

Hydrological disturbance benefits a native fish at the expense of an exotic fish

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Summary

1. Some native fish in New Zealand do not coexist with introduced salmonids. Previous studies of disjunct distributions of exotic brown trout *Salmo trutta* and native galaxiids demonstrated native extirpation except where major waterfalls prevented upstream migration of trout. In the Manuherikia River system, we predicted that water abstraction might be a further factor controlling the spatial distribution of both the invader and a native fish.

2. We applied multiple discriminant function analyses to test for differences in environmental conditions (catchment and instream scales) at sites with roundhead galaxias *Galaxias anomalus* and brown trout in sympatry and allopatry. We then used a supervised artificial neural network (ANN) to predict the presence–absence of *G. anomalus* and brown trout (135 sites). The quantification of contributions of environmental variables to ANN models allowed us to identify factors controlling their spatial distribution.

3. Brown trout can reach most locations in the Manuherikia catchment, and often occur upstream of *G. anomalus*. Their largely disjunct distributions in this river are mediated by water abstraction for irrigation, together with pool habitat availability and valley slope. Trout are more susceptible than the native fish to stresses associated with low flows, and seem to be prevented from eliminating galaxiid populations from sites in low gradient streams where there is a high level of water abstraction.

4. *Synthesis and applications.* In contrast to many reports in the literature, our results show that hydrological disturbance associated with human activities benefits a native fish at the expense of an exotic in the Manuherikia River, New Zealand. Water abstraction is also known to have negative impacts on native galaxiids, therefore we recommend restoring natural low flows to maintain sustainable habitats for native galaxiids, implementing artificial barriers in selected tributaries to limit trout predation on native fish, and removing trout upstream.

Key-words: biological invasion, disjunct distributions, disturbance, galaxiids, introduced trout, water abstraction

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Introduction

Biological invasions along with habitat loss are recognized as major threats to biodiversity world-wide

(Vitousek 1994; Clavero & García-Berthou 2005). Effects of exotic species are well documented and occur from individual to ecosystem level (Mack *et al.* 2000; Townsend 2003). At the population level, a comprehensive understanding of mechanisms leading to invasion success and impact is necessary to develop efficient management tools (Sakai *et al.* 2001). Effects may differ across sites (Palmer & Ricciardi 2004) and the ability to predict impacts requires information

about species' responses to local abiotic factors as well as to each other.

Brown trout *Salmo trutta* L. have been introduced for angling in many countries but have often had negative impacts on native fish populations (Krueger & May 1991; Crowl, Townsend & McIntosh 1992; Morita, Tsuboi & Matsuda 2004). The introduction of brown trout in 1864 to Australia and in 1867 to New Zealand coincided with declines and local extirpations of native galaxiid species through predation by trout (Townsend & Crowl 1991; Closs & Lake 1996) and competitive displacement (reviewed by McDowall 1968, 2003; Crowl, Townsend & McIntosh 1992). The strongest evidence of the effects of introduced brown trout on native galaxiids in stream ecosystems is provided by their non-overlapping distributions (Crowl, Townsend & McIntosh 1992; Closs & Lake 1996; McIntosh 2000).

The Otago region on the South Island of New Zealand has become recognized as a hotspot of non-migratory galaxiid diversity since the reinstatement of the roundhead galaxias *Galaxias anomalus* Stokell, previously confounded with *Galaxias vulgaris* Stokell, and the recognition of several new species (Department of Conservation 2004). According to the New Zealand threat classification list (Hitchmough 2002), these small (< 150 mm long) stream-dwelling species are in gradual decline, except for *G. vulgaris*. While habitat degradation caused by land-use change may be involved (Hanchet 1990), Townsend & Crowl (1991) found that land use in the Taieri River catchment (Otago Province) could not account for the observed galaxiid population fragmentation. Rather, it was large waterfalls (higher than 3 m) that prevented trout invasion and provided upstream refugia for the galaxiids. In the nearby Manuherikia River catchment, where *G. anomalus* is the dominant galaxiid, waterfalls are not such a marked feature but the diversion of stream water for irrigation is particularly widespread. Water was originally taken for gold mining but the associated rights were picked up by irrigators and the pattern of abstraction continued. In the dry Manuherikia region, droughts are a natural feature but have become extended and aggravated by the increase of water abstraction as a result of agricultural intensification. There is little previous work on the effects on fish of anthropogenically mediated drought (Matthews & Marsh-Matthews 2003).

As local abiotic conditions may mediate the effects of species' introductions (Holway, Suarez & Case 2002; Ricciardi 2003), we expected that low flow conditions associated with water abstraction might be a further factor controlling the spatial distribution of both brown trout and native galaxiids in the Manuherikia River catchment. We analysed a catchment-wide fish presence-absence data set with the following goals: (i) to identify the environmental factors that may mediate trout-galaxiid interactions, in order to predict the outcome of brown trout impacts, and thus (ii) to provide the basis for effective management. We made use of contrasting modelling techniques, but with special

emphasis on artificial neural networks (ANN), which have proved efficient in modelling species' distributions (Manel, Dias & Ormerod 1999) and predicting environmental impacts (Spitz & Lek 1999).

Method

The gravel-bed tributaries of the Manuherikia River (South Island, New Zealand), with their classic riffle-run-pool structure, rise in steep mountain country before flowing through developed farmland where water is taken for stock and irrigation. The main stem of the river flows south-west for 85 km to its confluence with the Clutha River at Alexandra. Its upper reaches have been dammed for irrigation purposes, while the middle and lower reaches have large water off-takes. The catchment has a harsh, dry climate, ranging from over 30 °C in mid-summer to -15 °C in mid-winter. Its fish fauna consists of two exotic salmonids (brown trout and the less common brook trout *Salvelinus fontinalis* Mitchill) and several native species: bullies *Gobiomorphus* spp., longfin eel *Anguilla dieffenbachii* Gray and the non-migratory alpine galaxias *Galaxias paucispondylus* Stokell (recorded at one site) and the yet to be named *Galaxias* sp. D. However, by far the most widespread native species is the roundhead galaxias *G. anomalus*.

FISH DATA SET AND ENVIRONMENTAL DATA

The data set contained 135 sites with both biological data (fish species presence-absence) and environmental data (Table 1). We extracted the occurrence of *G. anomalus* and brown trout from the New Zealand Freshwater Fish Database (NZFFD; McDowall & Richardson 1983; Joy & Death 2004). All sites have been sampled by electrofishing in summer since 1980, with 70% of samples taken since 2000. The percentages of the stream bed composed of particular channel units (pool, run, riffle and rapid) were also extracted from NZFFD. We extended the environmental data set by extracting stream order, valley slope and altitude from the River Environmental Classification (REC; Snelder, Biggs & Weatherhead 2004), a river reach-scale geographical information system (GIS). We also determined the relative distance of each site from the main channel as described by Schaefer & Kerfoot (2004), assigning a value of 0 to sites on the main channel and 1 to sites on headwater streams, and we identified the position of dams and natural waterfalls (greater than 3 m high) that could prevent the upstream migration of trout. Finally, we calculated an index of water abstraction in several steps using data from the Otago Regional Council.

The first step was to incorporate in the GIS all water abstraction locations in the Manuherikia catchment, each with its maximum permitted rate of water take (MWR; $L s^{-1}$). Records of actual water abstraction rates were not available. We also added 50 locations to the

Table 1. Mean and ranges for environmental variables described at the reach and site scales

Variable	Code	Minimum	Maximum	Mean	Data transformation
Reach scale					
Stream order	SO	1	7	3.30	None
Valley slope*	VS	1	3	2.16	None
Site scale					
Altitude (m)	ALT	170	1100	586.70	None
Relative distance from the main channel	RDM	0	1	0.53	Arcsinh
Index of water abstraction	IWA	1	6	2.56	None
% pool	%PO	0	100	28.60	Arcsinh
% riffle	%RF	0	100	21.62	Arcsinh
% run	%RN	0	100	38.42	Arcsinh
% rapid	%RP	0	100	11.37	Arcsinh

*Valley slope: 1, high gradient (slope > 0.04); 2, medium gradient (0.02 = slope = 0.04); 3, low gradient (slope < 0.02). The valley slope is based on Euclidean length (m m⁻¹).

GIS for which hydrological data were available, specifically the 7-day mean annual low flow (MALF; L s⁻¹), a measure of the risk of extended low discharge conditions (Richter *et al.* 1996). The MALF locations were reasonably evenly distributed in the catchment but did not correspond to the 135 fish sites. For each of the 48 fish sites subject to water abstraction upstream, we attributed a MALF value from the closest hydrological monitoring location. Then we divided the attributed MALF value by the sum of MWR upstream of each of the 48 sites. We chose MALF/MWR as the ratio of interest because the quantity of water permitted to be taken upstream was always greater than the MALF. Finally, the index of water abstraction was defined as follows:

$$IWA = 1 - \left(\frac{MALF}{MWR} \right)$$

This index ranges from 0 to 1 and the closer the index tends to 1, the greater the risk that the stream will dry up because of water abstraction. To include sites where no abstraction occurred, we transformed this index into a categorical series comprising six classes (class 1, no water abstraction; class 2, 0 = IWA < 0.2; class 3, 0.2 = IWA < 0.4; class 4, 0.4 = IWA < 0.6; class 5, 0.6 = IWA < 0.8; class 6, 0.8 = IWA = 1).

DATA ANALYSIS

Two types of analysis (classical multivariate and ANN) were performed to answer two different but complementary questions. First, we applied multiple discriminant function analysis (MDFA) on the environmental matrix (135 sites and nine variables; Table 1) to test for differences in environmental conditions found in streams with one of three fish groups (group 1, sites with *G. anomalus* alone; group 2, sites containing both *G. anomalus* and brown trout; group 3, sites with brown trout alone). We also employed a stepwise MDFA to identify variables most able to discriminate between the fish classification groups. The stepwise procedure consisted of alternating steps of forward selection and

backward elimination. Wilk's lambda was used to select variables and the maximum significance of the *F* to enter and *F* to remove criteria were, respectively, 0.05 and 0.1. The selected variables were then used to predict in which pre-defined fish group each site belonged. Finally, we assessed the accuracy of the stepwise MDFA model by applying a 'leave-one-out' cross-validation test (Efron 1983). This test consists of removing one observation from the original matrix followed by MDFA on the remaining observations to predict the group membership of the omitted observation. This operation was repeated for all the observations of the data matrix.

Secondly, to identify the environmental factors that may control the distribution of each species, we used a supervised ANN (Rumelhart, Hinton & Williams 1986; Lek & Guégan 1999). The ANN architecture consists of input, hidden and output layers with a one-way flow of information. The input layer of neurones represents the independent environmental variables (Table 1) and the output layer is a single neurone that represents the dependant variable (i.e. species occurrence). The number of neurones of the hidden layer (10) and the number of iterations for the back-propagation algorithm (500) were chosen by comparing different neural networks with various numbers of hidden neurones and iterations (Lek & Guégan 1999). These parameters were selected to optimize the accuracy of the model and minimize trade-off between network bias and variance. To standardize the scale of measurement, independent variables were converted to *z*-scores prior to training the models (i.e. the variables were centred and reduced to range between 0 and 1). Again we used the 'leave-one-out' cross-validation test (Efron 1983) to validate the accuracy of each ANN model (Guégan, Lek & Oberdorff 1998). Then we used different metrics reviewed by Fielding & Bell (1997) and Manel, Williams & Ormerod (2001) to evaluate the performance of the neural network models. The calculation of these metrics required the derivation of matrices of confusion that identified true positive, false positive, true negative and false negative cases predicted by each model. First, we explored receiver

operating characteristic (ROC) plots, obtained by plotting the proportion of true presences (sensitivity) against the proportion of false presences ($1 - \text{specificity}$) for varying decision thresholds over the entire range between 0 and 1. Two parameters were derived from the ROC plots. (i) The area under the curve (AUC), which is a robust indicator of model performance independent of the threshold probability at which the species' presence is accepted. AUC varies from 0.5 for a chance performance to 1.0 for a perfect fit. (ii) The optimal decision threshold, which maximizes the proportion of true presences (sensitivity) and true absences (specificity) that are correctly classified. The conventional decision threshold of 0.5 is arbitrary and may affect the outcome of a model (Manel, Dias & Ormerod 1999). Finally, we used Cohen's Kappa index, ranging from 0 to 1, to assess whether the performance of each model differed from expectations based on chance alone. This index is relatively independent of species' prevalence and values of 0.8–1 are generally considered to indicate excellent model performance (Manel, Williams & Ormerod 2001).

An important issue in model evaluation is determining the relative contribution (i.e. explanatory importance) of each predictive variable. To do this, we used the connection weight procedure (Olden, Joy & Death 2004), running each model 100 times (Joy & Death 2004), and displaying the relationships graphically by means of 'Lowess' smoothing plots (Trexler & Travis 1993) for the most strongly contributing variables (i.e. > 15% of contribution).

The ANN models were generated using Matlab® (Mathworks, Natick, MA, USA) software language. Other analyses were performed with SPSS for windows, version 11.0 (SPSS Inc., Chicago, IL). Data transformations were applied only for multivariate analyses as assumptions about linearity, normality and homogeneity of variance are not required for ANN methods.

Finally, we checked for spatial autocorrelation in model residuals for both MDFA and ANN modelling techniques. Autocorrelation analyses were based on Mantel's test, which determines linear relationships between pairwise distance matrices (Mantel 1967). The Euclidean distance was selected as a geographical distance between sites, and Euclidean distances between all pairs of sites were calculated with x - y coordinates. This measurement accounted for environmental conditions independently of river network structure, as this structure has been considered in both MDFA and ANN analyses. We measured Euclidean distance for ANN (continuous) residuals, and Jaccard distance for MDFA (binary) residuals. For this last analysis, misclassified sites were coded as one and properly classified sites were coded as zero. Spatial autocorrelation was then calculated on misclassifications within the overall pattern of sites. The significance of the normalized Mantel statistic (Legendre & Legendre 1998) was evaluated by comparing the observed value with a reference distribution of 1000 randomly permuted values.

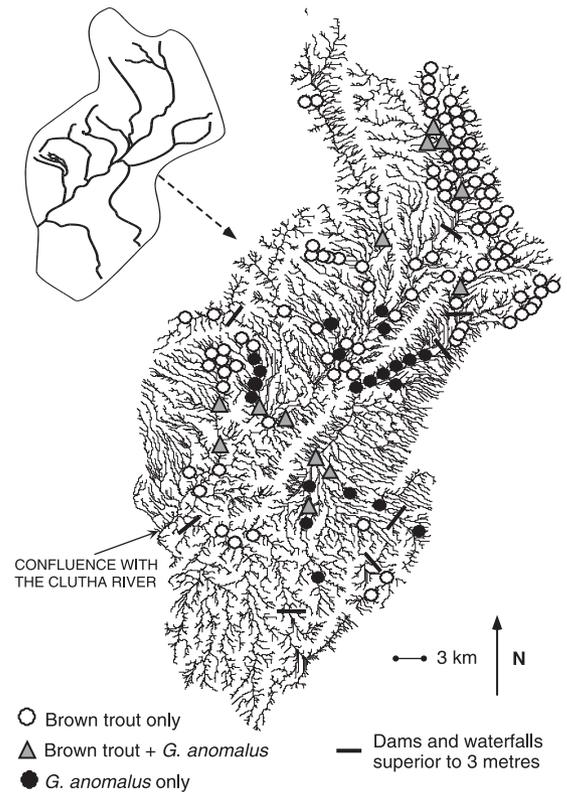


Fig. 1. Map showing the distributions of *G. anomalus* and brown trout in allopatry and sympatry in the Manuherikia River catchment.

Results

Among the 135 sites, brown trout occurred in 101 sites and *G. anomalus* in 34 sites, with the two species coexisting in only 13 sites (Fig. 1). Brown trout were capable of reaching most locations in the Manuherikia catchment, and often occurred upstream of *G. anomalus*. There were only three waterfalls and five dams present (Fig. 1); moreover, brown trout were present above and below each dam and two of the waterfalls. Therefore we decided to ignore dams and waterfalls in our analyses.

The MDFA showed that streams containing *G. anomalus* and brown trout in allopatry and sympatry were characterized by different environmental conditions (function 1, Wilk's lambda = 0.430, chi-square = 108.651, $P < 0.0001$; function 2, Wilk's lambda = 0.769, chi-square = 34.652, $P < 0.0001$). The plot of site scores for the first two discriminant functions (Fig. 2a) and the plot of loadings (Fig. 2b) indicated the environmental variables that were most strongly distinguished among the fish assemblages. Streams containing only *G. anomalus* were defined by a high percentage of pool habitat, high risk of drying up as a result of water abstraction and low to moderate valley slopes. In contrast, trout streams were characterized by a relative diversity of channel units (riffle, run, rapid) and little or no water abstraction (78% of sites with brown trout alone had no abstraction upstream). Moreover, 20% of sites containing only brown trout were located in

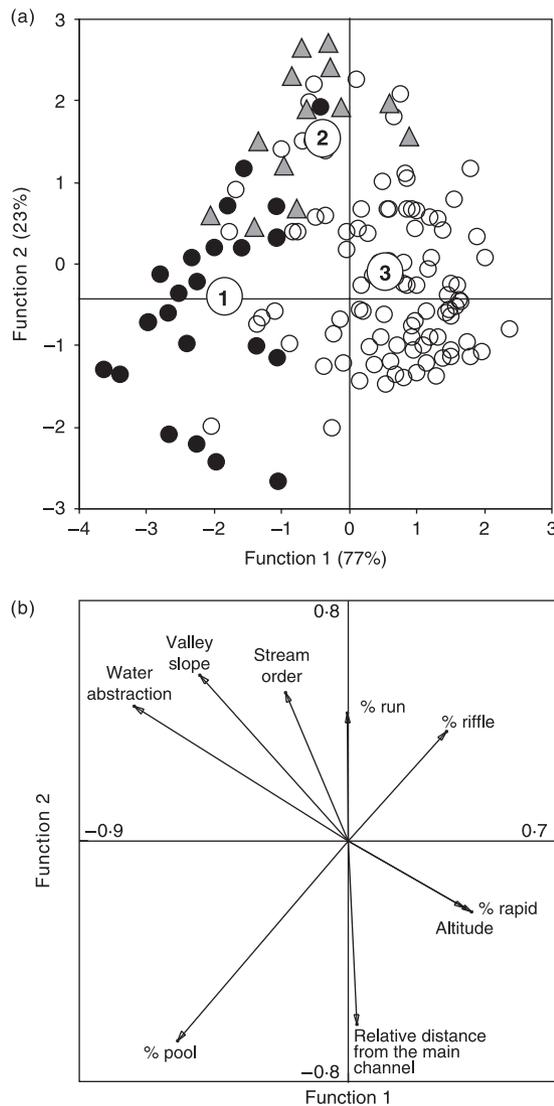


Fig. 2. (a) Plot of discriminant function scores for each of the 135 sites using the first two functions (black circles, 1, *G. anomalus* only; triangles, 2, *G. anomalus* and brown trout; white circles, 3, brown trout only; the white circles containing a number correspond to the group centroids). (b) Plot of correlations among discriminating variables and the standardized canonical discriminant functions.

tributaries far from the main stem of the river and were characterized by a high percentage of rapids and high altitude. The few sites with *G. anomalus* and brown trout in sympatry were characterized by a high risk of stream drying, low valley slope, good representation of riffles and runs, and medium to high stream order.

Stepwise discriminant function analysis confirmed that water abstraction ($F = 14.183$, $P < 0.0001$), percentage of pool ($F = 17.785$, $P < 0.0001$) and valley slope ($F = 4.089$, $P < 0.05$) were the most discriminating variables of the streams containing *G. anomalus* and brown trout in allopatry and sympatry, and most of the sites (76%) were classified correctly to each predefined fish group using only these variables (Table 2). The spatial autocorrelation analysis was not significant (Mantel test, $P = 0.895$).

The occurrence of both native *G. anomalus* and exotic brown trout was highly predictable based on neural network models (> 93% of sites correctly classified; Table 3), with sensitivity (presence correctly predicted) and specificity (absence correctly predicted) both exhibiting high values. Cohen's Kappa statistic and AUC were highly significant, with values indicating excellent performance of each model. For the three models, spatial autocorrelation analysis revealed independence between site residuals (Mantel test, $P = 0.182$ for *G. anomalus* model 1, $P = 0.439$ for *G. anomalus* model 2, $P = 0.111$ for brown trout model).

The percentage of pool and the index of water abstraction contributed most to predicting the occurrence of brown trout in the ANN models (Fig. 3a). The Lowess smoothing curve indicated that the probability of occurrence of brown trout decreased as the percentage of pool or the index of water abstraction increased (Fig. 4a). In other words, the few sites where brown trout were absent were characterized by a moderate to high percentage of pool and a maximum index of water abstraction. In the case of *G. anomalus*, two variables stood out: the index of water abstraction and valley slope (Fig. 3b). *Galaxias anomalus* occurred in sites with low valley slope (< 0.02) and maximal risk of drying up as a result of water abstraction (Fig. 4b). An increase in percentage pool corresponded with an increased probability of *G. anomalus* occurrence (Fig. 4b). Finally, when the occurrence of brown trout was added as a further independent variable to predict *G. anomalus* occurrence, this biotic variable contributed most to the ANN model (Fig. 3c).

Discussion

The distributions of *G. anomalus* and brown trout were largely non-overlapping at the reach scale in the Manuherikia River. Both MDFA and ANN models indicated that valley slope, the percentage of pool habitat

Table 2. Classification results obtained by stepwise discriminant function analysis and by 'leave-one-out' cross-validation. The number of correctly predicted sites is shown in bold

Group	No. of sites	Predicted group membership			Sites correctly predicted (%)
		1	2	3	
1 <i>G. anomalus</i> alone	21	13	5	3	62
2 <i>G. anomalus</i> and brown trout together	13	2	8	3	62
3 Brown trout alone	101	9	10	82	81
Total	135	24	23	88	76

Table 3. Performance of the ANN models to predict presence-absence of *G. anomalus* and brown trout according to a 'leave-one-out' cross-validation test (see text for the AUC and Kappa index). Brown trout and *G. anomalus* (model 1) models were built using the 10 predictors given in Table 1. The last model (*G. anomalus* model 2) includes the same input data, plus trout occurrence, considered here as a predictor

Species	Correct classification (%)	Optimal decision threshold	Sensitivity (%)	Specificity (%)	Kappa index	<i>P</i>	AUC	<i>P</i>
Brown trout	94.96	0.60	98.21	88	0.832	< 0.0001	0.909	< 0.0001
<i>G. anomalus</i> (model 1)	93.53	0.50	82.22	98.94	0.846	< 0.0001	0.974	< 0.0001
<i>G. anomalus</i> (model 2)	100	0.49	100	100	1	< 0.0001	1	< 0.0001

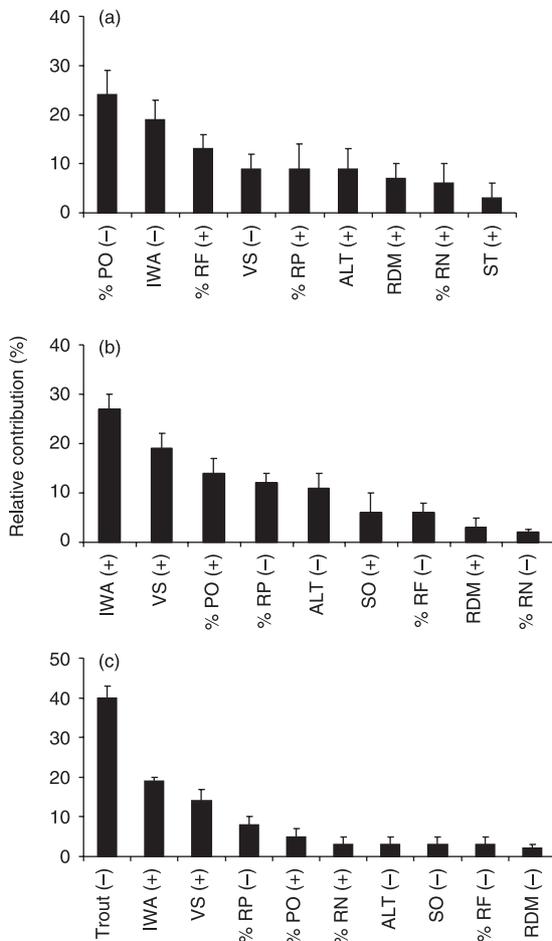


Fig. 3. Relative contribution of the independent variables in the ANN models. (a) Brown trout model, (b) *G. anomalus* model 1, (c) *G. anomalus* model 2 (occurrence of brown trout included as predictor variable). The direction of the relationship between predictors and predictions, extracted from the calculation of the connection weight algorithm, is indicated next to each environmental variable: positive '+', negative '-'. Definitions of variables provided in Table 1.

in the stream reach and, in particular, water abstraction could best account for their disjunct distributions. The absence of spatial autocorrelation in model residuals ensures the relevance of the independent variables used in the ANN models and the randomness of misclassifications in the stepwise MDFA model. As a consequence, the variables used in both MDFA and ANN models were appropriate to classify sites and predict species occurrence, respectively.

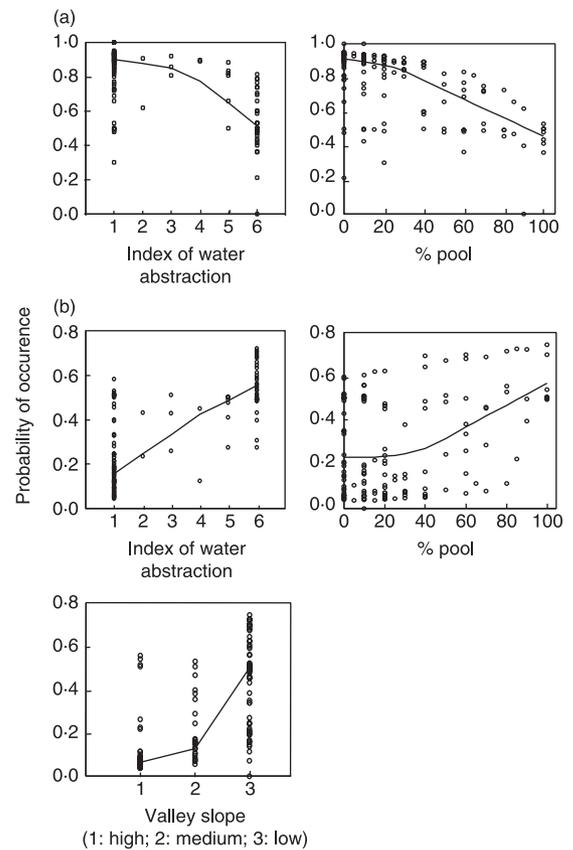


Fig. 4. Bivariate plots of predicted probability of fish occurrence against the most important contributing variables in the ANN models. The solid lines represent the Lowess curves used to fit the data. The proportion of samples perfectly fitted is indicated by the *f*-value (i.e. smoothing parameter). The *f*-values ranged from 0 and to 1 according to the sensitivity of the analysis: (a) brown trout (*f* = 0.8), (b) *G. anomalus* model 1, occurrence of trout not included as predictor (*f* = 0.8).

Brown trout occurred in low, medium and high gradient streams, but *G. anomalus* most often occurred in reaches with low valley slopes. This accords with the results for *G. anomalus* of Allibone & Townsend (1997) for the Taieri River. However, we have no record in the Manuherikia River of the extent to which *G. anomalus* may have been restricted to lower gradient sites before the arrival of brown trout. Old reports for the nearby Taieri River suggest that non-migratory galaxiids were historically much more widespread (Townsend & Crowl 1991).

The development of pastoral irrigation using historic gold-mining water races and water rights preceded the arrival of brown trout. The development of irrigation schemes during the early and mid-1900s was predominantly in low gradient valleys located in the middle and downstream reaches of each tributary. More recent expansion of irrigation in the drought-prone Manuherikia catchment has exacerbated the combined effects of these historical abiotic and biotic disturbances. At present, the permitted rate of water abstraction is considerable, with most sites where *G. anomalus* occurs alone having 7-day minimum annual low flows ranging from 30 to 300 L s⁻¹, whereas the sum of permitted water abstractions upstream varies from 500 to 2300 L s⁻¹. This very high proportion of natural flow abstracted means that farmers may actually take all the water from a tributary, and many reaches become dry during the low flows of summer. These reaches are also characterized by a high proportion of pool habitat, in contrast to the sites containing only brown trout. The predominance of pool habitat and the under-representation of riffles and runs is probably related to the reduction of stream discharge (Kraft 1972; Elliot 2000).

The resulting periods of low, or even no, flow are characterized by the presence of isolated pools and extreme conditions of high temperature (recorded up to 28 °C) and associated low oxygen concentrations, conditions that galaxiid fish tolerate (Richardson, Boubee & West 1994; Dean & Richardson 1999) better than salmonids (Closs & Lake 1996). Non-migratory galaxiids and especially *Galaxias eldoni* McDowall and *G. anomalus* have been recorded in Otago streams with temperatures above 28 °C (C. Arbuckle, personal observation). During low discharge, moreover, *G. vulgaris* (Dunn 2003) and *Galaxias cobitinis* McDowall and Waters (C. Arbuckle, personal observation) are capable of burrowing and surviving in the stream bed, a behaviour that may be shared by a number of non-migratory galaxiids. The response of brown trout to these extreme conditions may be death (the upper lethal limit for brown trout is 25 °C; Elliot 1994) or migration to upstream locations where abstraction does not occur. Large-scale migration in response to low flows is common in salmonid populations (Kraft 1972; Gowan & Fausch 1996).

Apart from these irrigation-impacted sites, brown trout occurred throughout the Manuherikia River catchment, even above some large waterfalls and dams. This is because of their introduction for sport fishing, particularly in upstream reaches and more recently in headwater reservoirs. Headwater introduction seems to promote catchment-wide invasion more than mainstream or low altitude stocking (Adams, Frissel & Rieman 2001). In the Manuherikia catchment, 92% of sites above dams contained only brown trout, while only five sites contained both species. It seems likely that *G. anomalus* were eliminated from the other sites by a combination of trout predation and competition. Four low-order sites, unimpacted by irrigation, contained

only *G. anomalus*, and these might conform to the pattern in the Taieri River where migration barriers leave upstream refugia for the natives (Townsend & Crowl 1991). One was located above a large waterfall that probably prevented trout invasion. The other sites were not upstream of large barriers but downstream irrigation water races comprised dams that may impede migration; stocking of trout may not have occurred in these sites.

The sites where *G. anomalus* and brown trout occurred in sympatry were associated with low valley slopes in high-order streams (in the main stem or close to it), where riffles and runs were well represented in a braided river structure. Downstream dispersal from higher altitude reaches seems not to be important because the galaxiids are generally not present above sites occupied by both trout and galaxiids (Fig. 1). More likely, bed instability in these braided sections promotes fish coexistence, as noted for similar locations in the Taieri River (Townsend 2003) and elsewhere in the South Island (McIntosh 2000). Promotion of the coexistence of native and exotic species by disturbance has also been reported for other stream fishes (Meffe 1984), amphibians (Doubledee, Muller & Nisbet 2003) and plants (Vujnovic, Wein & Dale 2002).

Overall, the negative association between *G. anomalus* and brown trout is mainly related to the level of hydrological disturbance. Thus local *G. anomalus* populations have not been excluded by brown trout in low gradient streams subject to significant water abstraction. Closs & Lake (1996) found that *Galaxias olidus* Günther were similarly protected from trout predation by severe drought in summer, observing that *G. olidus* survived in upstream reaches that tended to stop flowing while brown trout could only survive in downstream reaches less affected by drought. The pattern is reversed in the Manuherikia, where the risk of stream drying, because of abstraction for irrigation, occurs in the middle and downstream reaches.

Our findings run contrary to the idea that anthropogenic disturbance is more likely to facilitate invasions of exotic species (Minckley & Meffe 1987; Hobbs & Huenneke 1992; Moyle & Light 1996; Byers 2002). Whether a disturbance will facilitate an invasion depends on whether the disturbance is natural or human-induced (McIntosh 2000) and whether the exotic species (or the native), by virtue of its evolutionary history, is favoured by the changed conditions (Baltz & Moyle 1993; Moyle & Light 1996; Townsend 2003). Our results are consistent with the classical view that exotic species can only invade as far as their physiological tolerances permit (Moyle & Light 1996; Holway, Suarez & Case 2002; Facon *et al.* 2004). This underlines the need to identify niche components of exotic species to better forecast their distribution and impact on natives.

MANAGEMENT IMPLICATIONS

Exotic species management is particularly sensitive from a political point of view when the invader has a

high economic value, as is the case with brown trout for sport fishing in New Zealand. Consequently, eradication of brown trout at the catchment scale is not conceivable. In addition, management of water abstraction for irrigation of agricultural land, which has a regional economic importance, is currently focused on improving irrigation efficiency to lessen abstraction requirements and establishing minimum residual flows to maintain aquatic habitat. These developments must proceed with caution to ensure that the re-establishment of more natural flows, which will favour brown trout, do not threaten the native fish in their physically stressed refugia.

Key factors in the conservation of *G. anomalus*, in conjunction with water resource management, are the identification of locations where galaxiid reserves can be established, the encouragement of public education about the threats faced by the native fish and, where possible, the reduction of abstraction. Although water abstraction has created local abiotic conditions that seem to prevent *G. anomalus* extirpation by brown trout, we certainly do not advocate an increase in permitted abstraction for the sake of galaxiid populations. This type of hydrological disturbance can be expected to have negative impacts for *G. anomalus* by reducing the carrying capacity of the stream (Allibone 2000a), disrupting spawning habitats and juvenile recruitment, and reducing growth rates of larval fish (Allibone 2000b).

In its recovery plan for non-migratory galaxiids, the Department of Conservation (2004) emphasizes the need to maintain and improve fish barriers, to inform landowners of barriers and their importance, and to request them not to transfer trout above these barriers or allow others to do so. In the case of the Manuherikia River catchment, with only a very few exceptions, brown trout have already been introduced to streams above waterfalls and dams. Therefore we suggest that a number of tributaries should be chosen with habitat features appropriate to the different life-history stages of *G. anomalus*, where artificial barriers can be constructed to impede trout upstream migration. Trout should be removed by repeated electrofishing above the barriers, which should permit a *G. anomalus* population to recolonize the stream above. This was done successfully in a montane stream in south-eastern Australia, where a breeding population of *G. olidus* had become established 3 years after trout eradication (Lintermans 2000). Given the habitat requirements of *G. anomalus*, such streams are unlikely to support significant stocks of brown trout, so their removal will have little impact on the sports' angling resource. Only after reserves of galaxiid populations have been established, do we recommend restoring natural low flows. Indeed, if the natural patterns of low flow are restored to the trout-free streams that currently support galaxiid populations prior to the implementation of reserves for galaxiids, we foresee that brown trout will colonize and imperil the remaining galaxiid populations. Although Morita & Yamamoto 2001, showed that isolation can increase

the extinction probability because of inbreeding in stream-dwelling charr *Salvelinus leucomaenis* Pallas, this risk is probably reduced for small, sedentary fish that occur at high population densities in small stream reaches, such as *G. anomalus*. Moreover, when exotic species pose an immediate threat to the survival of native species, the risk of isolation is justified when seeking rapid protection of threatened native species from the negative effects of exotics (Moyle & Sato 1991; Shafer 1995; Novinger & Rahel 2003). Over a longer time scale, inbreeding risk should be properly assessed to ensure the sustainability of threatened populations.

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