

The implications of climate change for New Zealand's freshwater fish

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Abstract

Climate change is poised to reshape ecological communities globally by driving species into new environments and altering interactions between species. Conservation efforts should not only address current pressures but also plan for future pressures, such as sensitive species moving into degraded environments or arising problematic trophic interactions. This study sought to assess how climate change may affect the end-of-century distributions of New Zealand's native and nonnative freshwater fish, including consequences for the overlap between trout (a nonnative sports fish) and native species vulnerable to trout predation. Random forest modelling was used to predict end-of-century distributions for New Zealand's freshwater fish based on six hydrologically downscaled global climate models across four representative concentration pathways. Severe climate change impacts could drive nine native fish species to extinction or near-extinction and cause substantial declines in another eight native species. Seven nonnatives are also predicted to decline substantially, including a 30%–40% reduction in the extent of trout. To avert these potential extinctions, it is crucial to mitigate climate change severity and improve land use impacting freshwater ecosystems.

Key words: predation, trophic impacts, global warming, rainbow trout, brown trout, galaxiid,

1.0 Introduction

Although we know that climate change will wreak severe devastation on the world's biodiversity, we are still uncertain about which particular species will be most affected or how these pressures will interact with other ongoing anthropogenic stresses (Brooker et al. 2007; Death 2024). As global climate patterns shift, species are expected to undergo substantial changes in their geographical distributions, with native species often migrating to more suitable habitats in response to changing environmental conditions (Hellman et al. 2008; Mainka and Howard 2010; Pyšek et al. 2020). Such shifts in distribution can lead to ecological imbalances, including disruptions in food webs, nutrient cycling, and ecosystem services, all of which are critical to maintaining biodiversity and ecological resilience (Harvey et al. 2020; Turner et al. 2020; McDermott 2022). For example, climate-induced rewiring has been observed in north-temperate lake ecosystems that contain the cold-water lake trout (*Salvelinus namaycush*) (Guzzo et al. 2017; Bartley et al. 2019). While lake trout traditionally forage between shallow nearshore and deep offshore habitats, telemetry and diet data indicate that climate change-induced warming of nearshore waters is forcing them into deeper, cooler areas. This shift is disrupting carbon flows through the lake ecosystems and affecting lake trout growth,

condition, and population density. Similar behavioural and dietary shifts have also been observed in other co-occurring species, such as the planktivorous cisco (*Coregonus artedii*) and piscivorous walleye (*Sander vitreus*), indicating a broader pattern of food web rewiring in response to climate change (Guzzo et al. 2017; Bartley et al. 2019). If the habitat occupied under future distributions is degraded, then fish populations may also reduce and become more vulnerable to disturbances. For example, reduced rainfall in Australia's Murray–Darling basin could dry upstream refuge habitats and drive some species downstream to more polluted areas with less instream habitat (Balcombe et al. 2011; Pratchett et al. 2011). Predictive modelling could enhance fish conservation by enabling proactive planning to mitigate existing stressors in future habitats and implement measures to restrict unwanted migrations (Schweiger et al. 2008; Angert et al. 2013).

Climate change imposes complex, multifaceted pressures on riverine ecosystems, reshaping fish distribution patterns and altering key ecological dynamics (Olden et al. 2010; Woodward et al. 2010; Comte et al. 2013). A primary driver of these changes is the shift in thermal regimes, which directly affects the spawning, growth, and survival rates of fish species adapted to specific temperature ranges (Woodward et al. 2010). Rising water temperatures not only push species

beyond their optimal thermal limits but also reduce oxygen solubility, increasing the risk of hypoxic conditions detrimental to many aerobic organisms (Rabalais et al. 2010). Altered precipitation patterns and intensified hydrological cycles result in modified river flows—ranging from severe droughts to extreme flood events—that can disrupt the availability of suitable habitats and challenge the life-strategies of various fish species (Olden et al. 2010; Comte et al. 2013). Alterations in the timing of seasonal flows can misalign critical life events, such as migration and reproduction, with environmental cues, potentially compromising reproductive success (Aldous et al. 2011; Milner et al. 2013). As fish populations adapt to these pressures, many species may shift their ranges toward cooler waters or higher elevations, resulting in a reorganization of community structures and a reshaping of historical distributions (Brooker et al. 2007; Schweiger et al. 2008; Pecl et al. 2017). While some species may experience reduced distributions, others may experience increased distributions, ultimately resulting in new assemblage compositions and altered patterns of interspecific interactions.

In the context of New Zealand's freshwater ecosystems, climate projections suggest that rising temperatures and intensified westerly winds could lead to the continued earlier emergence of mean winter flows, particularly in the South Island, whereas streamflow in the North Island is projected to decline (Collins 2021; Queen et al. 2023). Temperature increases are anticipated to extend further south, accelerating the melting of alpine glaciers. Across the country, the frequency and intensity of floods are also projected to increase (Collins 2020; Serrao-Neumann et al. 2024).

Temperature and hydrological changes will impact New Zealand's freshwater fish and pose challenges for managing future species assemblages and their interactions. For example, Boddy and McIntosh (2017) predict that alpine galaxias (*Galaxias paucispondylus*) populations will fragment as they move into habitats currently occupied by trout, which may retreat from warming waters. Conversely, invasive species like brown bullhead catfish (*Ameiurus nebulosus*) and koi carp (*Cyprinus carpio*) are expected to expand their range, worsening sedimentation and algal growth in lowland rivers (Wu et al. 2013; Leathwick et al. 2016; Collier et al. 2017). Additionally, native fish like the warm-tolerant shortfin eel (*Anguilla australis*) may spread to new areas, preying on both native and introduced fish, further complicating ecosystem management (Sagar et al. 2005; Jellyman 2016; Stewart et al. 2024).

New Zealand's National Policy Statement for Freshwater Management (NPS-FM 2020) requires regional authorities to set pollution and water abstraction limits considering anticipated climate change impacts. However, limited understanding of climate change's effects on freshwater fauna may hinder authorities' ability to manage future impacts. Conservation managers also face the challenge of protecting both native species and introduced sports fish like trout, which are valued for recreation and funding freshwater advocacy but can harm native species. Identifying where these impacts are most severe in the future could enable more targeted conservation efforts without widespread trout eradication. To guide freshwater fish management decisions in New Zealand, this study aims to address the following questions:

1. How might the severity of climate change (indicated by the Intergovernmental Panel on Climate Change (IPCC) representative concentration pathways (RCPs) affect the potential end-of-century distributions of New Zealand's freshwater fishes?
2. For the predicted end-of-century distributions, how might climate change severity affect the overlap extent between introduced trout and native fish highly vulnerable to trout predation?

2.0 Methods

2.1 Fish data

Fish detection data were sourced from the New Zealand Freshwater Fish Database (NZFFD) (Richardson 1989), which is a national database compiling detection and nondetection data from freshwater fish surveys collected from a wide range of studies. To ensure a sufficient site selection for the models to learn habitat while reducing the influence of temporal changes in fish communities, only fish species that were present in at least 300 surveys (regardless of survey method used) since 1986 (the starting year of the climate baseline) were included, constituting 35 native and 10 non-native species (Table 1). Juvenile migratory galaxiids, known as "whitebait", were excluded to focus on predicting adult distributions as the migratory pathway covered by whitebait does not necessarily indicate suitable habitat. To account for potential temporal autocorrelation, observations made at the same site over time were aggregated into a single observation. A site is considered a single reach (typically ~700 m long), as mapped by the New Zealand's river environment classification system (Snelder et al. 2010). For each site, if at least one presence was recorded over the observation period, the site was considered as having a presence, ensuring each site was only represented once in the dataset, thereby minimizing temporal dependencies. Given that survey effort is not consistent across all database records, the dataset can only inform presence and nondetection, rather than true absence.

2.2 Environmental data

Two sets of environmental variables were compiled from multiple spatial datasets covering New Zealand's riverine network (Snelder et al. 2010), the first set (Table S1) was assumed to remain unchanged under future climate predictions, while the second set (Table S2) varied according to the climate scenario and climate model used. The first set contained 29 predictors (Table S1), containing a range of modelled and measured habitat and land use characteristics from the Freshwater Environments New Zealand geodatabase (Leathwick et al. 2010). Since water quality has varied both spatially and temporally during the fish data period, we focused on variables that are assumed to have changed little over this period, for example, geological or long-term hydrological variables. This reduces the likelihood of mismatch between species presence and environmental variables and improves model transferability (Werkowska et al. 2017).

Table 1. The scientific names and common names, native or introduced status, along with the number of New Zealand Freshwater Fish Database (Richardson 1989) observations (Obs.) of freshwater fish species modelled across New Zealand under different climate scenarios. NZTCS is the New Zealand Threat Classification System.

Status	Scientific name	Common name	NZTCS status	Vuln.	Int.	Obs.
Native	<i>Aldrichetta forsteri</i>	Yelloweye mullet	Least concern	Minor		546
	<i>Anguilla australis</i>	Shortfin eel	Near threatened	Minor		11 809
	<i>Anguilla dieffenbachii</i>	Longfin eel	Endangered	Minor		18 508
	<i>Cheimarrichthys fosteri</i>	Torrentfish	Vulnerable	Minor		2988
	<i>Galaxias anomalus</i>	Central Otago roundhead galaxias	Critically endangered		1	594
	<i>Galaxias argenteus</i>	Giant kokopu	Vulnerable	Moderate	1	1913
	<i>Galaxias brevipinnis</i>	Koaro	Least concern	Moderate	1	4473
	<i>Galaxias cobitinis</i>	Lowland longjaw galaxias	Critically endangered		1	971
	<i>Galaxias depressiceps</i>	Flathead galaxias	Vulnerable		1	
	<i>Galaxias divergens</i>	Dwarf galaxias	Endangered	Moderate	1	992
	<i>Galaxias eldoni</i>				1	614
	<i>Galaxias fasciatus</i>	Banded kokopu	Least concern	Minor	1	5740
	<i>Galaxias gollumoides</i>	Gollum galaxias	Critically endangered	Moderate	1	674
	<i>Galaxias macronasus</i>	Bignose galaxias	Critically endangered		1	654
	<i>Galaxias maculatus</i>	Inanga	Least concern	Minor		6594
	<i>Galaxias paucispindylus</i>	Alpine galaxias	Least concern	Moderate	1	1147
	<i>Galaxias postvectis</i>	Shortjaw kokopu	Endangered	Moderate	1	1055
	<i>Galaxias prognathus</i>	Upland longjaw galaxias	Critically endangered		1	383
	<i>Galaxias pullus</i>	Dusky galaxias	Critically endangered		1	407
	<i>Galaxias species D</i>	Clutha flathead galaxias	Nationally critical	High	1	842
	<i>Galaxias vulgaris</i>	Canterbury galaxias	Least concern	Moderate	1	3080
	<i>Geotria australis</i>	Lamprey	Data deficient	Minor		1004
	<i>Gobiomorphus basalis</i>	Crans bully	Least concern	Minor		1716
	<i>Gobiomorphus breviceps</i>	Upland bully	Least concern	Moderate		8356
	<i>Gobiomorphus cotidianus</i>	Common bully	Least concern	Minor		9672
	<i>Gobiomorphus gobioides</i>	Giant bully	Least concern	Minor	1	1131
	<i>Gobiomorphus hubbsi</i>	Bluegill bully	Vulnerable	Moderate	1	1347
	<i>Gobiomorphus huttoni</i>	Redfin bully	Near threatened	Minor	1	5969
	<i>Mugil cephalus</i>	Grey mullet	Least concern	Minor		339
	<i>Neochanna apoda</i>	Brown mudfish	Endangered	High	1	1105
	<i>Neochanna burrowsius</i>	Canterbury mudfish	Critically endangered		1	1546
	<i>Neochanna diversus</i>	Black mudfish	Endangered	High	1	880
	<i>Neochanna heleioides</i>	Northland mudfish	Critically endangered		1	1379
<i>Retropinna retropinna</i>	Common smelt	Least concern	Minor		2500	
<i>Rhombosolea retiaria</i>	Black flounder	Data deficient	Minor	1	419	
Introduced	<i>Ameiurus nebulosus</i>	Catfish				651
	<i>Carassius auratus</i>	Goldfish				1330
	<i>Cyprinus carpio</i>	Koi carp				563
	<i>Gambusia affinis</i>	Gambusia				2399
	<i>Oncorhynchus mykiss</i>	Rainbow trout				3339
	<i>Oncorhynchus tshawytscha</i>	Chinook salmon				436
	<i>Perca fluviatilis</i>	Perch				1041
	<i>Salmo trutta</i>	Brown trout				13 601
	<i>Salvelinus fontinalis</i>	Brook trout				328
	<i>Scardinius erythrophthalmus</i>	Rudd				741

Note: Vulnerability (Vuln.) to trout predation from Coughlan (2022) provided for native fish, along with an indication of intolerance (Int.) to anthropogenic stressors from Joy and Death (2004a) and the NZTCS conservation status (Dunn et al. 2018).

The second set of environmental variables contained 26 predictors (Table S2), composed of reach scale temperature and hydrological indicators calculated from climate-hydrology models by Collins (2020). Collins (2020), coupled a

TopNet hydrological model with six general circulation models (GCMs) to predict daily flows and catchment air temperature for both baseline or hindcast (1986–2005) and end-of-century (2080–2099) periods using four climate RCPs at

47 759 approximately equidistant reaches across the New Zealand River Environment Classification geospatial network (Snelder et al. 2010). Variables described in Table S1 were extracted from river reaches that corresponded to the same river reaches where climatic predictions were made. While the environmental variables in Table S1 were assumed to remain unchanged, their inclusion in modelling is necessary as water quality, physical habitat, and barriers to migration (such as dams), are often influential in determining the distribution of New Zealand's freshwater fish (Joy and Death 2004b; Leathwick et al. 2005; Canning 2018). For example, a large dam could prevent the movement of diadromous fish upstream (represented with the USDam variable), regardless of the hydrological and climatic suitability of the upstream environment. Pairwise Pearson correlations were used to assess collinearity between all variables across all distinct fish observation sites modelled and for each of the six climate models assessed, ensuring no variables were highly correlated ($r > 0.9$; Data S1), which can improve model transferability. The inclusion of spatially relevant covariates, such as altitude, distance from the coast, slope, temperature, precipitation, and vegetation cover, also help to account for potential spatial autocorrelation in our data (Joy et al. 2019).

2.2.1 Global climate models

The six GCMs used as part of the Coupled Model Intercomparison Project Phase 5 and included BCC-CSM1.1, CESM1-CAM5, GFDL-CM3, GISS-E2-R, HadGEM2-ES, and NorESM1-M (Collins 2020). The four future RCP scenarios used were a mitigation pathway (RCP2.6), two stabilization pathways (RCP4.5 and RCP6.0), and a high-end pathway (RCP8.5). Each RCP represents a different scenario of greenhouse gas emissions and concentrations, aerosols, and land use, extending to the year 2100. They are named based on their projected radiative forcing values for the year 2100, relative to pre-industrial levels (+2.6, +4.5, +6.0, and +8.5 $W \cdot m^{-2}$, respectively). Radiative forcing is a measure of the change in the balance of solar energy (measured in $W \cdot m^{-2}$) entering and leaving Earth's atmosphere due to factors like greenhouse gases or solar activity. Positive radiative forcing indicates an increase in net incoming energy, leading to a warming effect, while negative forcing implies a net loss of energy, resulting in cooling. These four RCP scenarios can be indicatively described as follows (Rogelj et al. 2012; IPCC 2014):

RCP2.6. This pathway is sometimes referred to as a “peak-and-decline” scenario. It represents a very stringent scenario where greenhouse gas emissions peak between 2010 and 2020, with emissions declining substantially thereafter. The goal of this pathway is to keep global warming likely below 2 °C above pre-industrial temperatures.

RCP4.5. This is a stabilization scenario where total radiative forcing is stabilized shortly after 2100, without overshooting the RCP4.5 level. It implies more modest reductions in emissions than RCP2.6 and is often considered an intermediate scenario. Under RCP4.5, the use of a mix of energy sources and technologies, including significant use of renewables, nuclear power, and fossil fuels with carbon capture and storage, is envisioned.

RCP6.0. This is another stabilization scenario where total radiative forcing is stabilized shortly after 2100, without overshooting the RCP6.0 level. It represents a scenario with no explicit climate target but where emissions peak around mid-century and decline thereafter.

RCP8.5. Often considered a “business as usual” scenario, it assumes continued high emissions leading to high greenhouse gas concentration levels. Under this scenario, there is no implementation of climate change policies, leading to high radiative forcing by the end of the century. This pathway is often used as a high-end scenario for risk assessment.

For each of the six GCMs and four RCP scenarios, all the temperature and hydrological variables in Table S2 were calculated for the hindcast and end-of-century periods using Collins (2020).

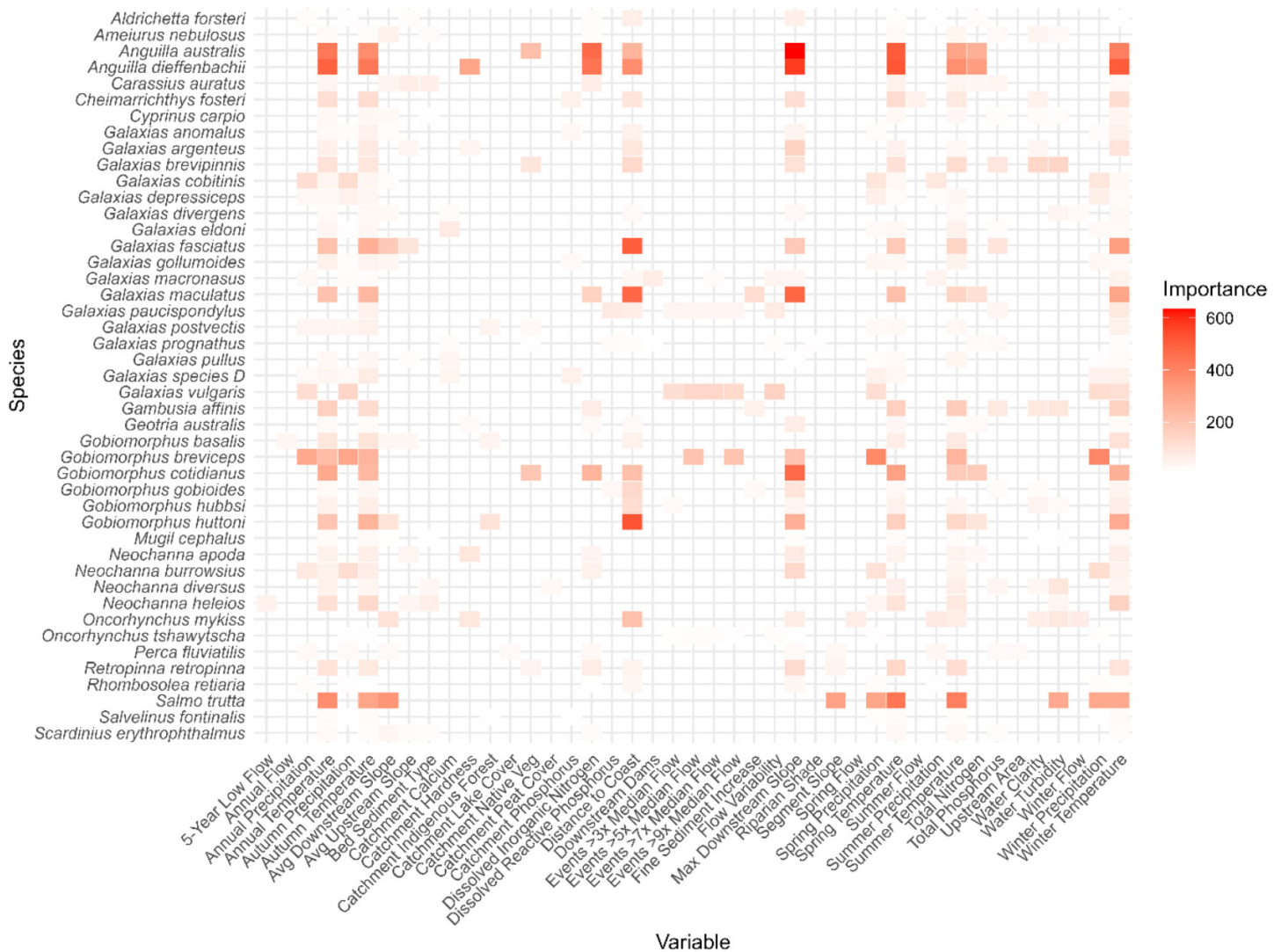
2.3 Data analysis

2.3.1 Predicting species distributions with climate change

Random forests is a machine learning method that uses a collection of classification and regression trees, whereby each tree is fitted to a bootstrapped sample (with replacement) and then validated on the out-of-bag sample. Random forest predictions are the average of the predictions of each tree. Classification and regression trees, and consequently random forests, work by partitioning observations at splits of predictors that minimize the sum of squares error. They have a high level of flexibility and can handle nonlinear relationships and complex interactions (Cutler et al. 2007).

For each fish species and each of the six climate models, random forests modelling was used to yield the probability of detection for all fish species using the potential predictor variables in Table S1 and the hydrological variables in Table S2 based on the hindcast climate scenarios. Each model was made using the “randomForest” function (trees = 500) from the randomForest package in R (Liaw and Wiener 2002; R Core Team 2024). The rfUtilities, psych, and pROC packages (Robin et al. 2011) were used to assess the performance (interrater reliability) of each model by calculating the average Cohen's Kappa coefficient and area under the receiver operating curves (AUC-ROC) using K-fold cross-validation ($N = 5$). The globally important variables were also identified using the “importance” function, which measures the decrease in Gini index from splitting on each variable, averaged over all trees. The thresholds for converting predicted probability to presence or background were determined using the *occurrence.threshold* function in the rfUtilities package to identify the thresholds that maximized the Kappa statistic (Evans and Murphy 2019). All species occurrence models were then used to predict the end-of-century distributions for each of the four RCP scenarios as determined by each of the six GCMs. Given the substantial increases in prediction uncertainty when extrapolating species distribution models to novel environments beyond the training data range, multivariate environmental similarity surfaces (MESS) analysis (Elith et al. 2010) was used to identify all river segments that contained environmental conditions outside the range of the training

Fig. 1. The mean variable importance for random forest models predicting the distributions of New Zealand's freshwater fish. Variable importance for random forest models was calculated within the *importance* function in the randomForest R package (Liaw and Wiener 2002), with higher values indicating greater influence as determined by the contribution to reduction in Gini coefficient. Six individual random forest models were created for each species using climate data from six global climate models; the mean variable importance values shown are the mean importance value across the six random forest models for each species.



data. This was conducted using the MESS function in the modEVA R package (Barbosa et al. 2016), involving the comparison of all hindcast training predictors for each climate model with each of the corresponding end-of-century climate scenario predictors. Negative values indicate areas where environmental conditions differ from the training data.

2.3.2 Overlap between trout and vulnerable native fish

Coughlan et al. (2024) developed a risk assessment matrix to systematically score and rank the vulnerability of New Zealand's native fish to the impacts of trout predation. Factors in the risk assessment matrix included the overlap of physical habitat where co-occurrence at reach level occurs, diel activity patterns, diet similarities, fecundity and egg

size, the age of reproductive maturity, larval dispersal ability, threatened species ranking, and adult body size. The vulnerability status from Coughlan (2022) is included in Table 1. For each of the climate scenario and climate-model combinations, the proportion of the end-of-century distributions predicted for each of the native fish species considered highly vulnerable to trout predation that overlaps with at least one trout species was estimated (Coughlan 2022).

3.0 Results

3.1 Predicting species distributions with climate change

All random forest models of present species distribution (using hindcast climatic conditions) showed very good or excellent performance as indicated by AUC-ROC values greater

than 0.8 and Cohen's Kappa values of at least 0.6 (Data S2). Variable importance, as indicated by the decrease in Gini index from splitting on each variable, is in Data S3. Overall, the most important variables for most species were the distance inland (river length) from the coast and the mean annual temperature (Fig. 1; Data S3). MESS analysis revealed that across climate scenarios and models, less than 0.28% of the end-of-century modelled river network was environmentally dissimilar to the hindcast training data.

Of the 35 native species modelled, four species (11%) are predicted to show a greater than 30% increased extent with an RCP8.5 scenario relative to hindcast extent in at least one climate model, native species predicted to have the greatest net increase in extent with increased radiative forcing compared to the hindcast scenario are *Mugil cephalus*, *Neochanna diversus*, *Gobiomorphus gobioides*, and *Retropinna retropinna*. Of the 10 nonnative fish modelled, four are predicted to have a large (>30%) net increase, with *Onchorhynchus tshawytscha* and *Cyprinus carpio* having the largest increases (Figs. 2 and 3). Among the native species modelled, 17 (49%) are projected to experience the greatest relative decline in extent with increased radiative forcing compared to the hindcast scenario. These species include *Galaxias depressiceps*, *Neochanna apoda*, *Galaxias species D*, *Galaxias gollumoides*, *Galaxias pullus*, and *Galaxias eldoni*. Additionally, seven nonnative species, including *Salvelinus fontinalis* and *Salmo trutta*, are also predicted to undergo significant reductions. Brown trout (*Salmo trutta*) are predicted to face reductions in current extent by between, on average, and between 12% and 43%, depending on the severity of climate change (Figs. 2 and 4). Rainbow trout (*Onchorhynchus mykiss*) are predicted to face reductions in current extent by between, on average, and between 17% and 24%, depending on the severity of climate change. As climate change severity increases, both brown and rainbow trout distribution reductions primarily occur southward and inland in the North Island, with minimal changes observed in the South Island (Fig. 3).

3.2 Overlap between trout and native fish

The native fishes considered highly vulnerable to trout predation by the Coughlan (2022) risk assessment, along with their change in extent and potential overlap with at least one trout species shown in Fig. 5. Despite increases in extent predicted for *Neochanna diversus*, *Neochanna burrowsius*, *Galaxias prognathus*, and *Galaxias macronasus* under more severe climate scenarios, expansion was consistently predicted in areas without trout overlap. *Neochanna apoda* and *Galaxias pullus* show varied results, with some models predicting both increases and decreases in extent, including scenarios with complete trout overlap. *Galaxias eldoni* and *Galaxias depressiceps* show potential decreases in extent with increased climate change severity, with high overlap with trout in all scenarios (Fig. 5).

4.0 Discussion

4.1 Species distribution models

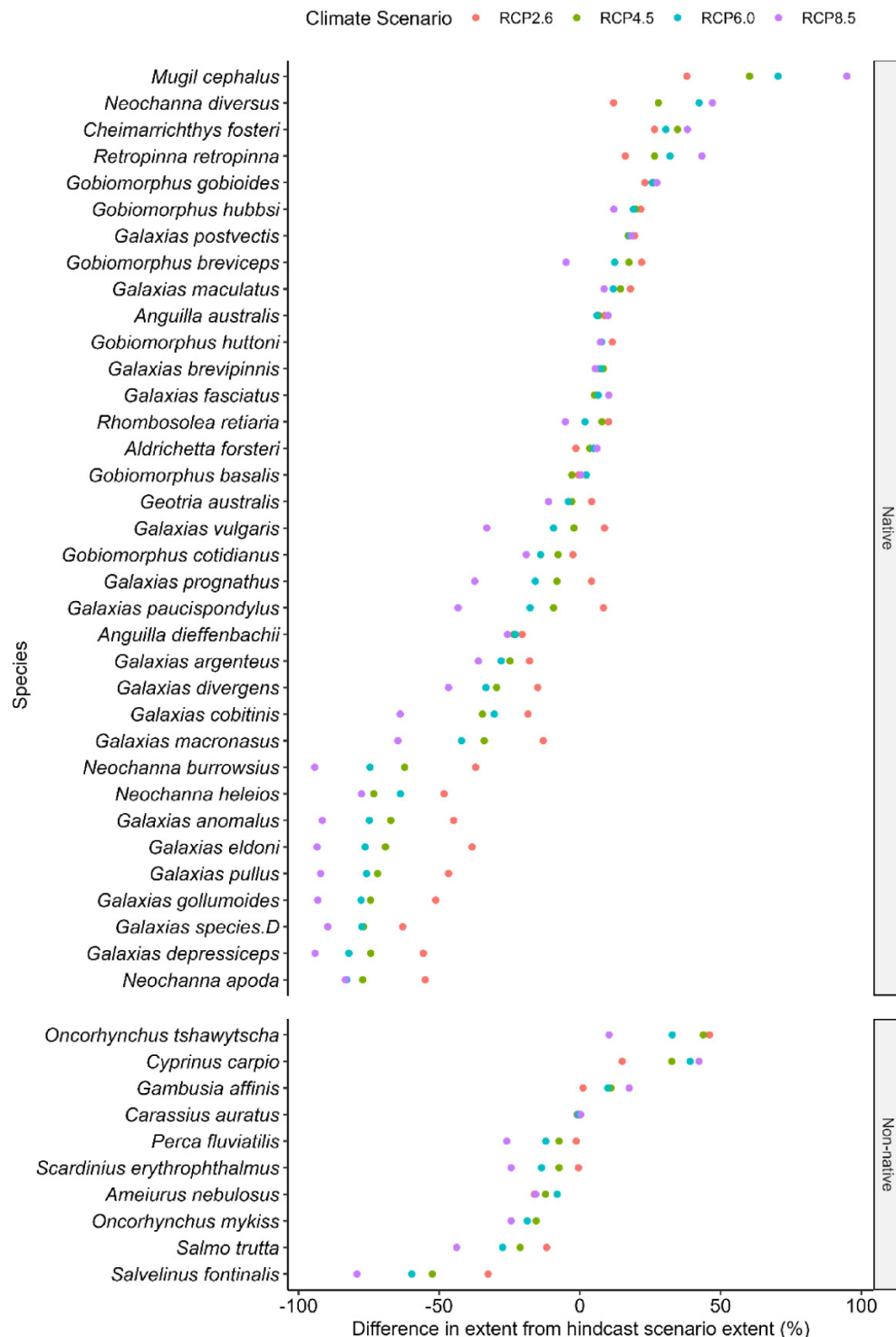
The present study used random forest models (Cutler et al. 2007) to predict how the distribution of New Zealand's fresh-

water fish might alter with climate change. The choice of modelling algorithm can significantly impact model transferability when extrapolating to novel conditions, such as those under climate change scenarios. While a model may perform well in predicting test data from the baseline conditions, it may not perform well in predicting unobserved conditions (García-Callejas and Araújo 2016; Morán-Ordóñez et al. 2017; Yates et al. 2018). For example, Charney et al. (2021) compared the transferability of 11 model algorithms when predicting the distribution of 108 tree species across the United States of America, and observed random forests to perform well within the range of training data and moderately when extrapolating to novel areas. Heikkinen et al. (2012) compared 10 model algorithms applied to bird, butterfly, and plant species in Finland. They showed that random forests were among the best performing models when assessing using Kappa, but showed intermediate performance (relative to the best and worst performing models) when assessing using the Area Under the Receiver Operating Curve (AUC)—though the difference in AUC performance from the best performing models was small (~0.03 reduction) (Heikkinen et al. 2012). There is also no universally accepted model algorithm that performs well in all instances when predicting both within and outside of the trained environmental space (Heikkinen et al. 2012; Norberg et al. 2019; Charney et al. 2021).

Relying on a single model algorithm is risky and potentially misleading, and decision-makers should compare predictions between different methodologies that use different source datasets, modelling algorithms, background data selection, cross-validation methods, and be mindful of the potential reasons for the differences. Random forests, as with all tree-based methods, tend to be conservative when extrapolating to novel environmental as they use predicted values from the closest observed tree split within the training range. In contrast, regression-based methods, such as generalized linear models, continue extrapolating the regression with the same slope derived from the training data, which may lead to extreme and unrealistic predictions (Elith and Graham 2009). Predicting beyond training data is challenging for any model, though Bayesian methods with priors informing species tolerance from experimental studies may be a promising avenue to improve the reliability of model transferability (Norberg et al. 2019; Schleuning et al. 2020; Bosch-Belmar et al. 2021). At present, there is limited published experimental data on the tolerance of New Zealand's fish to differences in temperature and hydrological regimes, and further research on fish tolerance should be prioritized to the species identified here as most at-risk (Richardson et al. 1994). Despite inevitable model difficulty predicting to entirely novel environments, the MESS analysis identified very few locations where environmental conditions are dissimilar to the range covered by the training dataset, likely owing to New Zealand's diverse climate and geology.

In addition to model methodology, future habitat and population changes may also affect the reliability future distribution predictions. Previous analysis has shown that nutrient enrichment, followed by downstream barriers (i.e., dams) and loss of riparian vegetation, but not the presence of introduced fish, currently accounts for the largest broad-scale de-

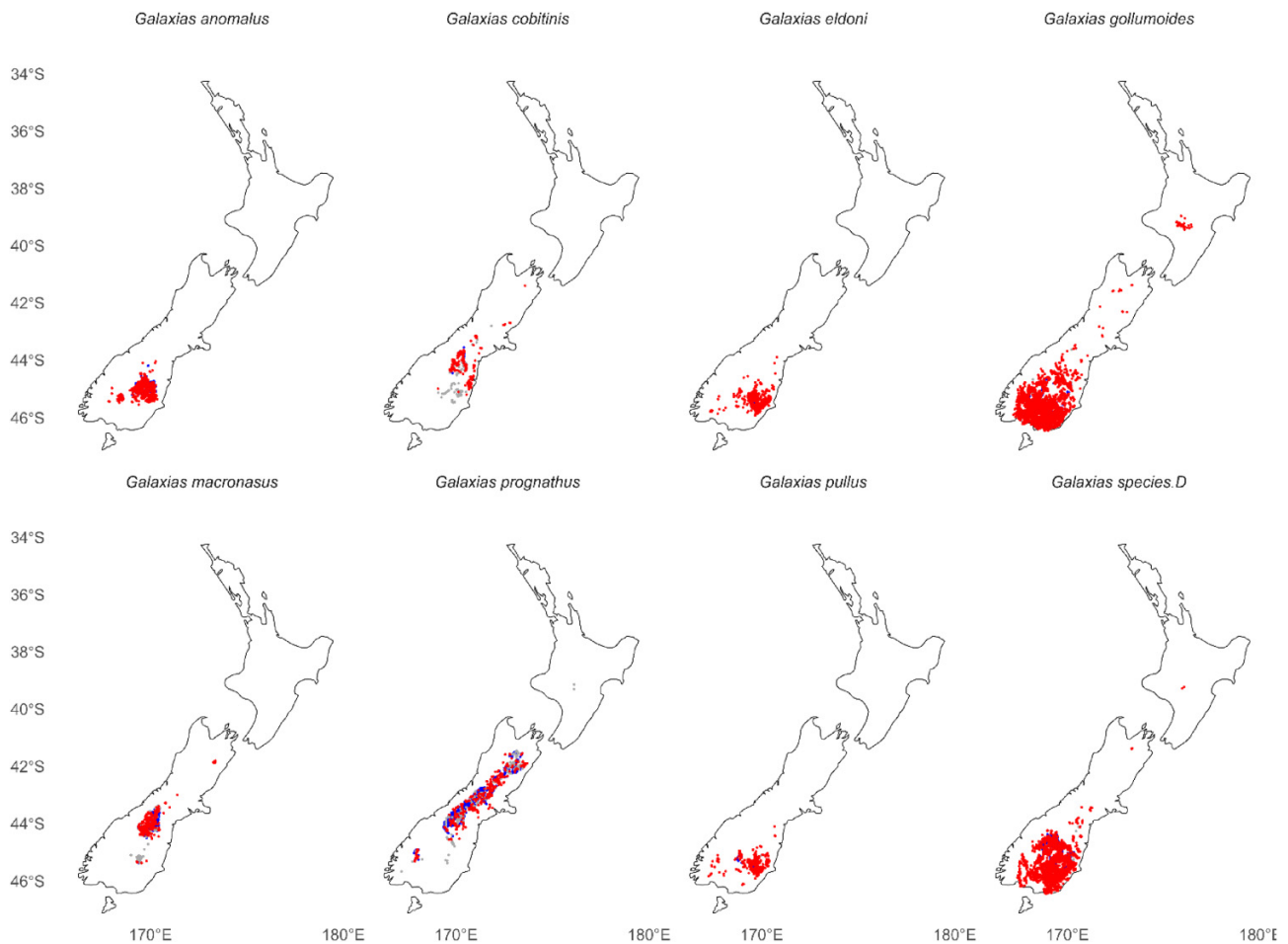
Fig. 2. The extent of the modelled hydrological network (%) across New Zealand predicted to be occupied by a given freshwater fish for four end-of-century climatic scenarios relative to the extent in the hindcast climate scenario (measured as percentage difference). Residuals within the climate scenarios are derived independently using six different global climate models. Groups compare native and nonnative fish. RCP, representative concentration pathway.



viation in freshwater fish distributions from that predicted to occur in reference conditions (Canning 2018), consistent with other research on the decline of New Zealand's freshwater fish (McDowall 2010; Dunn et al. 2018; Joy et al. 2019). Given that previous analysis also shows that frequent distur-

bances, owing to the short flood-prone nature of New Zealand rivers and streams, often limit the influence of biological interactions affecting species presence (Jowett and Richardson 1989; Death and Winterbourn 1995; Winterbourn 1997), this analysis did not use joint species distribution models (JSDMs).

Fig. 3. The predicted change in the extent of New Zealand's modelled hydrological network occupied by species currently classified by the IUCN as critically endangered (Dunn et al. 2018). Predictions are based solely on the Beijing Climate Center (BCC) climate modelling, contrasting a contemporary climate with a severe end-of-century scenario (RCP8.5). Red areas represent locations where the species are predicted to occur under the contemporary climate but not under the RCP8.5 scenario. Grey areas represent locations where the species are predicted to occur under the RCP8.5 scenario but not under the contemporary climate. Blue areas indicate locations where the species are predicted to occur under both climate scenarios. Classifications were plotted in order of occurrence in both places first, followed by future occurrence only, followed by hindcast only, as a result the hindcast only may mask appearance of other categories and visually emphasize loss.

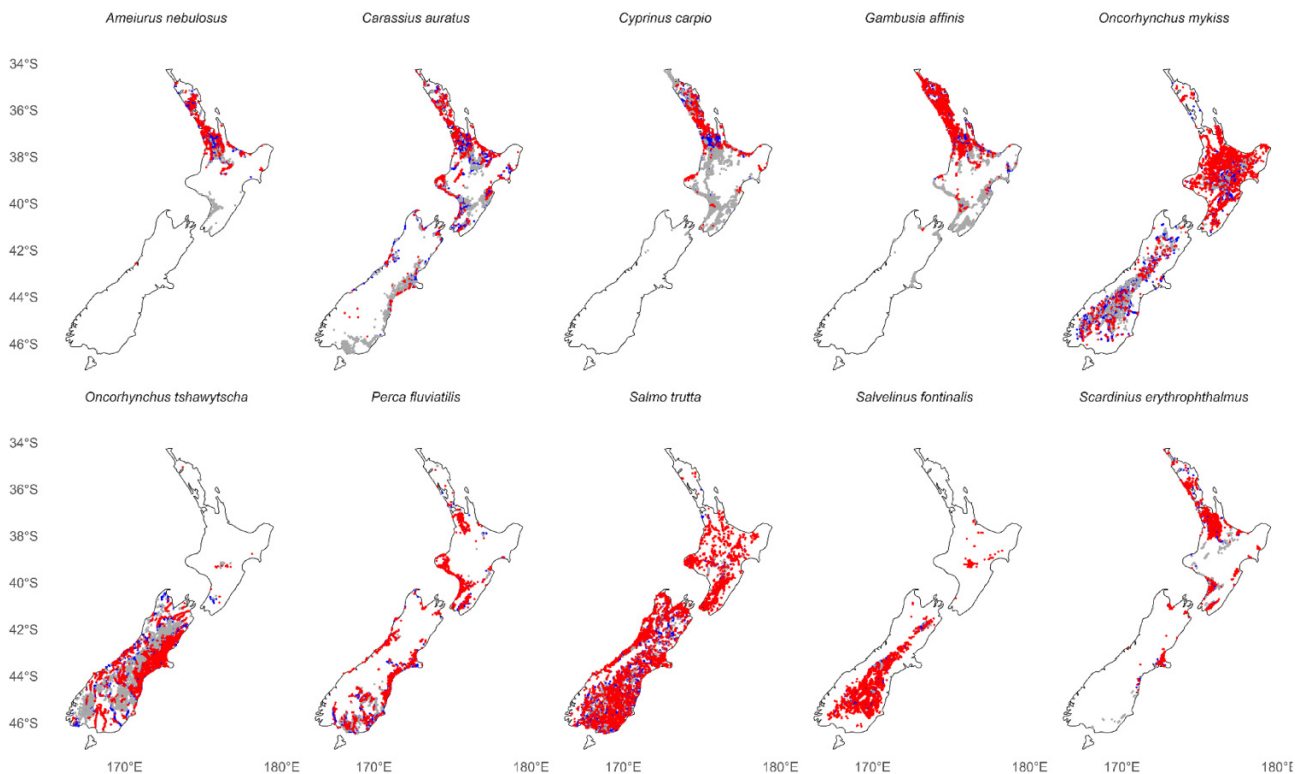


However, JSDMs may be a valuable exploration where population estimates are desired in environmentally stable locations or where environmental decline increases competition for resources (Woodward et al. 2016; Jellyman and McIntosh 2020). Although the *National Policy Statement for Freshwater Management* (NPS-FM; Ministry for Environment, 2020) requires regional management authorities to either maintain or improve the health of freshwater ecosystems, if that direction changes or is not enforced and future declines in freshwater health occur, then predictions made here are likely to underestimate declines in end-of-century distribution. Without any land use change, increased climatic variability could increase erosion and the sedimentation of freshwater habitats (Neverman et al. 2023). Extended periods of low rainfall or drought with fewer floods could reduce connectivity between riverine pools, disrupt migratory and spawning cues, increase water temperature in stagnant pools, and increase the likelihood of hypoxic events as algae and nutrients are

flushed less frequently (Woodward et al. 2010; van Vliet et al. 2023). Therefore, predictions presented may over-estimate future distributions or indicate distributions occupied by small and vulnerable populations unless efforts are taken to reduce nutrient enrichment and sedimentation and improve habitat quality.

As the models were trained using a dataset that collates surveys from many different studies using different methods, sampling intensity and study focus, the models only predict the probability of the product of occurrence and detection, which is not indicative of population density. It was also not possible to account for detection inadequacies or the true absence of species from any given site, instead models were trained by compared detected presence against background values where species may or may not be present. As a result, predictions may underestimate the true extent of species, particularly in locations where deep waters, in-stream structures, or turbidity make commonly used survey

Fig. 4. The predicted change in the extent of New Zealand's modelled hydrological network occupied by 10 introduced fish species is shown. Predictions are based solely on BCC climate modelling, contrasting a contemporary climate with a severe end-of-century scenario (RCP8.5). Red areas represent locations where the species are predicted to occur under the contemporary climate but not under the RCP8.5 scenario. Grey areas represent locations where the species are predicted to occur under the RCP8.5 scenario but not under the contemporary climate. Blue areas indicate locations where the species are predicted to occur under both climate scenarios. Classifications were plotted in order of occurrence in both places first, followed by future occurrence only, followed by hindcast only, as a result the hindcast only may mask appearance of other categories and visually emphasise loss.

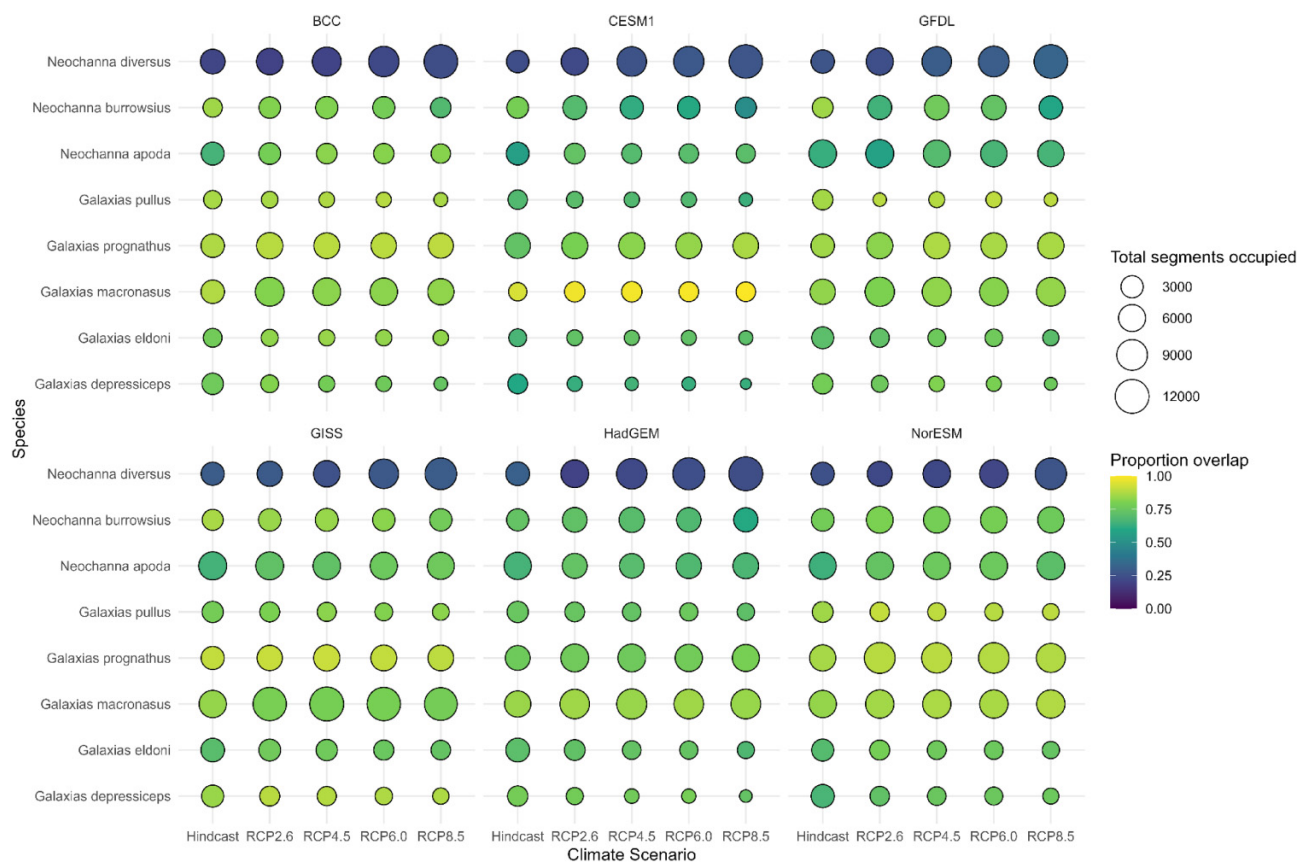


methods, such as electric fishing and spotlighting, difficult or where most surveys were collected focusing on a single species (not distinguished in the NZFFD). Nonetheless, the NZ Freshwater Fish Database remains the most comprehensive fish observation database across New Zealand. Although standardized and routine freshwater fish monitoring has historically been poor, a relatively recent directive to conduct standardized fish monitoring was given to all regional authorities from central government via the NPS-FM (Ministry for Environment, 2020). The directive requires councils to develop and implement a freshwater fish monitoring across wadeable rivers and stream, with sampling to occur at least annually between December and April (inclusive) following the protocols outlined in Joy et al. (2013), which builds on protocols by David et al. (2010). If successfully implemented, future analyses could explore modelling presence-absence, and relative abundance, as well as quantitative appraisals of spatio-temporal dynamics of fish assemblages and species interactions via JSDMs (Pollock et al. 2014; Tikhonov et al. 2017). Routine quantitative assessments of fish assemblages would improve impact assessments of changes in water quality, habitat, and species interactions, enabling managers to respond more effectively to detected declines.

4.2 Changes in species range

Nine native species are predicted to have end-of-century distributions reduced to less than 1% of the modelled network with a business-as-usual approach to climate change (RCP8.5 scenario). These species are all nonmigratory galaxiids or mudfish with very localized contemporary distributions and are critically endangered (Joy and Death 2013; Keegan et al. 2022). The substantial reductions in extent predicted to occur with a business-as-usual management of climate change may result in the extinction or near-extinction of these species. If populations are reduced to low levels in these localized areas, they become vulnerable to Allee effects, where reduced population fitness can lead to extinction (Berec et al. 2007; Walter et al. 2017). Small populations face heightened risks from demographic stochasticity, environmental stochasticity, and genetic factors. Random fluctuations in birth and death rates (demographic stochasticity) can cause significant declines in small populations, while unpredictable environmental events like floods and droughts (environmental stochasticity) disproportionately impact them (Bernhardt et al. 2020; Garant 2020). Genetic factors, such as inbreeding and reduced genetic diversity, further reduce their resilience to disturbances (Walter et al. 2017; Fenderson

Fig. 5. The proportion (colour) of the modelled river network across New Zealand where at least one species of trout is predicted to overlap with a given fish species considered highly vulnerable to trout predation (Coughlan 2022). Circle size is proportional to number of river reaches (segments) predicted to be occupied for a given native species, climate scenario, and global climate model. Within the climate scenarios, “Hindcast” approximates a contemporary climate, while RCP2.6–8.5 indicate potential end-of-century scenarios with values indicating the global radiative forcing ($W \cdot m^{-2}$).



et al. 2020; Hohenlohe et al. 2021). These combined pressures likely contributed to the extinction of the New Zealand grayling (*Prototroctes oxyrhynchus*). Deforestation, sedimentation, and pollution degraded their freshwater habitats, turning once optimal rivers into unfavourable ones, which, combined with overfishing, predation by introduced species, and the spread of *Saprolegnia parasitica*, led to their decline (Lee and Perry 2019). To prevent further extinctions of New Zealand’s freshwater fishes, efforts must focus on restoring and creating habitats, and mitigating threats near predicted distributions (Morris et al. 2006; Hodgson et al. 2011; Synes et al. 2020).

Included in the native species predicted to increase with increased radiative forcing are three of New Zealand’s five migratory galaxiid species known as “whitebait”—highly valued for their recreational and commercial fisheries (Rowe et al. 1992; Yungnickel et al. 2020). Furthermore, the black mudfish, which is currently considered At Risk—declining under the NZ Threat Classification System, is anticipated to have a substantially greater habitable distribution, particularly across the lowland Waikato River and the lowland Manawatu River. Despite potentially greater habitable distributions, the lack of connectivity between habitats and the

extensive loss of wetlands will likely constrain the potential habitat distribution from being realized (Davidson 2014; Dymond et al. 2021). In addition, to the increased extent of these native species, pest species including goldfish, carp, and mosquitofish will likely benefit from increased temperatures and changed flow regimes if biosecurity efforts are ineffective. Interestingly, some species with seemingly similar functional traits, such as short-fin and long-fin eels, and shortjaw kōkopu and giant kōkopu, are projected to increase and decrease, respectively. We are currently exploring what might be driving these differing responses in a companion publication (Death et al. in prep.).

4.3 Altered interspecific interactions

As climate change is predicted to substantially alter the composition of freshwater fish assemblages nationally, the food web interspecific interactions will also change. While existing predation pressures may reduce in some instances, new predation pressures may arise in other instances, as both native and nonnative predators move into new areas, e.g., if the introduced mosquitofish become established in the lower North Island, particularly in places like the Wairapapa Moana

Wetlands complex. If that spread is realized, then both native fish and introduced sports fish in those locations will be at risk of having their fins and eyes nipped by mosquitofish, potentially reducing their populations and causing trophic events, similar to those observed in Northland's Kai Iwi Lakes (Ling 2004; Rowe et al. 2018). The movement of native species into nonnative ranges can pose significant conservation challenges, as their impacts can mirror that of introduced species (Staudt et al. 2013; Van Zuiden et al. 2016; Guiden et al. 2019). For example, eels are predicted to move slightly into higher altitude river reaches, which would then increase predation pressures on smaller fish in those locations.

For nonmigratory species like the black mudfish, range shifts may require facilitated translocations to overcome geographical barriers and restore suitable habitats at new locations. Managing species movement, whether through assisted migration or natural range shifts, poses multiple challenges (Thomas 2011; Berger-Tal et al. 2020; Butt et al. 2021). While there are precedents for successful translocations to preserve endangered species, such as the South Island Takahē, the eastern barred bandicoot, and the Tasmanian devil, the ecological risks and unintended consequences of such interventions are well-documented, leading to significant hesitation in their application for climate adaptation (Miskelly and Powlesland 2013; Thalmann et al. 2016; Groenewegen et al. 2017). Socio-political challenges stem from high financial costs and societal concerns about species introductions, creating political risks for policymakers. Additionally, there is a potential values conflict when protecting native species that migrate into new areas due to climate change. While these species are native to their original habitats, they may be perceived and managed like introduced species in their new ranges, leading to ecological and ethical dilemmas (Coz and Young 2020; Glikman et al. 2022). This complicates traditional conservation paradigms focused on protecting native biodiversity and managing invasive species. Conservation managers will need detailed research into the ecological requirements of both the species at the destination and the species being relocated, including the timing around relocations to match climatic suitability, socio-political views, and the potential alteration of destination food webs (Miskelly and Powlesland 2013; Thalmann et al. 2016; Groenewegen et al. 2017). Even where detailed research has been completed, there is often considerable uncertainty in predicting suitable future habitats and potential ecological interactions, which hinders implementation (Pollock et al. 2014; Briscoe et al. 2019). Despite these barriers, advances in mechanistic and JSDMs, alongside adaptive management frameworks, offer pathways to mitigate uncertainties and balance ecological knowledge, societal engagement, and political will (Wyborn et al. 2021).

4.4 Native fish and valued sports fish

In New Zealand's unique context, introduced trout fisheries are a highly valued sports fishery that receive a high level of protection under conservation law, requiring populations to be maintained and enhanced. This can create

tension between conservation priorities, particularly in locations where trout have been implicated in the decline of native species via predation, competition, and behavioural mechanisms (McIntosh et al. 2010; Jellyman et al. 2018). Conversely, New Zealand's trout fishery generates substantial funding for conservation via licence sales, which have allowed the relevant statutory conservation agencies (Fish and Game councils) to become New Zealand's most active advocates for freshwater environments. The advocacy lobbies for strong environmental policies that benefit both introduced trout and native fisheries, and the licence-based funding model has afforded greater independence from government influence compared with the tax-funded Department of Conservation. For example, Fish and Game were responsible for securing 12 of the current 15 Water Conservation Orders, which are the highest level of protection a waterbody can be afforded in New Zealand. However, licence income has also funded the restoration of over 200 wetlands (Canning et al. 2021), far exceeding efforts made any other agency in New Zealand, and providing considerable habitat for native fauna (Garrett-Walker et al. 2020; Stewart et al. 2022). A balanced approach to managing both introduced trout and native fisheries likely involves prioritizing native fish protection in areas where they are particularly vulnerable to trout pressures.

Using the risk-assessment framework by Coughlan (2022), which identifies native fish most at risk from the pressures of trout, the potential end-of-century overlap between trout and highly vulnerable fish species was assessed. Overall, this overlap is predicted to reduce substantially with increasing climate change severity. It is estimated that the overlap with a radiative forcing of $8.5 \text{ W}\cdot\text{m}^{-2}$ (business-as-usual scenario) will be approximately half that of the "peak and decline" scenario where radiative forcing is limited to $2.6 \text{ W}\cdot\text{m}^{-2}$ (Fig. 5). This is attributed to a reduction in trout distribution, consistent with global observations of trout reduction (Kovach et al. 2016; Muhlfeld et al. 2019), as well as a reduction in the distribution of native fish that are highly vulnerable to trout predation. Of the latter, a business-as-usual scenario is predicted to reduce the distributions of 7 of the 10 highly vulnerable taxa almost entirely, potentially resulting in their extinction or near-extinction. This does not account for further declines in habitat quality or increased predation. At locations where trout may overlap with highly vulnerable native fish, conservation managers should consider mitigating interventions, such as reducing trout population pressures and increasing habitat for spawning and refugia.

While trout is predicted to reduce, Chinook salmon is predicted to have a considerable increase in extent. Chinook salmon hatch in cool, clean freshwater habitats with gravel substrates, where juveniles feed on small invertebrates before migrating to the ocean at 1–2 years old; once matured they returning to freshwaters to spawn and do not eat at this stage. As they typically spawn in waters below 10°C , warming of lowland South Island rivers where they currently spawn could push Chinook to migrate further upstream to cooler waters in lower order streams with longer cumulative length (Beer and Steel 2018; Fuhrman et al. 2018).

4.5 Intervention-forward adaptive management

An intervention-forward adaptive management approach is warranted for species facing extinction, significant range reductions, or high vulnerability to predation pressures. Intervention-forward adaptive management is an approach whereby, in the face of uncertainty, multiple interventions are planned and implemented early, followed by cyclical monitoring, evaluation, and adjustment as needed (Dickie et al. 2023). This iterative process allows managers to test hypotheses and adjust their approaches based on the outcomes observed, thereby improving the effectiveness of conservation efforts over time (Allen et al. 2011; Keith et al. 2011; Williams 2011). This involves long-term quantitative monitoring of affected native fish, trout, and their habitats in key overlap areas to assess intervention effectiveness. Intervention-forward adaptive management uses a precautionary approach and would be preferable over realized adaptive management, which relies on patterns of decline to establish first, which may take time to establish with confidence, particularly where natural variability is high and where monitoring capacity is limited.

In addition to local-scale mitigation efforts, reducing cumulative impacts from the broader catchment, and reducing climate change severity via a reduction in fossil fuel use, are also necessary. Showcasing the potential of reducing broader catchment stressors, Vaughan and Gotelli (2019) demonstrated that improving water quality effectively mitigated the adverse effects of significant temperature increases on aquatic macroinvertebrates in England and Wales between 1991 and 2011. Land use change, such as increasing vegetation cover, altering vegetation type, reducing impervious surfaces, and restoring wetlands, can also be used in key locations to mitigate climate-driven alterations in the severity of flooding and drought, as well as improve water quality and freshwater habitat availability. For example, Canning et al. (2022) examined the impact of creating 44 lagoons and sediment traps in a highly coordinated way across Australia's Tully-Murray catchment, which receives approximately 4 m of rainfall annually. Not only was widespread flooding across the catchment substantially reduced, but the lagoons provided habitat for at least 36 native freshwater fish, and landholder profitability increased. Thus, demonstrating the potential benefits of coordinated land use change and wetland restoration that could be observed more widespread in other catchments. Further research into catchment-based mitigation strategies at priority locations, considering both land management practices and land use, would be highly beneficial in informing more effective catchment management.

This study projected the potential end-of-century impacts of climate change on New Zealand's native fish. While predation pressures from trout are anticipated to reduce substantially with increasing climate change severity, the potential distributions for many of New Zealand's native fish are also anticipated to reduce. If aquatic habitats remain in their current condition and an RCP 8.5 climate scenario is observed, then climate change is predicted to result in approximately 10 native fish species being reduced to extinction or near-extinction. A further 18 species were predicted to have sig-

nificant reductions in extent, including the valued trout fisheries being reduced by approximately 30%–40%. These grim outcomes are likely only if a business-as-usual approach to climate change persists. Mitigating climate change severity and improving land use impacts on freshwater environments could prevent anticipated extinctions or near-extinctions.

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Data availability

Species climate prediction data can be accessed from a figshare repository at [10.6084/m9.figshare.27634824](https://doi.org/10.6084/m9.figshare.27634824).

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2024-0127>.

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