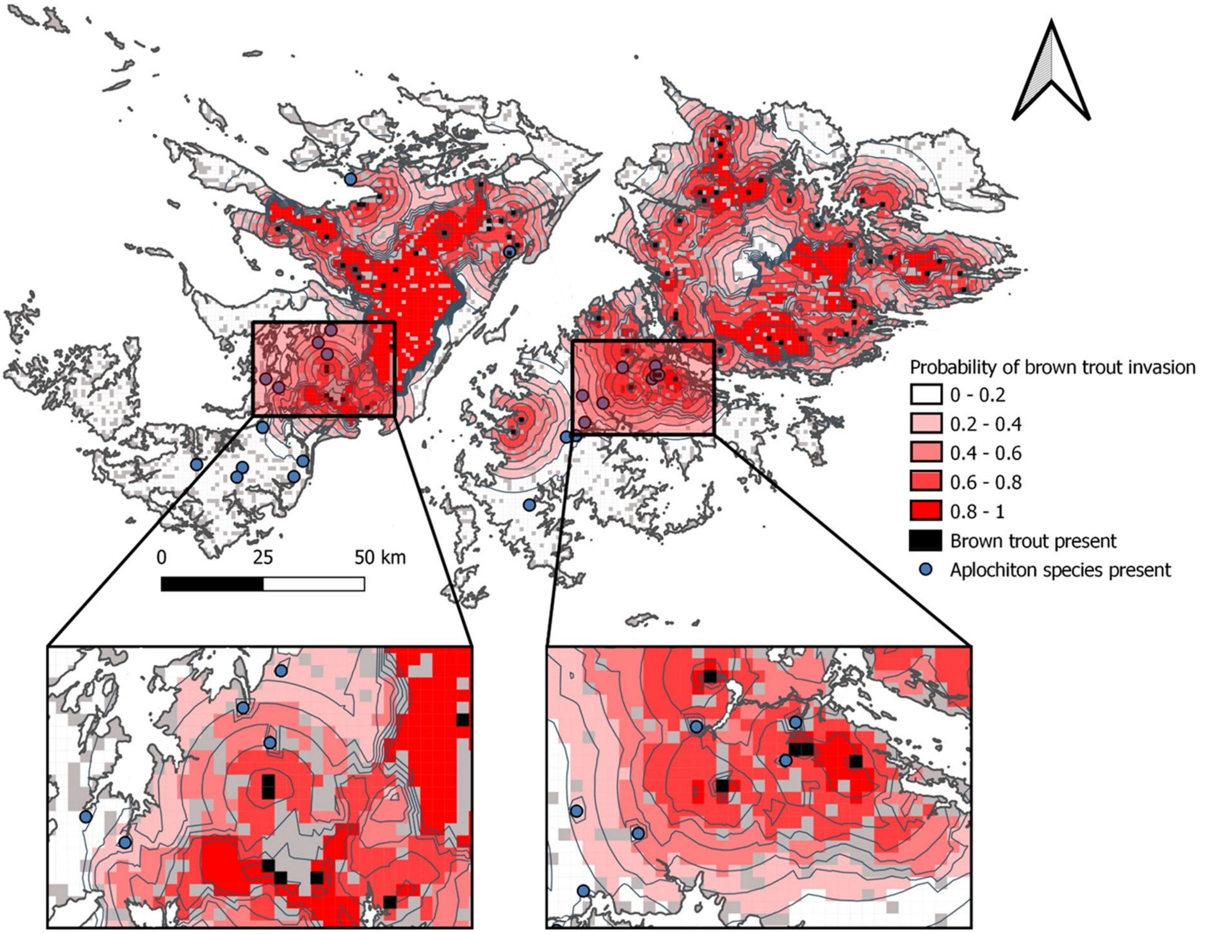

Fig. 3 Risk maps showing probabilities of brown trout invasion based on species distribution modelling. *Aplochiton* refugia at a high risk of brown trout invasion are shown in the insets

land-locked sites, where it could not have reached without human intervention. Transporting brown trout has been illegal in the Falklands since 1999, but some translocations must have taken place (McDowall et al. 2001). Indeed, our results indicate that brown trout presence was predicted by proximity to other invaded sites (overland, but not around the coast) and by the density of river-road crossings, which is consistent with secondary translocations facilitated by the road network, as seen in many other aquatic invasive species. For example, roads have facilitated the expansion of smallmouth bass (*Micropterus dolomieu*) in remote lakes in Canada (Kaufman et al. 2009) and of bluegill (*Lepomis macrochirus*) in Japan (Kizuka et al. 2014). The Falklands has ~ 800 km of roads that crisscross a dense river network, most of which were built over the last three decades (Fowler and Garcia de Leaniz 2012), and it is likely that this may have facilitated the expansion of brown trout.

Brown trout have expanded at a rate of 0.6 new sites/year or ~ 6 new sites per generation since they were first introduced, which is similar to the invasion rate found in the Kerguelen Islands where the species colonized 32 watersheds in ~ 50 years or 0.6 watersheds/year (Labonne et al. 2013; Lecomte et al. 2013). As found in the Kerguelen Islands, our simulations suggest that the speed of invasion is not constant over time. It may consist of two phases (Fig. 2), an initial phase characterized by rapid colonization, likely aided by low competition, fast growth and coastal dispersal (Jarry et al. 2018; Labonne et al. 2013; Minett et al. 2021b), and a second, slower

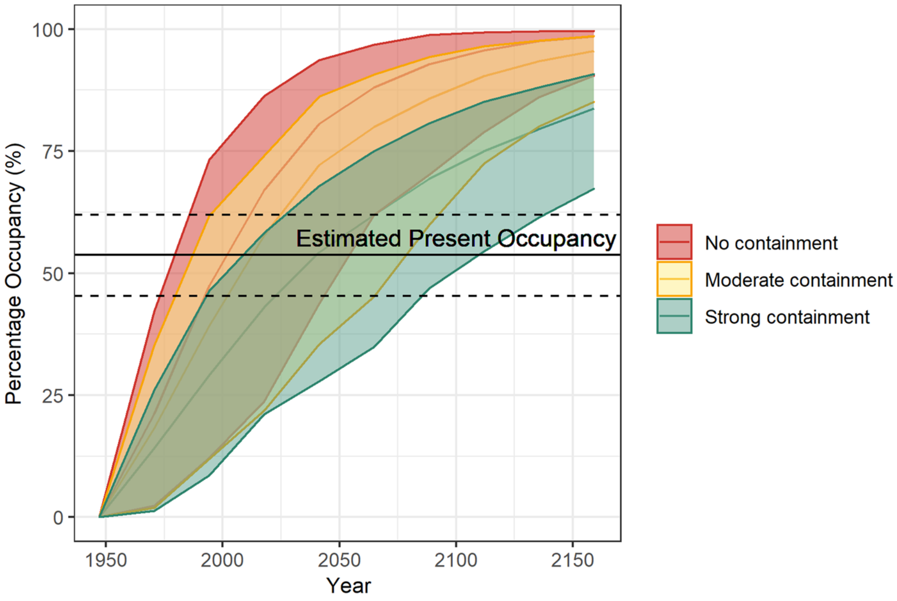

Fig. 4 Modelled expansion (% occupancy of suitable sites) of invasive brown trout in the Falkland Islands under three different management scenarios: (1) no containment (red), (2) moderate containment (yellow), achieved by reducing by 10% the probability of invasion at each cell, and (3) strong containment (green), achieved by reducing by 30% the probability of invasion at each cell. The envelopes denote the 95CIs around the three scenarios, and the dotted line the binomial 95CI around the present occupancy

phase seemingly being driven by density-dependence (Labonne et al. 2013). In Newfoundland, where brown trout is also invasive but where it competes with native Atlantic salmon, the species has expanded at rate of 4 km/year, and after ~ 135 years is still confined within a 500 km radius from the original sites of introduction (Westley and Fleming 2011). In contrast, recent eDNA analysis of water samples in the Falklands (Minett et al. 2021a) has detected brown trout in additional streams since our last survey, indicating that the species is still expanding at a rate of ~ 0.9%/year, suggesting it has not yet slowed down.

Other invasive salmonids are also threatening the native fish fauna of the Falklands. For example, both chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) are increasingly being caught off West Falkland (Fowler 2013), most likely originating from Chile or Argentina, highlighting the potential for further salmonid invasions. Similarly, the recent development of sea trout farming in open-net cages in the Falklands in 2013 poses a risk of escapees, which could further compromise the survival of native galaxiids, as seen in Patagonia (Consuegra et al. 2011; Vanhaecke et al. 2012a), particularly if sea cages are located close to *Aplochiton* refugia. Given the widespread ecological damage caused by invasive salmonids, being able to identify areas at high risk of invasion is critical for managing and curtailing their expansion. In this sense, our risk maps (Fig. 3) may aid conservation officers tasked with the protection of native fish fauna to monitor high risk areas and develop an integrated management strategy for invasive salmonids in the Falkland Islands.

Conclusions & recommendations

Galaxiids rank among some of the most severely threatened fish in the world due to the introduction of invasive salmonids (Cussac et al. 2020; McDowall 2006; Weyl et al. 2017). Our modelling suggests that without containment and strict measures brown trout will likely invade all remaining suitable freshwater bodies in the Falkland before the end of the century, putting the endangered native freshwater fish at high risk of extinction.

Existing legislation makes it illegal to transport or propagate brown trout in the Falkland Islands (Falkland Islands Government 1964), but this seems insufficient as the species is also afforded a protected status, and fishing for trout is widely promoted (Falkland Islands Government 2015), which may facilitate its spread. Promoting trout fishing can hamper galaxiid conservation if it serves to perpetuate the view that only fish that have utilitarian value are worth protecting (Garcia de Leaniz et al. 2010), and there is perhaps also a risk that creating and publicizing galaxiid reserves may attract those who might wish to propagate brown trout even further. Effective education and communication are therefore key (Ross 2009).

The road network appears to be a main route of human-assisted translocations, and it is essential that more stringent measures are put in place. This may involve making people more aware of the impacts of salmonid invasions and passing more stringent legislation. Exclusion barriers could also be deployed around galaxiid refugia to reduce the risk of salmonid invasions (Jones et al. 2021b), but care must be taken to ensure this does not impact native galaxiids, which may pose a challenge as even small barriers can have negative impacts on weak swimmers (Jones et al. 2021a). *Aplochiton* sp. includes both freshwater resident (land-locked) and migratory (amphidromous) populations, and both ecotypes are present in the Falkland Islands (McDowall 2006; Vanhaecke et al. 2012b). Maintaining connectivity and ensuring access to freshwater is essential for the viability of *Aplochiton* larvae migrating from the sea (McDowall et al. 2001) but this also means that they are very vulnerable to sea trout invasions, making barrier management particularly challenging in this case.

Changes to angling regulations might also be useful. Currently, brown trout anglers are subject to a daily bag limit and a strict fishing season, lifting these restrictions may help slow down the invasion front in some places. Intensive fishing could be used to eradicate brown trout and establish buffer zones around *Aplochiton* spp. refugia although this may not be effective if there is compensatory density-dependent mortality (Saunders et al. 2015). Analysis of eDNA from water samples could be used to delineate galaxiid refugia (Minett et al. 2021a), to serve as an early warning of brown trout invasions, and to establish whether containment or eradication measures have been successful.

Since McDowall's call for action 20 years ago (McDowall et al. 2001), brown trout has continued to expand while native galaxiids have continued to decline. *Aplochiton* spp. features on a Falklands postal stamp while *Galaxias maculatus* is called the 'Falklands minnow', testifying to their importance for local islanders, and their place in the natural and cultural heritage of the Falkland Islands. Brown trout has brought wealth and recreation opportunities to the Falklands, but has also caused the demise of native freshwater fish. Our study shows that urgent protection measures are needed to safeguard their survival.

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Data availability Availability of data and material. The data files for this paper have been stored in figshare https://doi.org/10.6084/m9.figshare.14798340.

Code availability Code is provided in Supplementary material, Table S5.

Declarations

Conflicts of interest The authors do not declare any conflict of interest.

Consent to participate NA.

Consent for publication The authors have approved the final version of the MS and agreed to be named as co-authors.

Ethics approval Ethics approval was granted by Swansea University Ethics Committee (Reference number SU-Ethics-Student-081217/307; SU-Ethics-Student-090118/299; SU-Ethics-Student-160118/463.

Human and animals Studies involving humans and/or animals. Fish sampling was carried out under permit number R18/2018 (17/04/2018) issued by the Falkland Islands Government (Falkland Islands Environmental Committee).

References

Arismendi I, Penaluna BE, Dunham JB, Garcia de Leaniz C, et al (2014) Differential invasion success of salmonids in southern Chile: patterns and hypotheses. Rev Fish Biol Fisheries 24:919–941. https://doi.org/10.1007/s11160-014-9351-0

Arndt E, Marchetti MP, Schembri PJ (2018) Ecological impact of alien marine fishes: insights from freshwater systems based on a compa rative review. Hydrobiologia 817:457–474. https://doi.org/10.1007/s10750-018-3511-5

Arrowsmith E, Pentelow FTK (1965) The introduction of trout and salmon to the Falkland Islands. Salmon and Trout Magazine 174:119–129

Baigún CRM, Quirós R (1985) Introducción de peces exóticos en la República Argentina. Informes Técnicos del Departamento de Aguas Continentales.. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar de la Plata, Argentina

Basulto S (2003) El largo viaje de los salmones: una crónica olvidada. Propagación y cultivo de especies acuáticas en Chile. Maval Limit ada Editores, Santiago de Chile, Chile

Consuegra S, Phillips N, Gajardo G, Garcia de Leaniz C (2011) Winning the invasion roulette: escapes from fish farms increase admixtur e and facilitate establishment of non-native rainbow trout. Evol Appl 4:660–671. https://doi.org/10.1111/j.1752-4571.2011.00189.x

Crawley MJ (2007) The R Book. John Wiley & Sons Ltd. Chichester, UK

Cussac VE, Barrantes ME, Boy CC et al. (2020) New insights into the distribution, physiology and life histories of South American galax iid fishes, and potential threats to this unique fauna. Diversity 12, 178. https://doi.org/10.3390/d12050178

Daciuk J (1975) La fauna silvestre de las Islas Malvinas. Anales de la Sociedad Científica Argentina 199:152–176

Davidsen JG, Bordeleau X, Eldøy SH et al. (2021) Marine habitat use and feeding ecology of introduced anadromous brown trout at the colonization front of the sub-Antarctic Kerguelen archipelago. Sci Rep 11:1–13. https://doi.org/10.1038/s41598-021-91405-x

Dormann CF, Elith J, Bacher S et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their perfor mance. Ecography 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Elgueta A, González J, Ruzzante DE, et al. (2013) Trophic interference by *Salmo trutta* on *Aplochiton zebra* and *Aplochiton taeniatus* in southern Patagonian lakes. J Fish Biol 82:430–443. https://doi.org/10.1111/j.1095-8649.2012.03489.x

Ewel JJ, Högberg P (1995) Experimental studies on islands. Springer, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-78963-2_18

Falkland Islands Government (1964) Trout and Salmon Fishing Regulations. Falkland Islands Government, Stanley

Falkland Islands Government (2015) Trout Fishing in the Falkland Islands. Falkland Islands Government Environmental Planning Department, Stanley

Faundez V, Blanco G, Vázquez E, Sánchez JA (1997) Allozyme variability in brown trout Salmo trutta in Chile. Freshw Biol 37:507–514. https://doi.org/10.1046/j.1365-2427.1997.00173.x

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49. https://doi.org/10.1017/S0376892997000088

Fish Loch Leven (2019) History of Loch Leven. http://www.fishlochleven.co.uk/history-of-fishing-on-loch-leven/

Fowler D, Garcia de Leaniz C (2012) Assessing the impact of culverts on population connectivity of endangered galaxiid fishes in the Falkland Islands. In: P Gough, P Philipsen, PP Schollema, H Wanningen (eds). From Sea to Source: International Guidance for the Restoration of Fish Migration Highways. Regional Water Authority Hunze en Aa's Postbus 195, 9640 AD Veendam, The Netherlands. pp 58–59

Fowler DM (2013) Brown trout in the Falklands: origin, life history, and public attitudes to an invasive species. MRes thesis, Swansea University, Swansea, UK

Garcia de Leaniz C, Gajardo G, Consuegra S (2010) From best to pest: changing perspectives on the impact of exotic salmonids in the southern hemisphere. Syst Biodivers 8:447–459. https://doi.org/10.1080/14772000.2010.537706

Halekoh U, Højsgaard S (2014) A Kenward-roger approximation and parametric bootstrap methods for tests in linear mixed models-the Rpackage pbkrtest. J Stat Softw 59:1–32. https://doi.org/10.18637/jss.v059.i09

Hooten MB, Hobbs NT (2015) A guide to Bayesian model selection for ecologists. Concep Synth 85:3–28. https://doi.org/10.1890/14-0661.1

Hulme PE (2015) Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. J Appl Ecol 52:1418–1424. https://doi.org/10.1111/1365-2664.12470

Jarry M, Beall E, Davaine P, et al (2018) Sea trout (Salmo trutta) growth patterns during early steps of invasion in the Kerguelen Islands. Polar Biology 41:925–934. https://doi.org/10.1007/s00300-018-2253-1

Jones PE, Closs GP (2015) Life history influences the vulnerability of New Zealand galaxiids to invasive salmonids. Freshw Biol 60:2127–2141. https://doi.org/10.1111/fwb.12637

Jones PE, Champneys T, Vevers J, et al. (2021a) Selective effects of small barriers on river-resident fish. Journal of Applied Ecology 58:1487-1498. https://doi.org/10.1111/1365-2664.13875

Jones PE, Tummers JS, Galib SM, et al. (2021b) The use of barriers to limit the spread of aquatic invasive animal species: a global review. Front Ecol Evol 9. https://doi.org/10.3389/fevo.2021.611631

Kaufman SD, Snucins E, Gunn JM, Selinger W (2009) Impacts of road access on lake trout (*Salvelinus namaycush*) populations: regionalscale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). Can J Fish Aquat Sci 66:212–223. https://doi.org/10.1139/F08-205

Kizuka T, Akasaka M, Kadoya T, et al (2014) Visibility from roads predict the distribution of invasive fishes in agricultural ponds. PloS One 9. https://doi.org/10.1371/journal.pone.0099709

Labonne J, Vignon M, Prévost E, et al (2013) Invasion dynamics of a fish-free landscape by brown trout (*Salmo trutta*). PLoS One 8. https://doi.org/10.1371/journal.pone.0071052

Lecomte F, Beall E, Chat J, Davaine P, Gaudin P (2013) The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. Polar Biol 36:457–475. https://doi.org/10.1007/s00300-012-1281-5

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN). p 12

MacCrimmon HR, Marshall TL (1968) World distribution of brown trout Salmo trutta. J Fish Res Board Can 25:2527–2548. https://doi.org/10.1139/f68-225

McDowall RM (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. Trans Am Fish Soc 132:229–238. https://doi.org/10.1577/1548-8659(2003)1322.0.CO;2

McDowall RM (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? Rev Fish Biol Fisher 16:233–422. https://doi.org/10.1007/s11160-006-9017-7

McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands fresh water fishes. Aquat Conserv Mar Freshwat Ecosyst 11:473–486. https://doi.org/10.1002/aqc.499

McIntosh AR, McHugh PA, Dunn NR et al (2010) The impact of trout on galaxiid fishes in New Zealand. N Z J Ecol 34:195–206

Minett JF, Garcia de Leaniz C, Brickle P, Consuegra S (2021a) A new high-resolution melt curve eDNA assay to monitor the simultaneous presence of invasive brown trout (*Salmo trutta*) and endangered galaxiids. Environ DNA 3:561–572. https://doi.org/10.1002/edn3.151

Minett JF, Garcia de Leaniz C, Sobolewska H, Brickle P, Crossin GT, Consuegra S (2021b) SNP analyses and acoustic tagging reveal multiple origins and widespread dispersal of invasive brown trout in the Falkland Islands. Evol Appl 14:2134–2144. https://doi.org/10.1111/eva.13274

Ortiz-Sandoval J, Gorski K, Sobenes C et al (2017) Invasive trout affect trophic ecology of *Galaxias platei* in Patagonian lakes. Hydrobiologia 790:201–212. https://doi.org/10.1007/s10750-016-3030-1

R Core Team (2019) R: A language and environment for statistical computing v. 3.5.3 R Foundation for Statistical Computing, Vienna, Austria.

Radcliffe L (1922) Fisheries and market for fishery products in Mexico, Central America, South America, West Indies, and Bermudas. Office UGP, Washington

Rodriguez-Rey M, Consuegra S, Borger L, Garcia de Leaniz C (2019) Improving species distribution modelling of freshwater invasive species for management applications. PLoS One 14:e0217896. https://doi.org/10.1371/journal.pone.0217896

Ross K (2009) Freshwater fish in the Falklands: conservation of native zebra trout. A report to the Falkland islands government and falklands conservation. Falkland Islands Government, Stanley, Falkland Islands

Salmon and Trout Association (2012) Falklands in the Family

Saunders WC, Budy P, Thiede GP (2015) Demographic changes following mechanical removal of exotic brown trout in an Intermountain West (USA), high-elevation stream. Ecol Freshw Fish 24:252–263. https://doi.org/10.1111/eff.12143

Stewart L (1973) Fisheries of the Falkland Islands. Overseas Development Administration, London, pp 104–124

Stewart L (1980) A history of migratory salmon acclimatization experiments in parts of the southern hemisphere and the possible effects of oceanic currents and gyres upon their outcome. Adv Mar Biol 17:397–466. https://doi.org/10.1016/S0065-2881(08)60305-3

Tabak MA, Piaggio AJ, Miller RS, et al (2017) Anthropogenic factors predict movement of an invasive species. Ecosphere 8. https://doi.org/10.1002/ecs2.1844https://doi.org/10.1002/ecs2.1844

Vanhaecke D, Garcia de Leaniz C, Gajardo G, Thomas CJ, Consuegra S (2012a) Metapopulation dynamics of a diadromous galaxiid fish and potential effects of salmonid aquaculture. Freshw Biol 57:1241–1252. https://doi.org/10.1111/j.1365-2427.2012.02794.x

Vanhaecke D, Garcia de Leaniz C, Gajardo G et al (2012b) DNA barcoding and microsatellites help species delimitation and hybrid identification in endangered galaxiid fishes. PLoS One 7:e32939. https://doi.org/10.1371/journal.pone.0032939

Westley PAH, Fleming IA (2011) Landscape factors that shape a slow and persistent aquatic invasion: brown trout in Newfoundland 1883–2010. Divers Distrib 17:566–579. https://doi.org/10.1111/j.1472-4642.2011.00751.x

Weyl OLF, Ellender BR, Ivey P, et al (2017) Brown trout introductions, establishment, current status, impacts and conflicts. In: Lobon-Cervia J, Sanz N (eds) Brown trout: biology, ecology and management. Wiley, pp. 623–629

Young KA, Stephenson J, Terreau A, Thailly A-F, Gajardo G, Garcia de Leaniz C (2009) The diversity of juvenile salmonids does not affect their competitive impact on a native galaxiid. Biol Invasions 11:1955–1961. https://doi.org/10.1007/s10530-008-9372-5

Young KA, Dunham JB, Stephenson JF, et al (2010) A trial of two trouts: comparing the impacts of rainbow and brown trout on a native galaxiid. Animal Conservation 13:399–410. https://doi.org/10.1111/j.1469-1795.2010.00354.x