

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

J. F. Minett¹, D.M. Fowler¹, J.A.H. Jones¹, P. Brickle², G.T. Crossin³, S. Consuegra¹,
C. Garcia de Leaniz^{1*}

¹Swansea University, CSAR, Swansea SA2 8PP, UK

²South Atlantic Environmental Research Institute, Stanley, Falkland Islands

³Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4R2
Canada

*corresponding author: c.garciadeleaniz@swansea.ac.uk

Keywords: Invasive species, translocations, risk management, invasion risk
competitive exclusion

Abstract

Non-native salmonids are protected in the Southern hemisphere where they sustain aquaculture and valuable sport fisheries, but also impact on native galaxiid 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. Our results indicate that establishment success was ~88%, and that dispersal was facilitated by proximity to introduction sites and density of stream-road crossings, suggesting it was human assisted. Brown trout has 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.

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 19th century (McDowall 2006), despite being responsible for the demise of native fish fauna (Garcia de Leaniz et al. 2010; Young et al. 2010).

Human activities have not only been responsible for the introduction of invasive species, but have also helped in many cases with their expansion (Hulme 2015). Yet, the importance of human assisted dispersal of non-native species is often difficult to assess due to lack of accurate introduction records and confounding environmental factors (Tabak et al. 2017). Islands provide ideal scenarios to examine the dispersal of invasive species 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 Högborg 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; Young et al. 2010), New Zealand (McDowall 2003), and the Falkland Islands, where it has benefitted from protected status (McDowall et al. 2001). This has created a conservation conundrum because protecting non-native salmonids to boost sport fishing may have put native fish at risk (Garcia de Leaniz et al. 2010).

Three surveys, conducted 10 and 20 years ago, concluded that brown trout had severely impacted two of the three native galaxiids, *Aplochiton zebra* and *Aplochiton taeniatus* (Fowler 2013; McDowall et al. 2001; Ross 2009), which appear to have contracted their range and are threatened by secondary releases. However, little is known about the current distribution of the endangered galaxiids, or the roles that natural and human-mediated dispersal may have played in the dispersal of brown trout following the initial introductions.

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 also derived risk maps under different management scenarios to help conservation agencies identify galaxiid populations at high risk of invasion and prioritise the establishment of freshwater refugia.

Methods

Reconstructing the introductions of brown trout

Historical records of the introduction of salmonids in the Falkland Islands (Table S1) were compiled and cross-referenced from (Arrowsmith and Pentelow 1965) and (Stewart 1973; Stewart 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 had dispatched salmonid eggs across the world.

Sampling of freshwater fish

A database of presence/absence records of the four species of freshwater fish present in the Falklands (three native galaxiids, *A. zebra*, *A. taeniatus*, and *G. maculatus*; and the non-native brown trout) was compiled by cross-checking records from (McDowall et al. 2001; Ross 2009), expanded with information from angler reports and our own sampling (Fowler 2013). McDowall's (McDowall et al. 2001) fish survey employed seine, gill and fyke netting, spotlighting at night, and electrofishing of ~50 m stream reaches. Ross (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).

Species distribution modelling

We divided the Falkland Islands into 8,813 1×1 km² 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). Brown trout presence was modelled using 13 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 QGIS 3.4. We excluded three predictors with VIF>3 to reduce collinearity, and randomly divided equal numbers of presence and absence records into training and testing datasets from 134 sites (Table S2) to train and test the model.

Brown trout distribution was modelled via a generalized linear model and the Leave One Out Cross Validation (LOOCV) (Hooten and Hobbs 2015). The *drop1* function in R3.5.3 (R Core Team 2019) was used to test the significance of individual predictors and arrive at a minimal adequate model based on changes in AIC. Model performance was assessed using the under the curve (AUC) criterion and compared against a null model built using the same testing and training datasets used for the final model (Rodriguez-Rey et al. 2019) using parametric bootstrapping (1,000 simulations).

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 used presence/absence data for brown trout and the three native galaxiids to assess how the presence of brown trout influenced the presence of native galaxiids by calculating relative risks. To visualize invasion risk, we used QGIS 3.10.3 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.

Predictive modelling of brown trout invasions under different management scenarios

We modelled the occupancy of brown trout since 1950 and predicted its future dispersal over a 130-year period (~30 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).

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 to obtain a mean percentage occupancy and 95% binomial confidence intervals. 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).

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) parents 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 it 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 (Table S1), but three rivers – all within a 25 km radius of the capital Stanley - received most of the introductions.

Establishment success

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, $P = 0.004$).

Modelling of brown trout distribution

At the time of the last survey (2012), brown trout occupied 54% of all sampled 1km² grid cells, with *Aplochiton* spp. only occupied 18%, confined to the South of the Islands (Fig. 1). Brown trout occurrence was predicted by distance to the nearest invaded point in a straight line (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 (LRT = 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* sp. Calculation of relative risk indicated that *Aplochiton* sp was 4.5 times less likely to persist in streams invaded by brown trout than in uninvaded streams (95CI = 1.8-11.2, $P < 0.001$). For *Galaxias maculatus*, the presence of brown trout decreased the probability of occurrence 2.9 fold (95CI = 2.0-4.2, $P < 0.001$).

Invasion risk

A risk map generated from the probability of occurrence of brown trout identified 21% of 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 9 sites at a high or very high risk of invasion where preventive measures should be prioritised to exclude brown trout and protect native freshwater fish (Fig. 3).

Invasion under different management scenarios

Our simulations indicate that if nothing is done (scenario 1) brown trout will likely 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%) and to 69% (95CI = 47-81%) with strong containment (scenario 3, Fig. 4). Thus, occupancy is predicted to increase under all the three scenarios, but only with strong containment can current *Aplochiton* refugia be protected from 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 on native freshwater fish. Streams invaded by brown trout were 2.9 times less likely to harbour *Galaxias maculatus* and 4.5 times less likely to contain *Aplochiton* sp. than uninvaded streams, suggesting 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). Our simulations suggest that unless more stringent measures are put in place, brown trout will likely invade nearly all the suitable freshwater habitats in the Falklands within the next ~70 years. Given that endangered *Aplochiton* sp. only occupy ~18% of the area, mostly confined to southern part of the Islands, this could drive the species to extinction.

The establishment success of brown trout in the Falklands was very high (88%), as seen elsewhere in the Southern Hemisphere (Arismendi et al. 2014; Young et al. 2010). For example, in Argentina no failed introduction of brown trout was ever reported (Baigún and Quirós 1985). Several factors may help explain this. Firstly, our study shows that brown trout introduced into the Falklands originated from at least four different origins with two life history strategies, which resulted in genetic admixture (Minett et al. 2021b). 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. Another reason for the success of brown trout in the Falklands may lie in their high phenotypic plasticity and facility for marine dispersal, which seems to have facilitated the colonization of coastal rivers in the Falklands, a point recently confirmed by acoustic tracking (Minett et al. 2021b).

However, marine dispersal alone cannot explain the current distribution of brown trout in the Islands; secondary translocations must have also taken place because the species is now found in 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 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 road tracks crisscrossing a dense river network, most of which have been 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. Recent eDNA analysis of water samples (Minett et al. 2021a) has revealed the presence of brown trout in additional streams since our last survey, suggesting that the species is expanding at a rate of ~0.9%/year.

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 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. 2012), 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 allows conservation officers to identify high risk areas, and could be used as part of an integrated management strategy for managing invasive salmonids in the Falklands.

Conclusions & Recommendations

Galaxiids rank among the most severely threatened fish in the world due to the introduction of invasive salmonids (Garcia de Leaniz et al. 2010; McDowall 2006). Our modelling suggests that without containment and strict measures brown trout will likely invade all remaining suitable water bodies in the Falklands before the end of the century, putting the endangered freshwater fish of the Islands at a high risk of extinction.

Existing legislation makes it illegal to transport or propagate brown trout in the Falklands, 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. The road network appears to be a main route of human-assisted translocations, and 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 on native galaxiids, which may pose a challenge as even small barriers can have negative impacts on weak swimmers (Jones et al. 2021a). Brown trout is subject to a bag limit and a strict fishing season and it might be useful to consider lifting these restrictions in some places to slow down the invasion front. Intensive fishing could be used to eradicate brown trout and establish buffer zones around *Aplochiton* refugia; analysis of eDNA from water samples could be used to delineate such refugia (Minett et al. 2021a), to serve as an early warning of brown trout invasions, and to establish whether containment 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* sp. features in a postal stamp of the Islands while *Galaxias maculatus* is called 'Falklands minnow', testifying to their importance for local islanders, and their place in the natural and cultural heritage of the Islands. Salmonids have brought wealth and recreation opportunities to the Falklands, but have also caused the demise of native freshwater fish. Our study indicates that urgent protection measures are needed to safeguard their survival.

Acknowledgements

We thank William P. Kay for help calculating distance around the coast, Supercomputing Wales for use of the Sunbird cluster, and Falkland Islands Government IMS-GIS Centre and SAERI for providing GIS data. Funding from Fortuna Ltd. and Swansea University College of Science is gratefully acknowledged.

References

- Arismendi I., Penaluna B.E., Dunham J.B. *et al.* (2014) Differential invasion success of salmonids in southern Chile: patterns and hypotheses. *Reviews in Fish Biology and Fisheries* **24**, 919-941.
- Arrowsmith E., Pentelov F.T.K. (1965) The introduction of trout and salmon to the Falkland Islands. pp. 119-129. *Salmon and Trout Magazine*.
- Baigún C.R.M., Quirós R. (1985) Introducción de peces exóticos en la República Argentina. p. 93. *Informes Técnicos del Departamento de Aguas Continentales*. Instituto Nacional de Investigación y Desarrollo Pequero, Mar del Plata, Argentina.
- Basulto S. (2003) *El largo viaje de los salmones: una crónica olvidada. Propagación y cultivo de especies acuáticas en Chile*. . Maval Limitada Editores, Santiago, Chile.
- Consuegra S., Phillips N., Gajardo G., Garcia de Leaniz C. (2011) Winning the invasion roulette: Escapes from fish farms increase admixture and facilitate establishment of non-native rainbow trout. *Evolutionary Applications* **4**, 660-671.
- Daciuk J. (1975) La fauna silvestre de las Islas Malvinas. *Anales de la Sociedad Científica Argentina* **199**, 152-176.
- Elgueta A., González J., Ruzzante D.E., Walde S.J., Habit E. (2013) Trophic interference by *Salmo trutta* on *Aplochiton zebra* and *Aplochiton taeniatus* in southern Patagonian lakes. *Journal of Fish Biology* **82**, 430-443.
- Ewel J.J., Högborg P. (1995) *Experimental studies on islands*. Springer Berlin Heidelberg.
- Falkland Islands Government. (2015) Trout fishing in the Falkland Islands.
- Faundez V., Blanco G., Vázquez E., Sánchez J.A. (1997) Allozyme variability in brown trout *Salmo trutta* in Chile. *Freshwater Biology* **37**, 507-514.
- Fish Loch Leven. (2019) History of 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. pp. 58-59 in P. Gough, P. Philipsen, P.P. Schollema, H. Wanningen editors. *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.
- Fowler D.M. (2013) Brown trout in the Falklands: origin, life history, and public attitudes to an invasive species. pp. 1-110.
- 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. *Systematics and Biodiversity* **8**, 447-459.
- Hooten M.B., Hobbs N.T. (2015) A guide to Bayesian model selection for ecologists. *Concepts and synthesis* **85**, 3-28.
- Hulme P.E. (2015) Invasion pathways at a crossroad: Policy and research challenges for managing alien species introductions. *Journal of Applied Ecology* **52**, 1418-1424.
- Jones P., Champneys T., Vevers J. *et al.* (2021a) Selective effects of small barriers on river-resident fish. *Journal of Applied Ecology*.

- Jones P.E., Tummers J.S., Galib S.M. *et al.* (2021b) The use of barriers to limit the spread of aquatic invasive animal species: a global review. *Frontiers in Ecology and Evolution*.
- Kaufman S.D., Snucins E., Gunn J.M., Selinger W. (2009) Impacts of road access on lake trout (*Salvelinus namaycush*) populations: Regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 212-223.
- Kizuka T., Akasaka M., Kadoya T., Takamura N. (2014) Visibility from roads predict the distribution of invasive fishes in agricultural ponds. *PLoS ONE* **9**.
- 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 p. 12. Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN)
- MacCrimmon H.R., Marshall T.L. (1968) World distribution of brown trout *Salmo trutta*. *J Fish Res Board Can* **25**, 2527-2548.
- McDowall R.M. (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society* **132**, 229-238.
- McDowall R.M. (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries* **16**, 233-422.
- McDowall R.M., Allibone R.M., Chadderton W.L. (2001) Issues for the conservation and management of Falkland Islands fresh water fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**, 473-486.
- Minett J.F., 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. *Environmental DNA* **3**, 561-572.
- Minett J.F., Garcia de Leaniz C., Sobolewska H., Brickle P., Crossin G.T., Consuegra S. (2021b) SNP analysis and acoustic tagging reveal multiple origins and widespread dispersal of invasive brown trout in the Falkland Islands *Evolutionary Applications*.
- 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.
- Ross K. (2009) Freshwater fish in the Falklands: conservation of native zebra trout. *A report to the Falkland Islands Government and Falklands Conservation*.
- Salmon, Trout A. (2012) Falklands in the Family.
- Stewart L. (1973) Fisheries of the Falkland Islands.
- 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.
- Tabak M.A., Piaggio A.J., Miller R.S., Sweitzer R.A., Ernest H.B. (2017) Anthropogenic factors predict movement of an invasive species. *Ecosphere* **8**.
- Vanhaecke D., Garcia de Leaniz C., Gajardo G., Thomas C., Consuegra S. (2012) Metapopulation dynamics of a diadromous galaxiid fish and potential effects of salmonid aquaculture. *Freshwater Biology* **57**, 1241-1252.
- Young K., Dunham J., Stephenson J. *et al.* (2010) A trial of two trouts: comparing the impacts of rainbow and brown trout on a native galaxiid. *Animal Conservation*, 1-10.

Young K.A., 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. *Biological Invasions* **11**, 1955-1961.

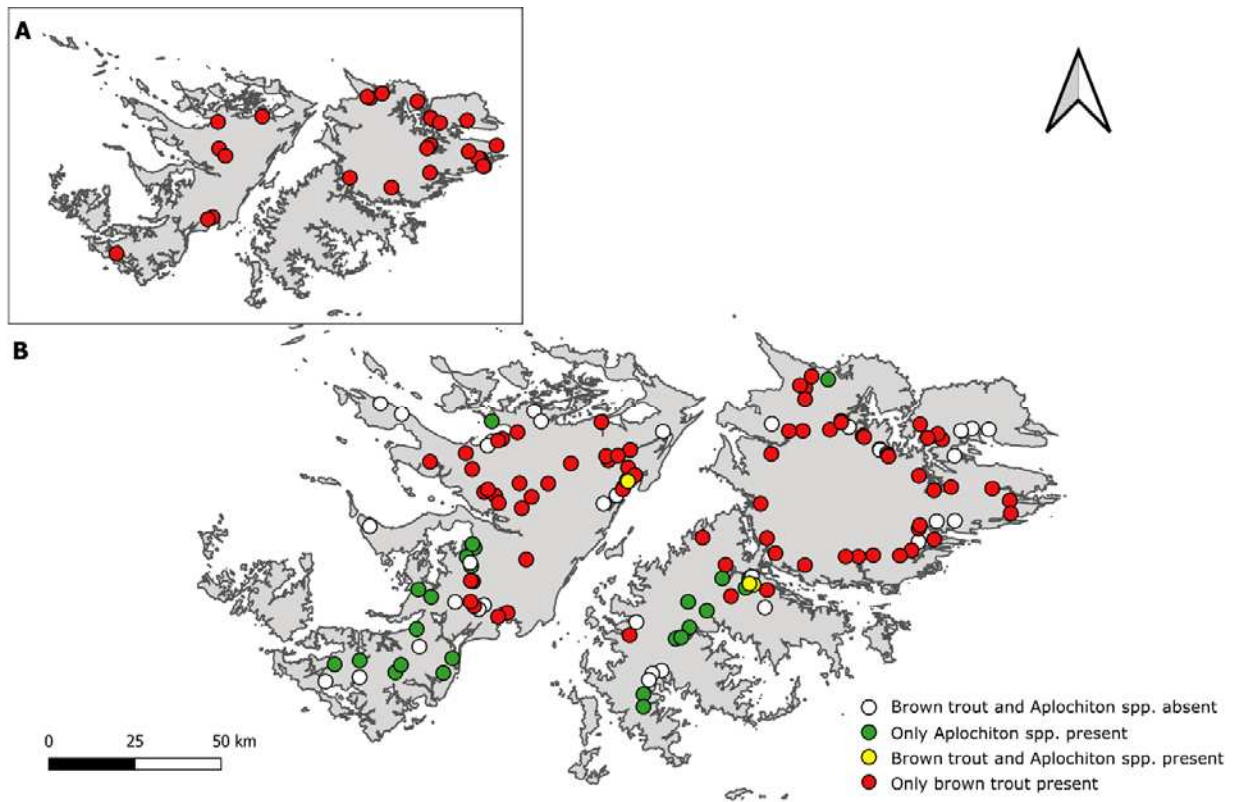


Figure 1. Map of the Falkland Islands showing (A) sites of the historical introductions of brown trout during 1944-1962 (details given in Table S1) and (B) presence/absence of brown trout and native *Aplochiton* sp. based on 1999-2012 surveys (detailed in Table S2) with 6 additional sites sampled in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

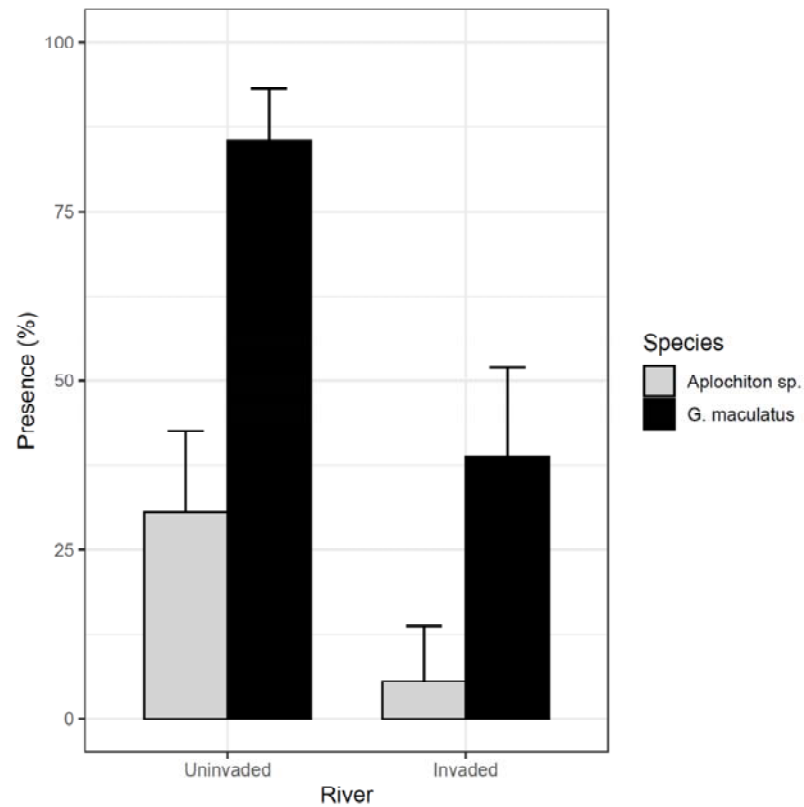


Figure 2. Frequency of occurrence (%) and binomial upper 95CI) of native galaxiids (*Galaxias maculatus* and *Aplochiton* sp.) in streams invaded by brown trout (N=62) and in uninvaded streams (N= 72).

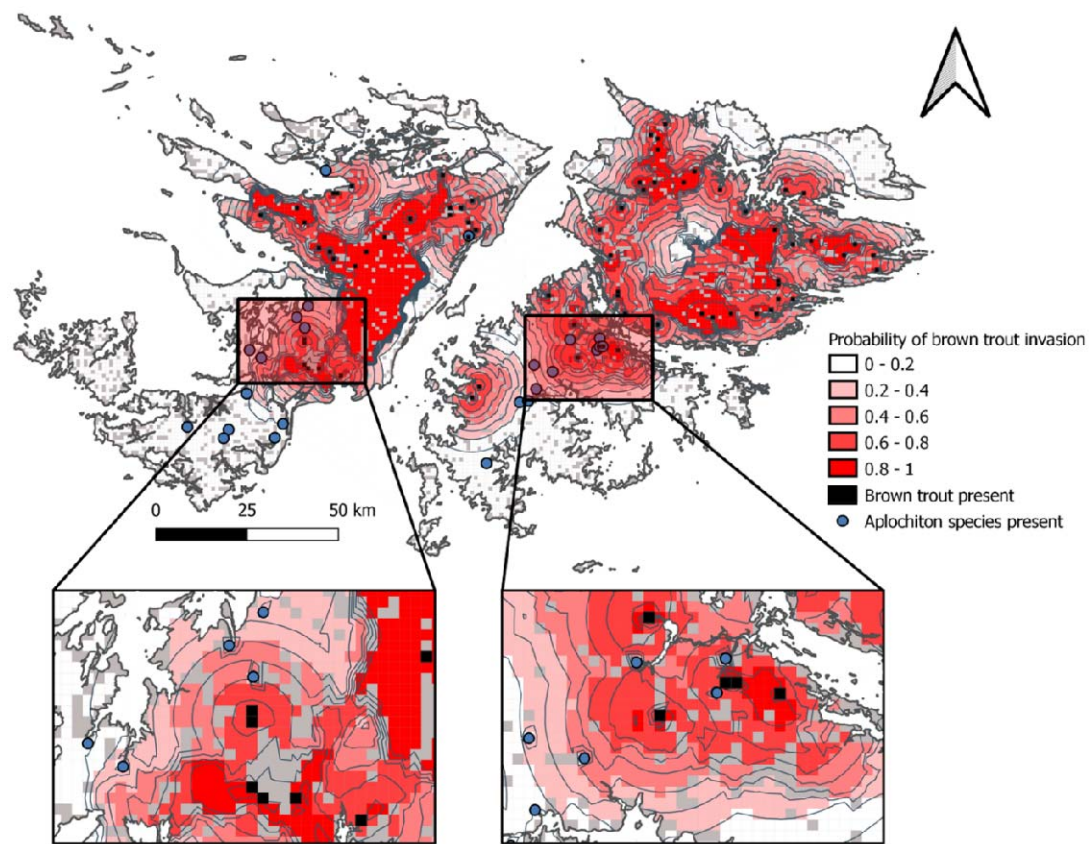


Figure 3. Risk maps showing probabilities of brown trout invasion based on species distribution modelling. *Aplochiton* refugia at a high risk of brown trout invasion are shown in the zoomed insets.

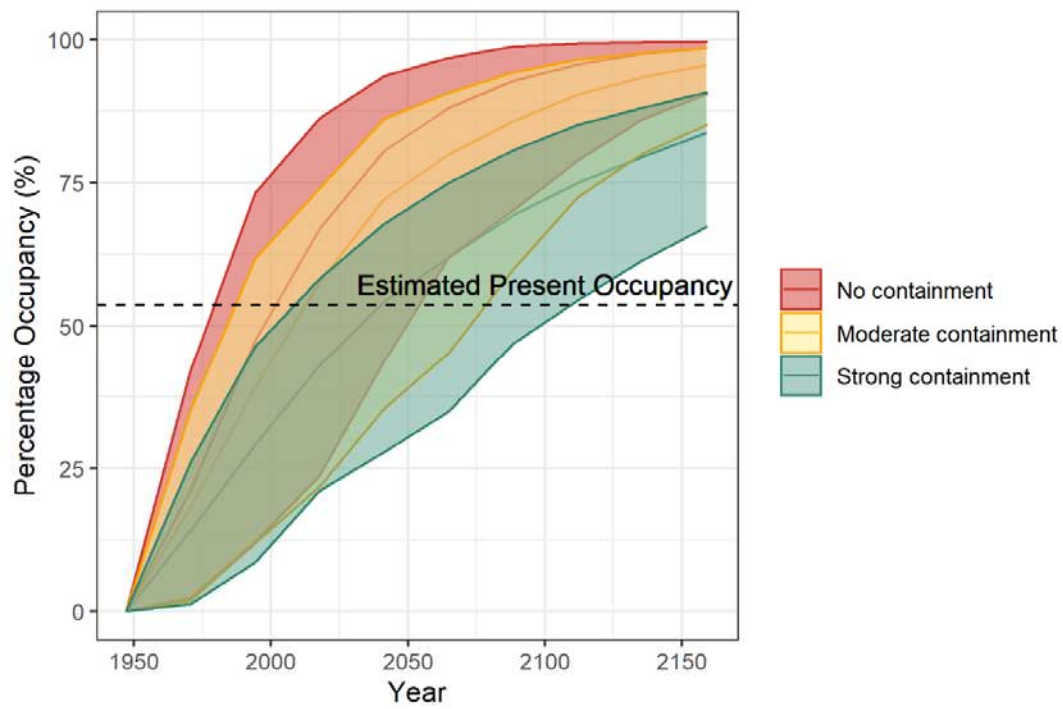


Figure 4. Modelled expansion of brown trout in the Falkland Islands under three different management scenarios.

Table S1. Introduction of brown trout eggs in the Falkland Islands, 1944-1962.

Stock origin	Year	Quantity	Introduction Site (code)	Latitude	Longitude
Unknown (likely Germany via Chile; non-anadromous)					
	1944	'Small quantities'	Unknown	Unknown	Unknown
			Moody Brook	-51.6857	-57.9222
			Moody Brook	-51.6857	-57.9222
Lautaro Hatchery (Chile, German Stock; non-anadromous)					
	1947	30,000	Moody Brook	-51.6857	-57.9222
			Malo River	-51.6171	-58.3018
			Murrell River	-51.6535	-57.9951
Surrey Trout Farm (UK; non-anadromous)					
	1948	10,000	Malo River	-51.6171	-58.3018
			Murrell River	-51.6535	-57.9951
			Hill Cove	-51.4736	-59.9764
			Chartres River	-51.6428	-59.9283
			Port Howard/Warrah R.	-51.4554	-59.6245
Surrey Trout Farm or Pentlands (UK; non-anadromous)					
	1949	15,000	Port San Carlos	-51.5095	-58.8220
			Elephant Beach	-51.3807	-58.7690
			Head of the Bay	-51.6061	-59.0142
			Lorenzo Pond	-51.3497	-59.6700
			Swan Inlet	-51.8239	-58.6161
			Fitzroy River	-51.7546	-58.3068
			Kidney Pond	-51.6251	-57.7739
			Pebbly Pond	-51.7270	-57.8740
			Johnsons Harbour	-51.4995	-58.0044
			Fox Bay East	-51.9421	-60.0500
			Fox Bay West	-51.9510	-60.0897
			Hill Cove	-51.4736	-59.9764
Surrey Trout Farm or Pentlands (UK; non-anadromous)					
	1950	10,000	Darwin (Camilla Creek)	-51.7711	-58.9457
			Malo River	-51.6171	-58.3018
			Port San Carlos	-51.5095	-58.8220
			Fitzroy River	-51.7546	-58.3068
			Pebble Island	-51.3199	-59.5741
			Chartres River	-51.6428	-59.9283
			Hill Cove	-51.4736	-59.9764
			Port Howard/Warrah River	-51.4554	-59.6245
			Port Stephens	-52.0980	-60.8321
Surrey Trout Farm or Pentlands (UK; non-anadromous)					
	1951	10,000	Malo River	-51.6171	-58.3018
			Swan Inlet	-51.8239	-58.6161
			Darwin (Camilla Creek)	-51.7711	-58.9457
			North Arm	-52.1291	-59.3709
			Port San Carlos	-51.5095	-58.8220
			Murrell River	-51.6535	-57.9951
Surrey Trout Farm or Pentlands (UK; non-anadromous)					
	1952	10,000	Murrell River	-51.6535	-57.9951
			Malo River	-51.6171	-58.3018
			Johns Brook	-51.4865	-58.2932
			Lorenzo Pond	-51.3497	-59.6700
			Fitzroy River	-51.7546	-58.3068
			Swan Inlet	-51.8239	-58.6161
			North Arm	-52.1291	-59.3709
			Pebbly Pond	-51.7270	-57.8740
			Kidney Pond	-51.6251	-57.7739
Middleton Hatchery – Lancashire Fisheries Board (UK; anadromous)					
	1961	20,000	Chartres River	-51.6428	-59.9283
			Mac's Paddock Brook	-51.4849	-58.2927

		Pasa Maneas	-51.6338	-58.3261
		Malo River	-51.6171	-58.3018
		Port San Carlos	-51.5095	-58.8220
		Port Howard/Warrah River	-51.4554	-59.6245
Middleton Hatchery – Lancashire Fisheries Board (UK; anadromous)				
1962	8,000	Felton's Stream	-51.6894	-57.9033
		Mile Pond	-51.7214	-57.8835
		Round Pond	-51.7268	-57.8835
		Pebbly Pond	-51.7270	-57.8740
		Salvador Camp	-51.4020	-58.3954

Table S2. Presence/absence of brown trout (*St*), *Aplochiton* sp. (*Ap*) and *Galaxias maculatus* (*Gm*) in the Falkland Islands. Sites marked with an asterisk denote brown trout introduction sites (see Table S1).

Sample Site	Island	Date last sampled	Lat.	Long.	<i>St</i>	<i>Ap</i>	<i>Gm</i>	Reference
Arrow Harbour Arroyo	East	2011	-51.9062	-58.9508	+	-	+	Fowler (2013)
Arroyo Pedro	East	1999	-51.5111	-58.5346	+	-	-	McDowall et al. (2001)
Big Pond	East	2018	-51.8433	-51.7522	+	-	+	Minett (unpubl.)
Bodie Creek	East	2011	-51.9191	-59.1042	+	-	+	Fowler (2013)
Bull Pass Stream	East	2011	-51.8909	-59.0074	+	+	+	Fowler (2013)
Clay Ditch	East	1999	-51.4925	-58.6700	+	-	-	McDowall et al. (2001)
Colorado Pond	East	2018	-51.7136	-58.4717	+	-	-	Minett (unpubl.)
Comoda Ditch	East	1999	-51.8219	-58.5003	+	-	-	McDowall et al. (2001)
Congo Ponds Area	East	2009	-51.9787	-59.5072	-	-	-	Ross (2009)
Dan's Shanty Stream	East	1999	-51.5236	-58.2020	+	-	+	McDowall et al. (2001)
Darwin (Camilla Creek) *	East	1999	-51.7711	-58.9457	+	-	-	McDowall et al. (2001)
Deep Arroyo	East	2011	-51.9553	-59.2080	-	+	+	Fowler (2013)
Ditches into New Haven	East	2009	-51.7646	-59.2166	+	-	+	Ross (2009)
Duffins Bridge Stream	East	2009	-52.1078	-59.4073	-	-	+	Ross (2009)
Elephant Beach Pond*	East	1999	-51.3807	-58.7690	+	-	+	McDowall et al. (2001)
Elmer's Ditch Tributary	East	1999	-51.4939	-58.7840	+	-	-	McDowall et al. (2001)
Estancia Brook	East	2008	-51.6480	-58.1678	+	-	-	Fowler (2013)
Felton Stream*	East	NA	-51.6894	-57.9033	NA	NA	NA	Not sampled
Findley Creek Stream	East	2011	-51.8882	-59.0250	+	+	+	Fowler (2013)
Findlay Harbour (Wreck House)	East	2009	-52.0122	-59.5375	+	-	-	Fowler (2013)
Fitzroy River*	East	2012	-51.7546	-58.3068	+	NA	NA	Angler
Frying Pan	East	2011	-51.8111	-58.3387	+	-	-	Fowler (2013)
Gonzales Arroyo	East	2009	-51.9513	-58.9621	-	-	+	Ross (2009)
Green Pass Brook Tributary	East	1999	-51.4098	-58.7715	+	-	-	McDowall et al. (2001)
Head of the Bay*	East	2012	-51.6061	-59.9764	+	NA	NA	Angler
Head of the Creek Stream	East	1999	-51.4961	-58.0763	-	-	+	McDowall et al. (2001)

Hunter's Arroyo East 1999 -52.1147 -59.4470 - - + McDowall et al. (2001)

Table S2 (cont).

Sample Site	Island	Date last sampled	Lat.	Long.	St	Ap	Gm	Reference
John's Brook*	East	2018	-51.4834	-58.2930	+	-	NA	Minett (unpubl.)
Johnsons Harbour*	East	NA	-51.4995	-58.0044	NA	NA	NA	Not sampled
Kidney Pond*	East	NA	-51.6251	-57.7739	NA	NA	NA	Not sampled
Laguna Isla	East	2011	-51.8439	-58.7890	+	-	-	Fowler (2013)
L'Antioja Stream	East	2012	-51.8249	-58.5627	+	-	-	Fowler (2013)
Little Creek Stream	East	1999	-51.3504	-58.7418	+	-	-	McDowall et al. (2001)
Lorenzo Pond*	East	1973	-51.3593	-58.6730	-	+	+	Stewart (1973)
Mac's Paddock Brook*	East	NA	-51.4849	-58.2927	NA	NA	NA	Not sampled
Magellan Pond	East	1999	-51.4995	-58.0062	-	-	+	McDowall et al. (2001)
Malo River*	East	1999	-51.6171	-58.3018	+	-	+	McDowall et al. (2001)
Mary Hill Quarry	East	2018	-51.6844	-57.7894	+	-	-	Minett (unpubl.)
Mile Pond*	East	NA	-51.7214	-57.8835	NA	NA	NA	Not sampled
Moody Brook*	East	2012	-51.6857	-57.9222	+	-	-	Fowler (2013)
Mullet Creek	East	1999	-51.7187	-57.9185	+	-	+	McDowall et al. (2001)
Murrell River*	East	2013	-51.6535	-57.9951	+	-	-	Fowler (2013)
North Arm*	East	2011	-52.1291	-29.3709	-	-	+	Fowler (2013)
Northwest Arm House Stream	East	2018	-52.1674	-59.4874	-	+	+	Minett (unpubl.)
Northern Stream	East	1999	-51.5018	-58.1223	-	-	+	McDowall et al. (2001)
Orequta Arroyo	East	2011	-51.8373	-59.1229	+	-	-	Fowler (2013)
Pasa Maneas*	East	NA	-51.6338	-58.3261	NA	NA	NA	Not sampled
Pebbly Pond*	East	NA	-51.7270	-57.8740	NA	NA	NA	Not sampled
Round Pond*	East	NA	-51.7268	-57.8835	NA	NA	NA	Not sampled
Rumford Brook	East	2011	-51.6557	-58.2399	+	-	-	Fowler (2013)
Salvador Camp*	East	NA	-51.4020	-58.3954	NA	NA	NA	Not sampled
San Carlos River at Ford*	East	2018	-51.5095	-58.220	+	-	-	Minett (unpubl.)
Shepherds Brook	East	1999	-51.6808	-58.9688	+	-	+	McDowall et al. (2001)
Spots Arroyo	East	2018	-52.0260	-59.3432	-	+	+	Minett (unpubl.)

Stream at Colorado Pass	East	2009	-51.8702	-59.0137	-	-	+	Ross (2009)
Table S2 (cont).								
Sample Site	Island	Date last sampled	Lat.	Long.	St	Ap	Gm	Reference
Stream at Gibraltar Gate	East	1999	-51.4933	-58.8417	+	-	-	McDowall et al. (2001)
Stream near Hunter Arroyo	East	1999	-52.1303	-59.4622	-	-	+	McDowall et al. (2001)
Stream, Caneja Creek	East	1999	-51.5190	-58.2621	+	-	-	McDowall et al. (2001)
Stream, at Fitzroy	East	1999	-51.7838	-58.2425	+	-	+	McDowall et al. (2001)
Stream, Douglas Creek	East	1999	-51.4704	-58.6229	+	-	-	McDowall et al. (2001)
Stream, Elephant Beach Pond*	East	2018	-51.3731	-58.7911	+	-	+	Minett (unpubl.)
Stream, Fitzroy	East	1999	-51.7887	-58.3085	-	-	-	McDowall et al. (2001)
Stream, Monty Dean's Creek	East	1999	-51.5669	-58.1515	-	-	+	McDowall et al. (2001)
Stream, Mount Pleasant	East	1999	-51.8243	-58.3878	+	-	-	McDowall et al. (2001)
Stream, NW of Teal Inlet	East	1999	-51.5456	-58.4638	-	-	+	McDowall et al. (2001)
Stream NW of Teal Inlet	East	1999	-51.5481	-58.4629	-	-	+	McDowall et al. (2001)
Stream, Salt House Creek	East	2009	-52.1997	-59.4894	-	+	+	Ross (2009)
Stream, SE of Teal Inlet	East	1999	-51.5580	-58.4330	-	-	-	McDowall et al. (2001)
Stream, Smylie's Brook	East	1999	-51.4738	-58.9129	-	-	-	McDowall et al. (2001)
Stream, Teal Inlet	East	1999	-51.5654	-58.4278	+	-	-	McDowall et al. (2001)
Stream, SE of Teal Inlet	East	1999	-51.5622	-58.4294	-	-	+	McDowall et al. (2001)
Swan Inlet*	East	2012	-51.8239	-58.6161	+	NA	NA	Angler
Teal Creek Arroyo	East	2009	-51.8106	-58.9121	+	-	+	Ross (2009)
Third Corral Brook	East	1999	-51.5520	-58.9182	+	-	-	McDowall et al. (2001))
Trib., Halfway House Arroyo	East	2011	-51.9977	-59.2836	-	+	+	Fowler (2013)
Turners Stream	East	1999	-51.5137	-58.5277	+	-	-	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.8726	-59.1386	-	+	+	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.9311	-59.2855	-	+	+	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.4869	-58.5905	-	-	-	McDowall et al. (2001)
Unnamed Stream	East	1999	-52.0228	-59.3197	-	+	+	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.8987	-59.0414	-	+	+	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.8753	-59.0254	-	+	+	McDowall et al. (2001)

Unnamed Stream Table S2 (cont).	East	1999	-51.7461	-58.3020	+	-	-	McDowall et al. (2001)
Sample Site	Island	Date last sampled	Lat.	Long.	St	Ap	Gm	Reference
Unnamed Stream	East	1999	-51.7366	-58.2306	-	-	+	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.7357	-58.1542	-	-	-	McDowall et al. (2001)
Unnamed Stream	East	1999	-51.4747	-58.6230	+	-	-	McDowall et al. (2001)
Pebble Island*	Pebble	NA	-51.3199	-59.5741	NA	NA	NA	Not sampled
1 st Arroyo	West	2009	-52.0838	-60.5346	-	+	-	Ross (2009)
2 nd Pass Stream	West	1999	-51.6253	-60.1260	+	-	-	McDowall et al. (2001)
2 nd Arroyo	West	2009	-52.0647	-60.5092	-	+	+	Ross (2009)
Arroyo Chico	West	1999	-51.9208	-60.1891	+	-	-	McDowall et al. (2001)
Arroyo Malo	West	1999	-51.9194	-60.1471	-	-	-	McDowall et al. (2001)
Ballan Stream	West	2009	-51.6471	-59.5714	-	-	+	Ross (2009)
Beach Stream	West	1999	-51.6258	-59.5402	+	-	+	McDowall et al. (2001)
Bull Hill Stream	West	1999	-51.5764	-59.5194	+	-	-	McDowall et al. (2001)
Bull Stream	West	1999	-51.4888	-60.0413	+	-	-	McDowall et al. (2001)
Campbell Creek Stream	West	2009	-52.0197	-60.4278	-	-	+	Ross (2009)
Cemetery Creek Estuary	West	1999	-51.5961	-59.4913	+	-	+	McDowall et al. (2001)
Chartres River*	West	1999	-51.6428	-59.9283	+	-	-	McDowall et al. (2001)
Daddy's Ditch	West	2009	-51.4195	-59.9033	-	-	+	Ross (2009)
Dean's River	West	2009	-52.0914	-60.6869	-	-	+	Ross (2009)
Dirty Ditch at the High Tide	West	1999	-51.5401	-60.3470	+	-	+	McDowall et al. (2001)
Double Stream	West	2009	-51.6677	-59.6277	-	-	+	Ross (2009)
Doyle River Tributary	West	1999	-51.7695	-60.1764	-	+	+	McDowall et al. (2001)
Dunbar Creek	West	2009	-51.4124	-60.4556	-	-	+	Ross (2009)
Edye Creek	West	2012	-51.8711	-60.4206	-	+	+	Fowler (2013)
Fish Creek 1	West	2012	-52.0538	-60.2908	-	+	+	Fowler (2013)
Fish Creek 2	West	2018	-51.8918	-60.3681	-	+	+	Minett (unpubl.)
Fox Bay East* (Doctors Creek)	West	2018	-51.9421	-60.0500	+	-	NA	Minett (unpubl.)
Fox Bay West*	West	2012	-51.9510	-60.0897	+	NA	NA	Angler

Gibraltar Stream Table S2 (cont).	West	2009	-52.0913	-60.3318	-	+	+	Ross (2009)
Sample Site	Island	Date last sampled	Lat.	Long.	St	Ap	Gm	Reference
Green Hill Stream	West	2009	-51.5552	-59.6012	+	-	-	Ross (2009)
Herbert Stream	West	1999	-51.5222	-60.1959	+	-	-	McDowall et al. (2001)
Hawk's Nest Stream	West	1999	-51.8055	-59.9614	+	-	-	McDowall et al. (2001)
Hill Cove*	West	2008	-51.4736	-59.9764	+	-	-	Fowler (2013)
House Creek	West	1999	-51.6097	-59.5267	+	+	+	McDowall et al. (2001)
House Stream	West	2012	-51.6116	-59.5221	+	+	+	Fowler (2013)
Lake Sullivan, Outflow	West	2009	-51.7922	-60.2111	-	+	+	Ross (2009)
Lake Sullivan North	West	2011	-51.8167	-60.1941	-	+	+	Fowler (2013)
Lake Sullivan North Outflow	West	1999	-51.8073	-60.1976	-	-	+	McDowall et al. (2001)
Lake Sullivan South	West	2011	-51.8567	-60.1891	+	-	+	Fowler (2013)
Larger Stream, Hill Cove	West	1999	-51.4945	-60.0843	-	-	+	McDowall et al. (2001)
Leicester Stream	West	2009	-51.9084	-60.2682	-	-	+	Ross (2009)
Main Point Creek	West	2009	-51.4474	-59.8757	-	-	+	Ross (2009)
Many Branches Stream	West	1999	-51.5303	-59.5083	+	-	+	McDowall et al. (2001)
Mickey Doolan's Ditch	West	1999	-51.9292	-60.1703	-	-	+	McDowall et al. (2001)
Mt Adam Stream	West	1999	-51.6355	-60.0802	+	-	-	McDowall et al. (2001)
Mt Donald Pond Inflow	West	1999	-51.5643	-60.1720	+	-	-	McDowall et al. (2001)
Neil Clark Nature Reserve	West	2018	-51.6324	-59.5452	+	-	NA	Minett (unpubl.)
Poncho Valley Stream	West	2012	-51.9736	-60.4357	-	+	+	Fowler (2013)
Port Howard/Warrah*	West	1999	-51.4554	-59.6245	+	-	-	McDowall et al. (2001)
Port Stephens*	West	2009	-52.0980	-60.8321	-	-	+	Ross (2009)
River Doyle	West	2009	-51.7588	-60.1845	-	+	+	Ross (2009)
Rous Creek Stream	West	2009	-51.7006	-60.6122	-	-	+	Ross (2009)
Skull Pass Stream	West	1999	-51.5444	-59.6095	+	-	-	McDowall et al. (2001)
Stewart's Brook	West	2009	-52.0482	-60.6826	-	+	+	Ross (2009)
Stream by Mt Rosalie House	West	2009	-51.4856	-59.3685	-	-	+	Ross (2009)
Stud Paddock Stream	West	1999	-51.9416	-60.0497	-	-	+	McDowall et al. (2001)

Teal House River Table S2 (cont).	West	2018	-51.6194	-60.1103	+	-	NA	Minett (unpubl.)
Sample Site	Island	Date last sampled	Lat.	Long.	St	Ap	Gm	Reference
Teal Ponds & Waterfall Stream	West	1999	-51.6557	-60.0672	+	-	+	McDowall et al. (2001)
Top Hog Ground Stream	West	1999	-51.6711	-59.9714	+	-	-	McDowall et al. (2001)
Unnamed Stream	West	1999	-51.5443	-59.5602	+	-	-	McDowall et al. (2001)
Unnamed Stream	West	1999	-51.9092	-60.2030	+	-	-	McDowall et al. (2001)
Unnamed Stream	West	2012	-51.6098	-59.8563	+	-	-	Fowler (2013)
Unnamed Stream, Hill Cove	West	1999	-51.5053	-60.1034	-	-	+	McDowall et al. (2001)
Unnamed Stream, Hill Cove	West	1999	-51.4928	-60.0587	+	-	-	McDowall et al. (2001)
Warrah River	West	1999	-51.5598	-59.7581	+	-	-	McDowall et al. (2001)
Waterfall Stream	West	2009	-51.3817	-60.5421	-	-	+	Ross (2009)
Weedy Outlet	West	1999	-51.8548	-60.1980	+	-	+	McDowall et al. (2001)
West Lagoons	West	2013	-51.4421	-60.0817	-	+	+	Fowler (2013)
Whisky Creek	West	2009	-52.0546	-60.7896	-	+	-	Ross (2009)

Table S3. Predictors used to generate a species distribution model of brown trout in the Falkland Islands. Predictors shown in **bold** had a VIF < 3 and were included in the model.

Predictor	Description	Source
Anthropogenic predictors		
Eucl_dist_inv	Euclidean distance to nearest invaded site in a straight line (km)	Own creation
Coast_dist_inv	Distance to nearest invaded site around the coast (km)	Own creation
Eucl_dist_intro	Euclidean distance to nearest introduction site in a straight line (km)	Own creation
Coast_dist_intro	Distance to nearest introduction site around the coast (km)	Own creation
Intro_site	Introduction site (y/n)	Table S1
Intro_basin	Introduction basin (y/n)	Table S1
Settle_dist	Distance to nearest settlement (km)	Own creation, FIG IMS-GIS Centre
Road_dist	Distance to nearest road (km)	Own creation, FIG IMS-GIS Centre
Road_cross_no	Number of river-road crossings in the river basin	Own creation, FIG IMS-GIS Centre
Road_cross_dist	Distance to nearest river-road crossing (km)	Own creation
BFL	Barrier Free Length, length of river between consecutive culverts (km)	Own creation
BFL_share	Proportion of total river length free of culverts	Own creation
Bioclimatic predictors		
Ap	Presence of <i>Aplochiton</i> (y/n); coded no if unknown	Table S2
EW	East or West Island	Own creation
Slope	Mean slope of grid cell	USGS
Alt	Mean altitude of each grid (m)	USGS
River_dens	River network in the basin (km)	Own creation, FIG IMS-GIS Centre
Flow_accum	Mean flow accumulation scaled by max flow accumulation in basin	Own creation, FIG IMS-GIS Centre
Min_winter_temp	Minimum winter temperature (°C)	FIG IMS-GIS Centre
Rain	Annual precipitation (mm)	FIG IMS-GIS Centre
LC	Land cover/substrate type	FIG IMS-GIS Centre, DPLUS065 Project