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Development and application of a predictive model of freshwater fish assemblage composition to evaluate river health in eastern Australia

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Abstract

Multivariate predictive models are widely used tools for assessment of aquatic ecosystem health and models have been successfully developed for the prediction and assessment of aquatic macroinvertebrates, diatoms, local stream habitat features and fish. We evaluated the ability of a modelling method based on the River InVertebrate Prediction and Classification System (RIVPACS) to accurately predict freshwater fish assemblage composition and assess aquatic ecosystem health in rivers and streams of south-eastern Queensland, Australia. The predictive model was developed, validated and tested in a region of comparatively high environmental variability due to the unpredictable nature of rainfall and river discharge. The model was concluded to provide sufficiently accurate and precise predictions of species composition and was sensitive enough to distinguish test sites impacted by several common types of human disturbance (particularly impacts associated with catchment land use and associated local riparian, in-stream habitat and water quality degradation). The total number of fish species available for prediction was low in comparison to similar applications of multivariate predictive models based on other indicator groups, yet the accuracy and precision of our model was comparable to outcomes from such studies. In addition, our model developed for sites sampled on one occasion and in one season only (winter), was able to accurately predict fish assemblage composition at sites sampled during other seasons and years, provided that they were not subject to unusually extreme environmental conditions (e.g. extended periods of low flow that restricted fish movement or resulted in habitat desiccation and local fish extinctions).

Introduction

In response to growing concern about the deleterious effects of water infrastructure developments, flow regulation, water pollution and land use practices on aquatic ecosystems (ANZECC & ARMCANZ, 2000; Norris et al., 2001), quantitative procedures for assessing aquatic ecosystem 'health' and monitoring biotic responses to remedial management are receiving increasing attention from scientists and catchment managers around Australia. Approaches to biotic assessments of environmental degradation in aquatic systems include toxicity-testing, use of biomarkers and a range of methods based on biotic community structure and ecosystem function (Bunn, 1995; Harris, 1995). Reference to the expected natural state (the reference condition

approach, Reynoldson et al., 1997; Bailey et al., 2004), whereby disturbance induced change is distinguished from variation in biotic assemblages along natural environmental gradients, is now a common approach to bioassessment. Multivariate predictive models of biotic community composition (e.g. Wright, 1995; Clarke et al., 1996; Simpson & Norris, 2000; Oberdorff et al., 2001b) and of summary metrics of community structure and function (e.g. Index of Biotic Integrity – IBI, Karr, 1981; Karr et al., 1986) form the basis of this approach.

In Australia, considerable research effort has been directed toward the adoption of aquatic macroinvertebrate communities as indicators of river health using a referential approach (Davies, 2000). Predictive models have been developed that enable site-specific predictions of benthic macroinvertebrate community composition expected in the absence of major human disturbance. The expected fauna is derived using a small number of environmental characteristics as predictors of species composition. By comparing the expected fauna at a new site, with that observed, an evaluation of the biological integrity of the site is obtained. This method, based on a predictive modelling procedure originally developed for assessing the biological quality of rivers in the United Kingdom using aquatic macroinvertebrates – the RIVPACS method (Wright et al., 1984), has been packaged as AUSRIVAS (the Australian River Assessment Scheme) and is now implemented widely throughout Australia under the National River Health Program (Simpson & Norris, 2000). Similar predictive models of diatoms and stream habitat have also been developed with a view to evaluate their potential use as indicators of river health in Australia. However, bioassessment procedures based on fish are however not well advanced in Australia, despite the well-documented responses of fish to a wide range of human disturbances (e.g. Fausch et al., 1990; Harris, 1995; Karr & Chu, 1999; Hughes & Oberdorff, 1999; Simon, 1999, 2003).

Harris (1995) suggested that multi-metric methods such as the IBI were potentially applicable to stream health assessment in Australia and the IBI has been tested and applied in several rivers of southern Australia (Harris & Silveira, 1999; Murray Darling Basin Commission, 2004). Yet, the development of multivariate predictive models of fish assemblage composition and their utility in stream bioassessment programs in Australia has received little attention. These fish-based predictive modelling methods have been demonstrated to provide a sensitive tool for biomonitoring river health in Europe (Oberdorff et al., 2001b) and New Zealand (Joy & Death, 2000, 2002, 2003). Joy and Death (2002, 2003) developed predictive models based on variations of the RIVPACS approach for low diversity fish fauna's in New Zealand streams. These authors concluded that accurate site-specific predictions of fish species composition were possible using the models, and that outputs from the models could provide a sensitive measure of human impact at disturbed sites.

In common with other biological indicators, there are several potential impediments to the use of fish assemblages as indicators of river health. The ability to accurately define an expected fish assemblage in the absence of anthropogenic disturbance is critical, and requires that relationships between natural environmental conditions and biota are sufficiently strong that species composition can be predicted accurately. Both local and regional scale factors may be important determinants of local variation in fish species composition, abundance and biomass (Jackson & Harvey, 1989; Schlosser, 1991; 1995; Schlosser & Angermeier, 1995; Poff, 1997; Angermeier & Winston, 1998). However, the ability to detect species associations (Angermeier & Schlosser, 1989) and relationships with environmental conditions (Pusey et al., 2000; Williams et al., 2003) may be more difficult in systems characterised by high environmental variability, such as that associated with high flow variability, a characteristic of many Australian steams (McMahon, 1986; Lake, 1995; Puckridge et al., 1998). Predictive approaches to defining the reference condition typically also rely on the assumption that the reference communities from which predictions are derived are stable through time, permitting valid comparisons to be made with tests sites often sampled years afterwards (Barmuta et al., 2003). The implications of long-term variation in species assemblages arising from natural or human-induced variations in environmental conditions related to major climatic cycles or climate change (Meyer et al., 1999; Mol et al.,

2000; Puckridge et al., 2000; Metzeling et al., 2002) is rarely addressed. Another potential difficulty is that low numbers of species available for modelling (e.g. local fish assemblages are typically much less diverse than aquatic macroinvertebrate assemblages) have the potential to bias bioassessments given that the failure to detect a single species during sampling could result in considerable deviations in expected and observed assemblages and result in a low sensitivity of predictive models to detect disturbance at mildly disturbed sites (Smith et al., 1999; Turak et al., 1999).

This paper forms part of a program designed to develop indicators of biotic structure and ecosystem function for incorporation into a broad-scale ecosystem health monitoring program for freshwater streams and rivers of south-eastern Queensland Australia. Here, we construct a predictive model of fish assemblage composition based on relationships with a small number of catchment scale and local scale environmental features. We construct the model using a set of least-disturbed reference sites sampled on one occasion during one season. We evaluate the effect of low species richness on model performance and validate the predictive capacity of the model using two sets of temporally sampled data from reference sites in two rivers. We also evaluate the sensitivity of the model to detect disturbance at a set of independent sites sampled along known gradients of human disturbance brought about by land use pressures.

Methods

Study area

The study area was confined to coastal south-eastern Queensland, Australia (Fig. 1), a temperate/subtropical area constituting a single biogeographic region based on freshwater fish distributions (Unmack, 2001; Pusey et al., 2004). The majority of rainfall and streamflow occurs in the summer months of January to March, often followed by a second minor peak in discharge between April and June (Pusey et al., 1993, 2004). The flow regime of many streams and rivers in south-eastern Queensland is highly variable on an inter-annual and seasonal basis: low and high flows can occur at any time of year, and some tributaries may cease to flow for extended periods (Pusey et al., 1993, 2000). Before European settlement, the region was dominated by sclerophyll forests with substantial areas of sub-tropical rainforest and coastal 'wallum' (*Banksia* heathlands). Human land use practices associated with extensive land clearing, cattle grazing, agricultural cropping and large urban and industrial developments, have led to substantial degradation of local riparian, in-stream habitat and water quality conditions in many streams and rivers of the region. In addition, some of the major rivers are regulated by large dams and many contain barriers to fish movements (Kennard et al., 2005).

Reference, validation and test site datasets

A dataset comprising 82 reference sites (least-affected by human activity) was used to develop and validate the predictive model. Reference sites were located in the Mary, Brisbane, Logan and Albert Rivers (Fig. 1). We selected reference sites that represented the best condition available within each river (i.e. undisturbed riparian vegetation, bank and channel structure in natural condition, natural hydrograph, *sensu* Hughes (1995)) ensuring that such sites were arrayed sufficiently widely throughout each catchment to encompass as much of the natural biological and environmental variation as possible. Site selection was constrained by sampling methodology (backpack electrofishing) and sites were only included if they were not close to major urban areas, extractive industries (i.e. mines, quarries and sand/gravel extraction), intensive agriculture and point source pollutants, or located upstream of barriers to fish movement (e.g. dams and weirs that did not drown-out periodically or lacked fish passage devices). Potential reference sites were also excluded if they contained high relative abundances of alien fish species (i.e. >20% the total number of individuals in a sample).

Seventy-two sites selected randomly from the reference site database were used for model construction. Most of these reference sites were sampled seasonally (winter, spring and summer) between 1994 and 1997, but numbers of samples varied among sites and rivers. We constructed the predictive model using data collected on the first

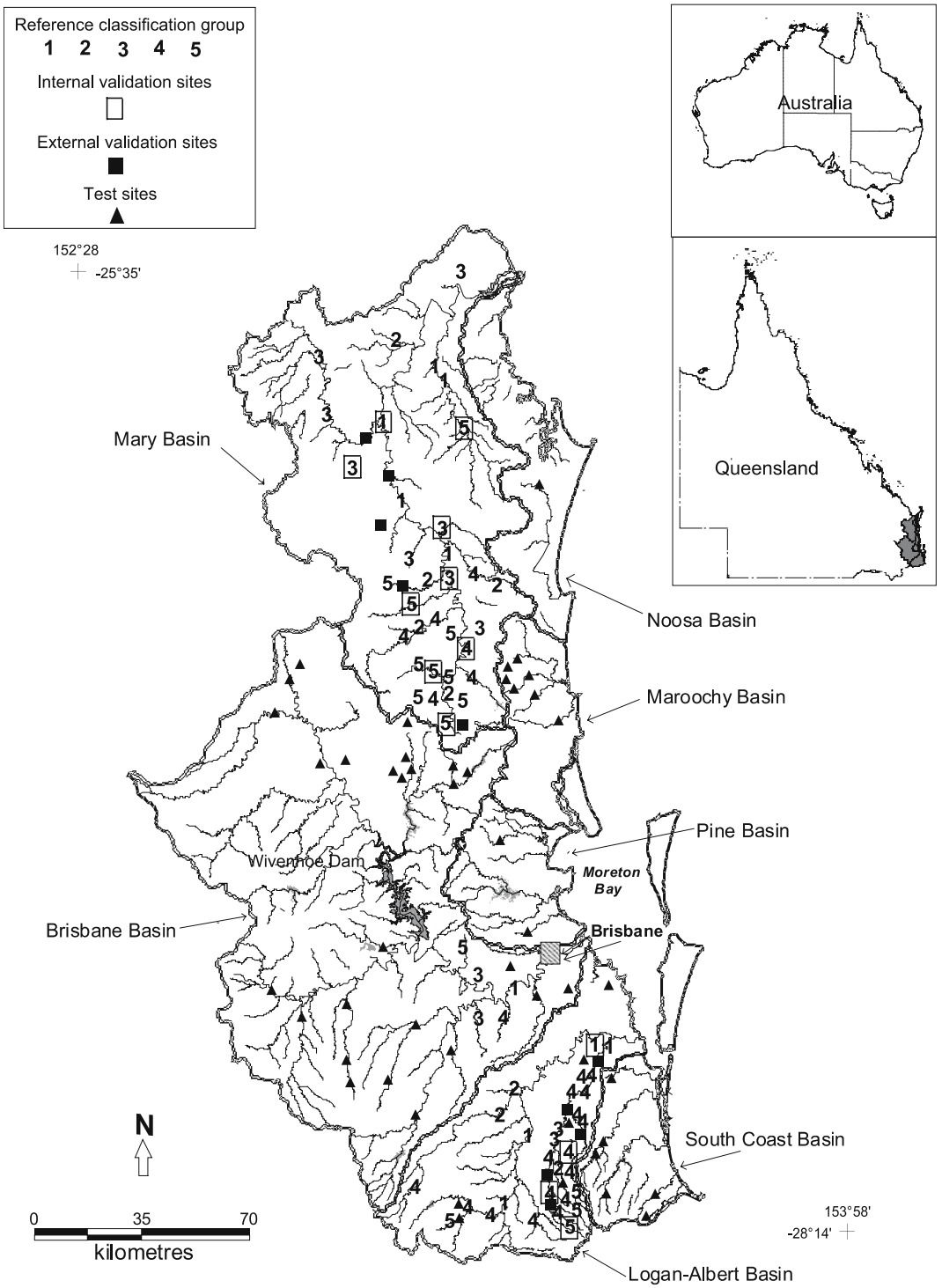

Figure 1. Location of reference sites (numbered by classification group membership), validation sites and test sites in south-eastern Queensland (Note: some sites located close together overlay each other and hence may not visible on map). Major impoundments are also depicted. The inset shows the location of the study area in Queensland, Australia.

winter sampling occasion for each site and river. During the 4-year sampling period, some rivers of the study regions experienced several discharge extremes including an 8-year annual return interval flood in January 1996. Furthermore, some tributaries of the Mary River experienced the longest period of zero flows on record. We chose the winter sampling period (between June and August) as hydrological conditions are more likely to be characterised by low and stable flows (Pusey et al., 2000, 2004), but are sufficiently elevated to allow fish unrestricted longitudinal movement among river reaches and habitat types. The reference data used to constructed the model therefore comprised 25 sites in the Mary River and 16 sites in the Albert River sampled during winter 1994, 11 sites in the Mary River and six sites in the Albert River sampled in winter 1995, nine sites in the Logan River sampled during winter 1996 and five sites in the Brisbane River sampled in winter 1997.

We evaluated the predictive capacity of the reference model (based on sites sampled once only in winter) to predict assemblage structure for time periods outside of the range used to develop the model using two validation datasets. The first comprised a random subset of the original reference sites that were sampled during spring, summer and winter between 1994 and 1997 (hereafter termed 'internal' validation samples). This dataset included nine sites from the Mary River sampled on nine occasions, and four sites from the Albert River sampled on seven occasions. Five of these sites (three in the Mary River and two in the Albert River) were also sampled again during September 2000 ($n = 114$ samples). The second dataset comprised the remaining 10 least-disturbed reference sites withheld from the original reference dataset and not used to construct the model (hereafter termed 'external' validation samples). These sites were also sampled seasonally between 1994 and 1997 (five sites in the Mary River sampled on nine occasions and five sites from the Albert River and sampled on six occasions ($n = 86$ samples). Three internal validation sites and two external validation sites were situated on streams that experienced extended periods of zero flow and so enabled evaluation of the effects of flow variability on model predictions.

Forty-eight test sites from six river basins in south-eastern Queensland were selected to test the predictive model and to examine whether differences in observed *versus* predicted fish assemblage composition was related to known gradients in human disturbance (particularly impacts associated with catchment land use and associated local riparian, in-stream habitat and water quality degradation). These test sites ranged from minimally disturbed to highly impacted; see Kennard et al. (2005) for further description of test sites. Test sites were sampled once between September and October 2000. The range of variation in environmental conditions at the reference sites was generally similar to, or greater than, the range at validation and test sites (Table 1). The exception to this was a small number of test sites located on streams with slightly smaller catchment areas (3 sites), or were closer to the river mouth (4 sites). The spatial separation of reference sites from test sites in some river basins (i.e. Noosa, Pine Brisbane and South Coast) was in part due to a lack of acceptable reference sites in these catchments (particularly the Brisbane Basin) and the funding conditions under which the test site data were collected. Although this has potential to bias predictions for sites in these basins, all study rivers were located within a single bioregion based on freshwater fish distributions and the reference sites included a broad range of stream types and habitats; we therefore considered that the three datasets (reference, validation and test sites) were acceptable for initial model development, validation and testing.

Fish sampling methods

The fish assemblage within an entire meander wavelength or riffle-run-pool sequence (Newbury & Gaboury, 1993) was sampled in each stream reach using a standardised protocol that was consistent among reference, validation and test sites. Three contiguous individual mesohabitat units (i.e. riffles, runs or pools) within each reach were sampled separately and data subsequently combined to represent each site. Each mesohabitat unit was blocked upstream and downstream with weighted seine nets (11 mm stretched-mesh) to prevent fish movement into or out of the study area. The mesohabitat unit was sampled using a combination of repeated pass electrofishing (Smith-Root model 12B Backpack

Table 1. Range and median values of environmental predictor variables at reference, validation and test sites

Predictor variable	Site type	*N*	Minimum	Median	Maximum
Catchment area (km^2)	Reference	72	12	145	9734
	Internal validation	13	18	141	4851
	External validation	10	23	136	3884
	Test	48	7	110	930
Distance from source (km)	Reference	72	7	34	261
	Internal validation	13	10	33	211
	External validation	10	11	36	181
	Test	48	8	26	94
Distance to mouth (km)	Reference	72	28	149	310
	Internal validation	13	31	147	292
	External validation	10	39	125	292
	Test	48	14	127	301
Elevation (m.a.s.l.)	Reference	72	0	80	250
	Internal validation	13	0	80	220
	External validation	10	20	60	180
	Test	48	1	96	247
Mean width (m)	Reference	72	1.02	7.30	42.73
	Internal validation	114*	0	7.29	45.50
	External validation	86*	0	7.85	26.20
	Test	48	1.18	6.98	19.70
Mean depth (m)	Reference	72	0.12	0.37	0.85
	Internal validation	114*	0	0.36	0.93
	External validation	86*	0	0.38	0.83
	Test	48	0.15	0.49	0.84
Mean velocity ($m\ s^{-1}$)	Reference	72	0	0.16	0.75
	Internal validation	114*	0	0.13	0.80
	External validation	86*	0	0.13	0.74
	Test	48	0	0.02	0.32

N indicates the number of sites for catchment-related variables that were static in time. For environmental variables that varied through time (at validation sites sampled on multiple occasions), *N* refers to the number of samples (indicated by *).

Electroshocker) and seine netting until few or no further fish were collected following the protocol described and evaluated in Pusey et al. (1998). These authors showed that intensive sampling using multiple-pass electrofishing plus supplementary seine netting yielded significantly more accurate and precise estimates of total species richness and species composition within individual mesohabitat units (riffles, runs or pools) in comparison to less intensive sampling using a single electrofishing pass only. In a separate study to be published elsewhere, we evaluated the length of stream (i.e. number of mesohabitats) required to gain accurate and precise estimates of species richness and species composition at the stream reach scale. Intensive sampling (using multiple pass electrofishing plus seine netting) of three mesohabitat units yielded 95% of the total number of species and about 97% similarity in species composition to fish assemblage data obtained for more extensive sampling over six mesohabitat units (equivalent to 30 stream widths or 265 m stream length on average). To control for the effect of variation in channel morphology and hence the size of the study sites on fish catches, fish abundances at each site were transformed to species densities (number of individuals $10\ m^{-2}$).

Estimation of environmental variables

Catchment and local scale environmental characteristics of the study sites were estimated according to a standard protocol described in Pusey et al. (2004) (Table 1). These variables were considered to be least affected by human activity and so could be used as predictors of species composition. Catchment descriptors for each site were estimated from 1:100,000 topographic maps using a digital planimeter or from Geographical Information Systems (GIS) databases. Site physical characteristics including mean wetted stream width, mean and maximum water depth, and mean and maximum water velocity were calculated from a series of 40–60 point measurements located randomly throughout the site.

We characterised the potential sources and intensity of anthropogenic disturbance at each test site using a set of variables intended to reflect disturbance mechanisms operating at both large and local scales. Catchment land use was characterised by the percentage of the catchment upstream of each site affected by land clearing, cattle grazing, agricultural cropping and urbanisation. We hypothesised that these large-scale land use impacts would result in localised changes to water quality, riparian habitat, and in-stream habitat conditions that would, in turn, influence the distribution and abundance of freshwater fish. A set of basic water chemistry variables (conductivity, turbidity, pH, total nitrogen, total phosphorus, diel range in dissolved oxygen and temperature) and several simple measures of riparian and in-stream habitat conditions (riparian vegetation cover, percentage of mud substrate, and the abundance of aquatic macrophytes, filamentous algae and submerged vegetation – mostly terrestrial invasive weeds) were assessed at each site to describe these potential sources of disturbance. We recognise that many of the variables used to characterise the disturbance gradient may vary along natural environmental gradients, however we did not have the capacity to account for this natural variation in the present study. We assumed that all disturbance variables were likely to increase in magnitude with increasing human disturbance intensity except pH (increase or decrease) and riparian cover (decrease). Smith & Storey (2001) and Kennard et al. (2005) provide further justification and rationale for the use of these variables to describe the disturbance gradient.

Statistical methods

We developed a multivariate predictive model of fish species composition based on the RIVPACS modelling approach (Wright et al., 1984; Moss et al., 1987) and its derivative AUSRIVAS (Simpson & Norris, 2000). Detailed descriptions of the statistical procedures can be found in Wright (1995) and Clarke et al. (1996); only a brief outline is given here. The 72 reference sites were first classified into groups with similar species composition using an agglomerative hierarchical fusion technique (unweighted pairwise group arithmetic averaging in the PATN pattern analysis package – Belbin, 1995). This classification was performed on a site-by-site association matrix derived using the Bray-Curtis dissimilarity measure (Bray & Curtis, 1957), following the recommendation of Faith et al. (1987). Classification of the 24 species data set (one species present at one site only was excluded from the database) was based on $\log_{10}(x+1)$ transformed species densities at each site as preliminary classification based on the presence or absence of fish species resulted in less well-defined classification group structure. Groups of sites were selected by viewing a dendogram representation of the classification. Stepwise discriminant analysis (using the STEPDISC procedure in SAS; SAS Institute, 1988) was used to identify those environmental variables best able to discriminate between reference site groups derived from the classification analysis. All environmental variables were $\log_{10}(x+1)$ transformed to help satisfy the assumptions of discriminant analysis that predictor variables are normally distributed and that within-group variances are homogenous (Tabachnik & Fidel, 1989). Environmental variables that contributed significantly ($p < 0.05$) to group discrimination were classed as predictor variables for subsequent model development, validation and testing. Multiple discriminant functions analysis with cross-validation (using DISCRIM procedure in SAS; SAS Institute, 1988) was used to estimate probabilities of group membership for each reference site on the basis of those significant environmental predictor variables

identified above. The discriminant functions model was then used to calculate probabilities of group membership for the validation sites and test sites on the basis of their environmental characteristics. The probability of occurrence (PO) of a species at a new site was estimated by weighting the frequency of occurrence of each fish species in each of the reference site groups (i.e. the proportion of sites in each group in which the species occurs) by the probability with which the site belonged to each reference group (from the discriminant functions model) (Wright, 1995). We considered all species with greater than 0% probability of occurrence (PO_0) and 50% probability of occurrence (PO_{50}) in order to examine whether the removal of taxa with a low chance of occurrence improved the accuracy and precision of the model (Simpson & Norris, 2000). We chose this somewhat arbitrary threshold as it is frequently used in RIVPACS-style applications in Australia and North America, and it allowed us to compare the accuracy and precision of our models. The number of taxa expected at each test site was equal to the sum of the individual probabilities of all the predicted taxa greater than the PO_0 and PO_{50} thresholds (the number of expected taxa is therefore always less than the number of predicted taxa as individual species may often have less than 100% predicted probability of occurrence). The number of observed taxa at each test site is that number of taxa predicted to occur and which actually do so. The number of observed taxa was divided by the number of expected taxa to give an O/E ratio for each PO threshold (i.e. O/E_0 and O/E_{50}). The O/E ratio gives an indication of the degree of fidelity between the fish assemblage observed at a test site with that expected and theoretically, is an indication of the predictive capability of the model (the closer to 1.0, the better the match between observed and expected assemblage) (see Moss et al., 1987; Wright, 1995).

We performed several internal tests of the accuracy and precision of the reference site model and whether the choice of PO threshold influenced model performance. For each PO threshold, we compared frequency distributions, means and standard deviations of O/E scores generated for the reference sites used to construct the model. We also compared variation in mean O/E scores generated for reference sites from each classification group, each river and each year of sampling to evaluate whether any systematic biases were apparent due to these factors. For each PO threshold, we also evaluated the match between O and E using simple linear regression models. We compared the amount of variance explained by each regression model (R^2) and compared the slopes and intercepts of the regression line (with the null hypothesis that the slope of the relationship is not significantly different from 1 ($p > 0.05$) and that the intercept does not differ significantly from 0). For each PO threshold we also compared the width of the 10th and 90th percentile of the distribution of reference site scores as a further test of model error and to establish reference thresholds for further model validation (hereafter termed 'reference' bands). We evaluated whether the total number of species at a site biased model predictions by regressing species richness against reference sites' O/E scores generated at each PO threshold and comparing the R^2 and slope of each relationship.

Model validation and the effect of temporal variation on model performance

For each validation data set we evaluated how well the reference model could predict species composition at new sites and samples by comparing the match between expected and observed species using simple linear regression. We used *t*-tests to determine if mean O/E scores for each validation data set differed significantly from those of reference sites. To examine the effect of temporal variation on the predictive capacity of the model, we used an approach similar to Barmuta et al. (2003). For each data set we examined whether the rank order of O/E scores for sites within each river was preserved over time (hereafter referred to as site concordance) using Friedman's two-way analysis of variance for ranks (Zar, 1996). For each data set and river, the O/E scores were ranked across sites within each sample period and the Friedman's analysis tests whether the ranked values are consistent across sampling periods. A significant value of the test statistic indicates that sites do not differ in their ranks. Kendall's coefficient of concordance was also calculated to quantify the degree of synchrony of the ranking of site O/E scores: 1 indicates perfect synchrony or concordance; 0 indicates no synchrony or

concordance. We also examined whether there were any strong, systematic trends in O/E scores through time using a one-way repeated measures analysis of variance using sites as "subjects", and Huynh-Feldt corrected *p*-values were used to assess linear, quadratic or cubic trends for each data set (Zar, 1996). Finally, we examined whether O/E score for temporal samples of validation sites remained within the reference band (based on the 90th–10th percentile of reference site O/E scores).

Model testing and sensitivity to disturbance

The sensitivity to human disturbance of our predictive model based on variation in fish assemblage composition was evaluated by predicting fish assemblage composition at the 48 test sites and generating O/E scores for each site. We used *t*-tests to determine if mean O/E scores for the test sites differed significantly from those of reference sites. We related test site O/E scores to a suite of variables describing the source and intensity of disturbance at the test sites. A Principal Components Analysis (PCA) was used to reduce the 16 disturbance variables ($\log_{10}(x+1)$ transformed) to a smaller number of orthogonal components, to avoid the potential problem of correlation between predictor variables. The PCA was based on the correlation matrix, and loadings of the original variables on each of the first five principal components were used to identify the dominant disturbance gradients in the dataset. Importantly, the disturbance gradients identified by the PCA analysis did not appear to be confounded by variation along the natural environmental gradients used to model fish species composition. No strong relationships existed between disturbance gradient principal component scores and catchment-scale descriptors (catchment area, elevation, distance to river mouth) and local site physical characteristics (mean wetted width, mean depth, mean velocity) (Spearman's correlations, $p > 0.05$, Kennard et al., 2005). We therefore assumed that any observed relationships between disturbance gradients and departures in species composition from that predicted at test sites were real and not artefacts due to co-variation along natural environmental gradients. Stepwise Generalised Linear Modelling (GLM) was used to predict O/E scores on the basis of the disturbance gradient principal components. The amount of variance (R^2) explained by the model was used as an indication of the ability of O/E scores to reflect the disturbance gradient. Non-parametric Kruskal–Wallace rank tests were used to further elucidate the relationship between the disturbance variables and the presence or absence of each species. The magnitude of individual disturbance variables at those sites where each species was predicted to occur but was not observed, were compared with corresponding values at sites where species were present as predicted, and at sites where species were present but not predicted to occur. These analyses were conducted using S-PLUS 2000 (Statistical Sciences, 1999).

Results

Freshwater fish fauna and biological characteristics of the reference data set

Quantitative sampling of the fish fauna in the 72 least-disturbed reference sites in the Mary, Brisbane, Logan and Albert Rivers resulted in the collection of 24 species and 18,431 individuals. Six species (*Retropinna semoni, Melanotaenia duboulayi, Craterocephalus marjoriae*, *Hypseleotris galii*, *Pseudomugil signifer* and *Anguilla reinhardtii*) collectively comprised 75% of the total number of fish collected. The most widespread species collected across the four reference rivers were *A. reinhardtii, M. duboulayi, Tandanus tandanus* and *R. semoni*, occurring in 75% of reference sites. *Pseudomugil signifer, H. galii C. marjoriae*, and *H. klunzingeri* were also relatively widespread, occurring in 50% of sites.

Model development: classification and discriminant analysis

We recognised five groups of samples from the UPGMA classification of the 72 reference sites based on fish assemblage structure ($\log_{10}(x+1)$ transformed species densities. Each classification group contained sites from each river (Fig. 1) and contained sites sampled in each year (data not shown) implying little biogeographic variation between rivers or systematic annual variation in species assemblages. Stepwise discriminant functions analysis revealed that six environmental

Table 2. Mean density (number of fish 100 m^{-2}) (±SE) and frequency of occurrence (percentage of sites) of the 24 fish species within each of the five reference site groups defined by UPGMA classification

UPGMA reference group	1	2	3	4	5	
Number of sites	11	8	13	26	14	
Fish taxa						
Anguillidae						
Anguilla reinhardtii	8.48 ± 6.22 (100)	1.48 ± 0.57 (75)	1.63 ± 0.27 (92)	9.88 ± 1.86 (96)	1.84 ± 0.68 (86)	
A. australis	0.05 ± 0.04 (18)		0.05 ± 0.05 (8)	0.05 ± 0.02 (15)	0.11 ± 0.11 (7)	
Retropinnidae						
Retropinna semoni	0.27 ± 0.13 (36)	0.86 ± 0.72 (38)	12.70 ± 5.91 (62)	24.81 ± 4.53 (100)	14.36 ± 7.13 (93)	
Plotosidae						
Tandanus tandanus	0.31 ± 0.11 (64)	2.28 ± 0.65 (88)	5.18 ± 1.11 (85)	3.10 ± 0.74 (81)	1.60 ± 0.60 (86)	
Neosilurus hyrtlii		0.39 ± 0.39 (13)	0.05 ± 0.05 (8)	0.01 ± 0.01 (4)		
Atherinidae						
Craterocephalus marjoriae	0.01 ± 0.01 (9)	0.02 ± 0.02 (13)	15.28 ± 7.66 (85)	7.90 ± 2.93 (81)	25.49 ± 10.29 (79)	
C. stercusmuscarum	0.08 ± 0.05 (18)	2.04 ± 1.87 (38)	5.87 ± 3.00 (69)	1.50 ± 0.87 (23)	0.17 ± 0.15 (14)	
Melanotaeniidae						
Melanotaenia duboulayi	0.92 ± 0.53 (73)	8.16 ± 2.98 (88)	22.57 ± 5.35 (100)	23.42 ± 5.20 (85)	9.54 ± 3.14 (93)	
Pseudomugilidae						
Psuedomugil signifer	1.65 ± 1.01 (82)	1.39 ± 0.86 (38)	16.14 ± 3.81 (100)	1.65 ± 0.60 (46)	16.79 ± 3.77 (86)	
Synbranchidae						
Ophisternon sp.					0.02 ± 0.02 (7)	
Scorpaenidae						
Notesthes robusta	0.07 ± 0.06 (18)					
Chandidae						
Ambassis agassizii	1.34 ± 1.07 (18)	5.06 ± 3.44 (38)	9.16 ± 2.83 (69)	1.61 ± 1.02 (23)	1.04 ± 0.81 (36)	
A. marianus	0.28 ± 0.28 (9)					
Therapontidae						
Leiopotherapon unicolor	0.04 ± 0.04 (9)	0.30 ± 0.27 (25)	1.75 ± 0.92 (46)	0.12 ± 0.09 (12)	0.01 ± 0.01 (7)	
Apogonidae						
Glossamia aprion	0.21 ± 0.19 (18)		1.72 ± 1.06 (54)	0.56 ± 0.56 (4)		
Eleotridae						
Gobiomorphus australis	1.76 ± 1.21 (36)	0.56 ± 0.48 (25)	0.21 ± 0.12 (23)	0.95 ± 0.49 (23)	0.07 ± 0.06 (14)	
G. coxii				0.05 ± 0.03 (15)		
Hypseleotris galii	0.79 ± 0.51 (27)	61.48 ± 21.38 (100)	20.50 ± 8.89 (92)	2.05 ± 0.71 (54)	2.06 ± 0.63 (64)	
H. klunzingeri	7.28 ± 4.83 (64)	7.03 ± 3.04 (63)	21.45 ± 7.34 (100)	3.21 ± 1.31 (54)	0.15 ± 0.09 (21)	
H. compressa	3.92 ± 2.58 (45)	0.09 ± 0.09 (13)	0.75 ± 0.65 (23)	0.03 ± 0.03 (4)	0.34 ± 0.34 (7)	
Mogurnda adspersa	0.63 ± 0.47 (36)	5.93 ± 5.32 (50)	9.92 ± 4.51 (77)		1.92 ± 0.98 (64)	
Philypnodon sp.	0.22 ± 0.16 (27)	0.06 ± 0.06 (13)	3.24 ± 2.40 (46)	0.11 ± 0.08 (12)	0.89 ± 0.62 (43)	
P. grandiceps	8.56 ± 8.41 (27)	0.03 ± 0.03 (13)	1.40 ± 1.22 (31)	0.53 ± 0.31 (27)	0.32 ± 0.24 (21)	
Gobiidae						
Redigobius bikolanus	0.30 ± 0.30 (9)					
Environmental variables						*F*
Elevation (m.a.s.l.)	33.6 ± 13.6	85.0 ± 21.6	67.7 ± 7.4	96.9 ± 11.3	101.4 ± 14.9	8.9
Distance to mouth (km)	118.9 ± 22.7	176.7 ± 27.9	182.1 ± 17.1	136.1 ± 15.4	202.2 ± 24.3	8.2
Mean velocity (m s^{-1})	0.16 ± 0.05	0.10 ± 0.04	0.08 ± 0.02	0.26 ± 0.03	0.20 ± 0.03	5.4
Mean depth (m)	0.51 ± 0.06	0.44 ± 0.06	0.38 ± 0.03	0.34 ± 0.02	0.36 ± 0.05	5.3
Mean width (m)	19.8 ± 3.4	7.4 ± 1.3	12.2 ± 3.3	8.7 ± 0.9	6.3 ± 0.6	4.7
Distance from source (km)	100.8 ± 22.9	29.7 ± 8.7	58.5 ± 9.7	45.4 ± 5.9	26.1 ± 4.9	3.9

Also shown are mean values (±SE) and *F* values for environmental variables identified by stepwise multiple discriminant analysis as being significant predictors of UPGMA classification group membership ($p < 0.001$).

variables could significantly discriminate between site groups (Table 2, $p < 0.001$). These results suggest a strong association between catchment scale (stream size and relative site position within the catchment) and local scale (mean depth and mean water velocity) environmental variables and fish assemblage structure. Lowland, main channel sites (e.g. group 1) were wide and deep and were characterised by the presence and/or high densities by the diadromous species *Anguilla reinhardtii*, *Notesthes robusta, A. marianus*, *Gobiomorphus australis*, *H. compressa* and *Redigobius bikolanus* (Table 2). Deep, slow flowing sites located higher in the catchment (e.g. group 2 and 3 sites) were characterised by the presence and/or high densities of *T. tandanus, C. s. fulvus*, *Ambassis agassizii*, *H. galii*, *H. klunzingeri* and *Mogurnda adspersa*. Shallow, fast flowing headwater sites (group 4 and 5 sites) contained *G. coxii* and had higher densities of *R. semoni, C. marjoriae*, *M. duboulayi* and *Gobiomorphus coxii*. Multiple discriminant functions analysis (MDFA), successfully classified 67% of the 72 reference sites into the groups to which they were assigned on the basis of similarities in fish assemblages. A further 15% of sites were allocated to the correct group with the next highest probability.

Internal consistency of predictive model

Mean Observed/Expected ratios calculated for the predicted and observed fish faunas at probability of occurrence thresholds >0% (PO_0) and >50% (PO_{50}) were close to unity (mean $O/E_0 = 0.99 \pm 0.25$ SD, $O/E_{50} = 1.00 \pm 0.20$) implying that overall, both PO thresholds produced unbiased estimates of the number of species at the reference sites (Table 3). However, comparisons of mean O/E scores between reference site classification groups indicated that the model tended to over-estimate the number of species expected at low diversity sites (mean O/E scores <1.0 for reference groups 1 and 2 where the mean numbers of species observed was lowest) and underestimate high diversity sites (group 3) (mean O/E scores >1 for group 3 where the mean number of species observed was highest) (Table 3). This bias was more apparent at PO_0 than PO_{50} (i.e. O/E_{50} scores were closer to unity than O/E_0). Mean O/E scores calculated for reference sites sampled in each river or year were close to unity, indicating relatively little systematic bias in estimates of species richness due to these factors (data not shown). The standard deviation of OE_{50} scores was lower than that of O/E_0 suggesting that there was greater error predicting rare species than common ones (Table 3). Frequency distributions of reference site O/E scores at PO_{50} were more tightly distributed around unity than those generated at PO_0 (Fig. 2), resulting in a narrower width of the reference band (90th–10th percentile) (Table 3), also suggesting greater precision in the match between observed and expected assemblages. The relationship between the number of species expected and observed was stronger for the PO_{50} level ($R^2 = 0.69$) in comparison to the PO_0 level ($R^2 = 0.43$) (Fig. 3a and b). Although not

Table 3. Means and standard deviations of the expected number of species (sum of the predicted species probabilities of occurrence), the observed number of species and Observed/Expected ratios for reference sites used to construct the model and calculated using probability of occurrence thresholds of PO > 0% and PO > 50%

	Probability of occurrence >0% (PO_0)			Probability of occurrence >50% (PO_{50})		
	Expected	Observed	O/E_0	Expected	Observed	O/E_{50}
All reference sites	8.29 ± 1.31	8.25 ± 2.76	0.99 ± 0.25 (0.63–1.34)	6.10 ± 1.56	6.15 ± 2.21	1.00 ± 0.20 (0.68–1.27)
Group 1	8.42 ± 0.83	7.18 ± 1.60	0.85 ± 0.21	5.31 ± 1.54	4.73 ± 1.10	0.89 ± 0.18
Group 2	8.17 ± 1.05	7.13 ± 2.47	0.86 ± 0.24	5.35 ± 1.06	4.88 ± 1.64	0.91 ± 0.17
Group 3	9.36 ± 1.02	11.62 ± 2.22	1.24 ± 0.20	7.74 ± 1.56	8.62 ± 2.02	1.11 ± 0.16
Group 4	7.62 ± 1.31	7.46 ± 2.21	0.98 ± 0.24	5.49 ± 1.19	5.65 ± 1.60	1.03 ± 0.16
Group 5	8.50 ± 1.37	8.07 ± 2.81	0.94 ± 0.24	6.58 ± 1.58	6.64 ± 2.44	1.00 ± 0.20

The width of the reference band (90th–10th percentile of all O/E scores) for each PO threshold is given in parentheses. Means and standard deviations for species metrics at reference sites within each classification group are also shown.

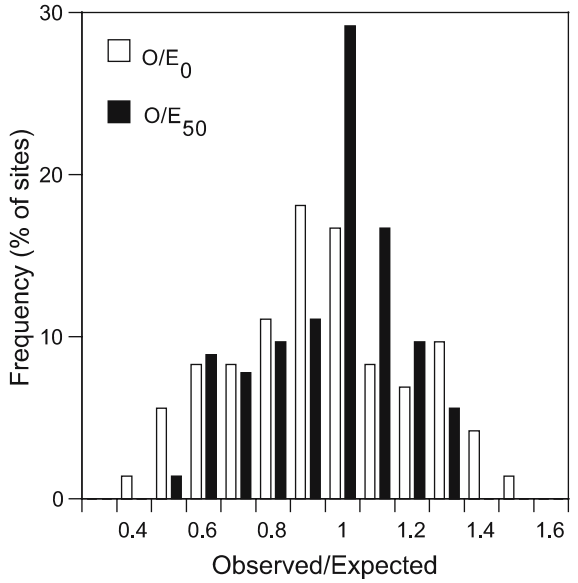

Figure 2. Frequency distributions of observed over expected ratios for the 72 reference sites at probability of occurrence thresholds of PO > 0% (open bars) and PO > 50% (closed bars).

significant ($p > 0.05$), the higher slope of the regression relationship between E and O (1.37 *versus* 1.16 for PO_0 and PO_{50}, respectively) and the lower intercept (−3.15 *versus* −0.92) suggest that PO_0 was more strongly biased than PO_{50}, tending to over-estimate the number of species expected when observed species richness was low and under-estimate when species richness was high, supporting the conclusion reached earlier (Fig. 3a and b). Evaluation of the effect of the total number of species per site on model performance and predictive accuracy further revealed the stronger relationship between the total number of species at a site and the corresponding O/E scores at the PO_0 level in comparison to the PO_{50} ($R^2 = 0.70$ *versus* 0.33), although the slopes of both regression relationships were significantly greater than zero ($p < 0.001$) (Fig. 3c and d). This indicates that O/E scores generated at each probability level are influenced by the total number of species present at a site but that this effect is greater when rare species are included in the prediction of the number of species expected. We conclude that PO_{50} produces more accurate and precise estimates of the number of species expect at a site and so use this probability of occurrence threshold for further model validation and testing.

Validation of predictive model and effect of temporal variation on model accuracy

The relationships between the number of species expected and observed at validation sites was strong both for reference sites used in model development and sampled subsequently ($R^2 = 0.59$, Fig. 4a) and for sites and samples foreign to the reference model ($R^2 = 0.62$, Fig. 4b). The slopes (not significantly different from 1, $p > 0.05$) and intercepts (not significantly different from 0, $p > 0.05$) of the regression lines for both sets of validation data, indicate little bias in the ability of the reference model to predict species composition at new sites and samples at PO_{50}. Mean O/E_{50} scores for internal and external validation data sets did not differ significantly from the mean of reference site O/E_{50} scores (internal validation mean $O/E_{50} = 0.97 \pm 0.27$ SD; $t = -0.76$, df = 184, $p > 0.05$; external validation mean $O/E_{50} = 1.04 \pm 0.18$ SD; $t = 1.26$, df = 155, $p > 0.05$). The apparent greater ability of the reference model to predict fish assemblage composition at sites and samples foreign to the model (i.e. external validation sites) seems counter-intuitive and we attribute this to the fact that these sites contained intermediate numbers of species which the model was least biased in being able to predict (see above).

The degree of temporal concordance and synchrony of ranked O/E scores was generally weak among rivers and validation data sets (Fig. 5, Table 4). Friedman's tests revealed that the ranking of sites from the Mary River was preserved through time to a greater degree (i.e. higher Friedman's test statistics) than sites in the Albert River for each validation data set, but this concordance was weakly significant ($p = 0.02$) only for the internal validation data set (Table 4). Little evidence of synchrony in temporal oscillations of ranked O/E scores was observed in each data set or river (Kendall's coefficients of concordance all <0.34). Despite this general lack of concordance, no significant trends in O/E scores for each river and data set were detected by one-way repeated measures ANOVA (Table 4). These results suggest that sites fluctuate though time, but in an inconsistent manner, and that the lack of any strong trends implies that systematic biases accruing over time are relatively weak. For most

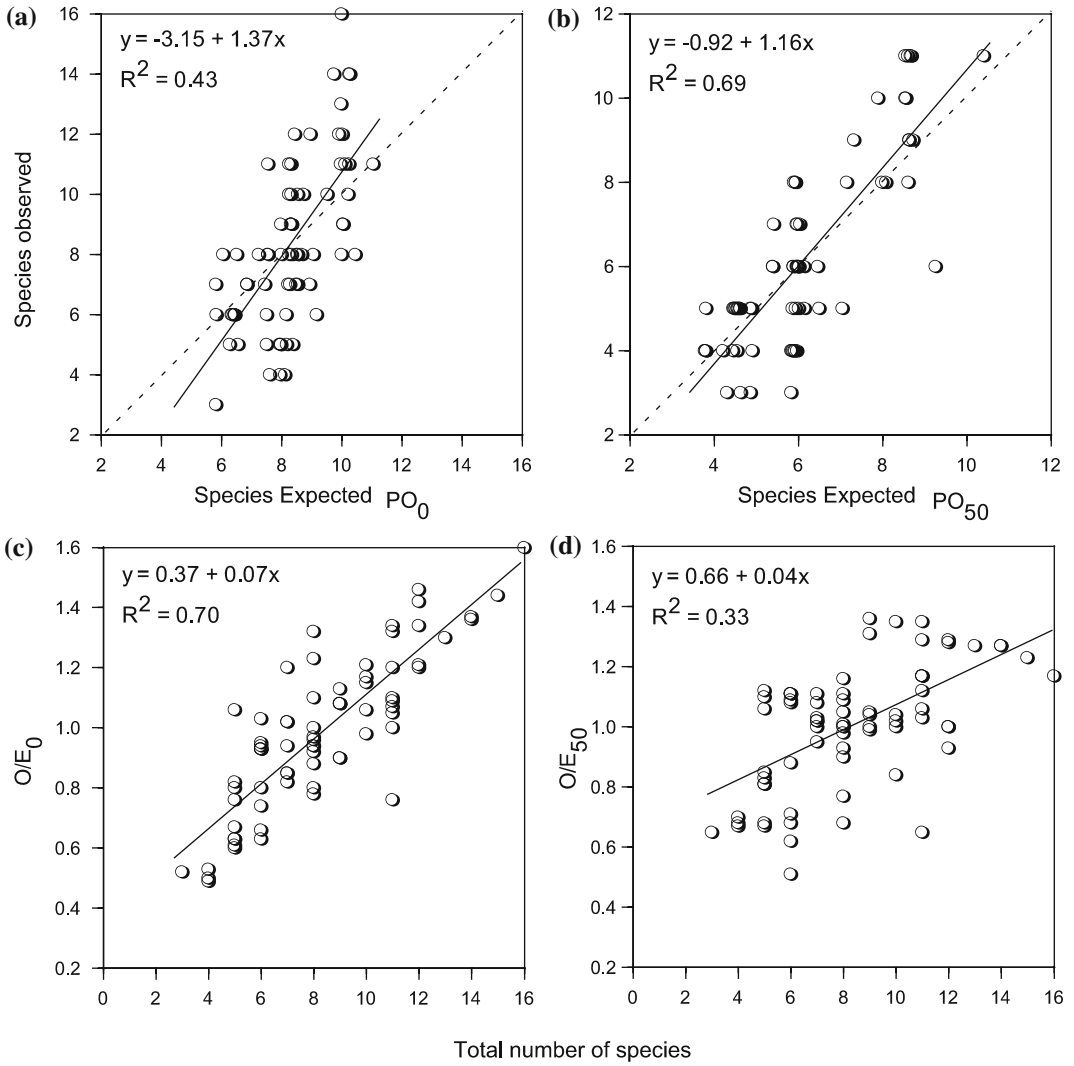

Figure 3. Relationship between expected and observed values for (a) PO_0 and (b) PO_{50} probability of occurrence thresholds at reference sites. The diagonal dashed lines represent the line of perfect agreement between the two measures. Regression lines and equations for each plot are also shown. For each PO threshold, $p > 0.05$ for H_o: slope = 1 and H_o: Intercept = 0. Also shown are the relationships between the total number of species observed at reference sites and (c) O/E_0 and (d) O/E_{50} scores. For each PO threshold, $p < 0.001$ for H_o: slope = 0.

sites O/E scores for each sampling occasion remained within the reference band (Figs. 5a, b and 6a), indicating that temporal variation was not marked enough to reduce the confidence of the model predictions based on one season (winter) when the model was applied to new sites and/or sampling occasions. O/E scores for the five internal validation sites sampled in spring 2000 were also within the reference band, indicating that the reference model could accurately predict forward in time (Fig. 5a). Four sites in the Mary River showed a very high degree of temporal variation, with O/E scores falling below the reference band on several occasions (Fig. 5a and b). These sites were located on tributary streams that ceased to flow for prolonged periods, becoming either small isolated pools or desiccating completely.

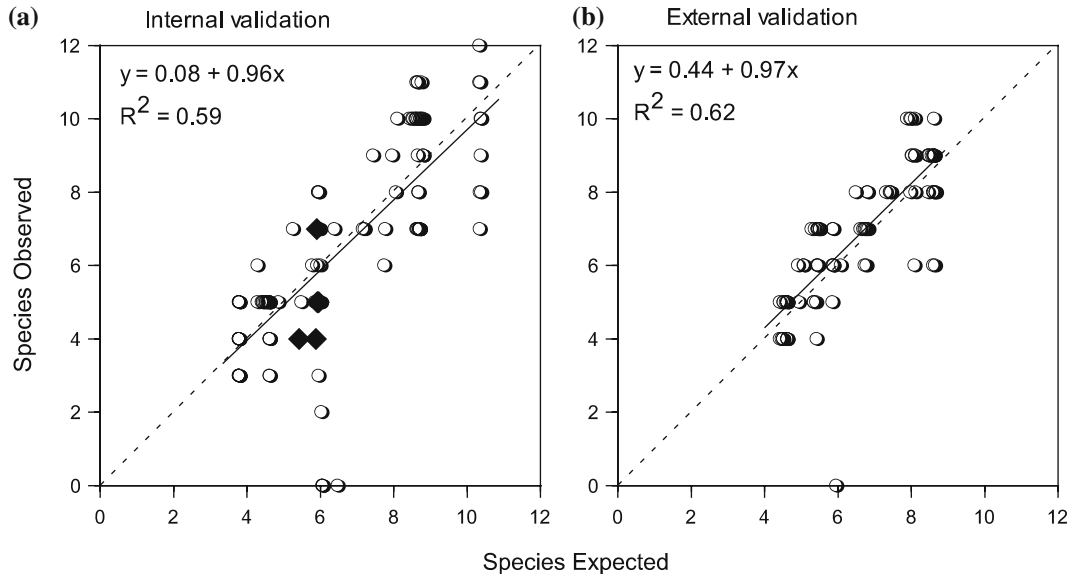

Figure 4. Relationship between expected and observed values for (a) internal validation samples and (b) external validation samples at the PO_{50} probability of occurrence threshold. The five internal validation sites sampled during spring 2000 are shown as black diamonds (note that two sites directly overlie each other on the plot). The diagonal dashed lines represent the line of perfect agreement between the two measures. Regression lines and equations for each plot are also shown. For each dataset, $p > 0.05$ for H_o: slope = 1 and H_o: Intercept = 0 .

Testing the ability of the predictive model to detect human disturbance

Fish assemblage composition at the 48 test sites subject to known gradients of disturbance was often substantially different from that predicted by the model. Mean O/E_{50} scores across all test sites (mean 0.64 ± 0.31 SD) were significantly lower than mean reference site scores ($t = -7.75$, df = 118, $p < 0.0001$) and O/E_{50} scores for 27 of the 48 sites were lower than the reference band (Fig. 6b): this latter result is suggestive of biological impairment at these test sites. A multiple regression model using disturbance gradient principal components (Table 5) as predictors of variation in O/E_{50} scores at test sites was highly significant ($p < 0.001$) and could explain 60% of the variance in the data (Table 6). The regression model selected three disturbance principal components as predictors, with the components describing catchment land use, water quality and in-stream habitat degradation (PC1, PC4 and PC5 – Table 5).

Examination of individual species predictions and patterns of occurrence revealed more detailed information about the sources of disturbance potentially affecting each species. For example, the Australian smelt (*R. semoni*) was predicted to occur at all 48 sites (at PO_{50}) but was observed at only 21 of these sites. Sites in which *R. semoni* was predicted to occur, but did not, had a significantly higher percentage of their upstream catchments subject to land use pressures (i.e. high % cropped and % urban), poor water quality (high conductivity, high diel dissolved oxygen fluctuations and high turbidity), and degraded in-stream habitat condition (high % mud) (Fig. 7). These results suggest that *R. semoni* is sensitive to a wide range of disturbances imposed at catchment to microhabitat scale. Land use factors were also associated with the absence of *A. reinhardtii*, *T. tandanus*, *M. duboulayi* and *H. klunzingeri*. Poor water quality was associated with the absence of *C. marjoriae, A. agassizii* and *H. klunzingeri* and abundant growths of filamentous algae and aquatic plants were associated with the absence of *M. duboulayi* and *P. signifer*, respectively (Fig. 7). Occasionally, species were present at some sites, despite not being predicted to occur there by the model. For example, *C. stercusmuscarum* was observed at seven sites in which this species was not predicted to occur (Fig. 7). These sites were characterised by a relatively high percentage of

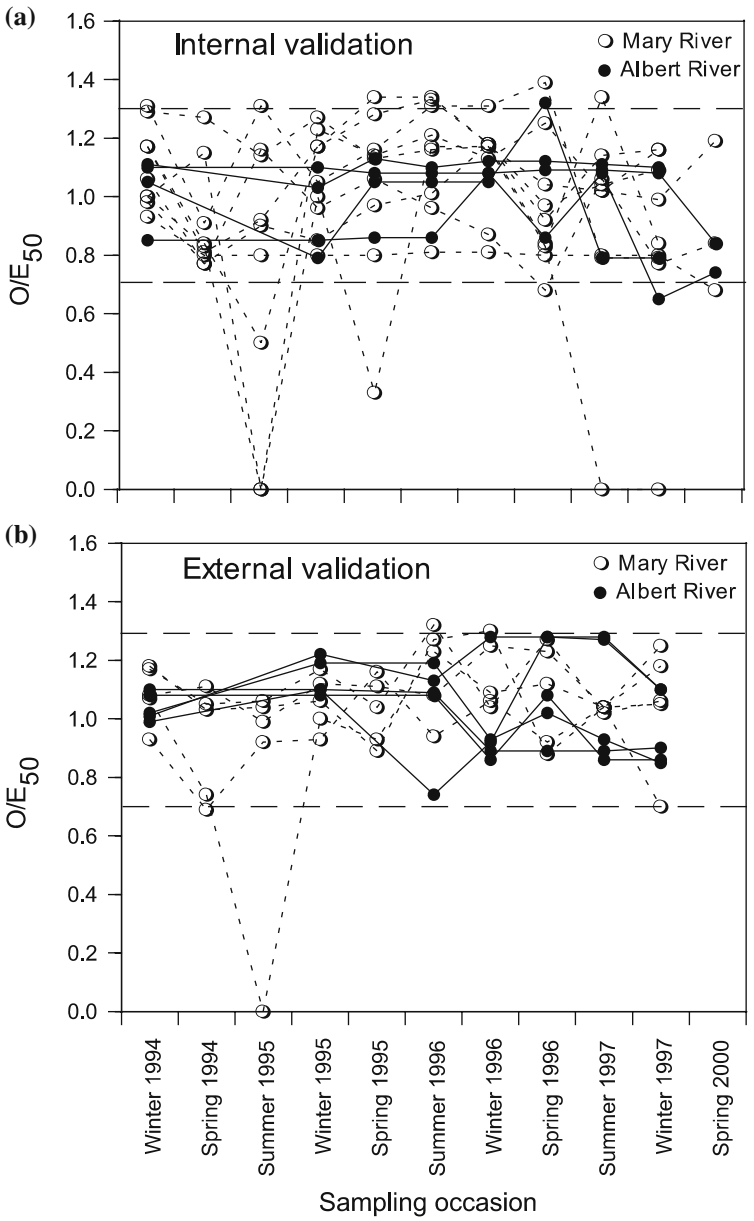

Figure 5. Temporal variation in O/E_{50} scores for (a) internal validation samples and (b) external validation samples in the Mary River (open circles) and Albert River (closed circles). The 90th–10th percentile reference band is depicted with horizontal dashed lines. Internal validation sites sampled in Winter 1994 (Fig. 5a) were included in the reference data set used to construct the model and were used to derive O/E_{50} scores for theses samples, all other samples were foreign to the model.

urban development in the catchment, high total nitrogen levels and high amounts of filamentous algae. These results may indicate that *C. stercus-muscarum* can successfully colonise sites affected by human activities that result in nutrient enrichment and abundant algal growths, or they may be indicative of inaccuracies in the predictive model.

Discussion

Humphrey et al. (2000) envisaged that regions subject to strongly seasonal and/or unpredictable environmental fluctuations would be less amenable to the development and application of predictive models of species composition as the basis for

Table 4. Results of Friedman's test of concordance (*FR*) and Kendall's coefficient of concordance (*KCC*) in OE_{50} scores at internal validation sites and external validation sites in the Mary and Albert Rivers

Data set	Internal validation		External validation	
River	Mary ($n=9$)	Albert ($n=4$)	Mary ($n=5$)	Albert ($n=5$)
Concordance				
Fr	20.26	8.75	15.19	5.66
d.f.	9	7	9	6
p	0.02	0.27	0.09	0.46
KCC	0.250	0.313	0.338	0.189
Trend				
Repeated Measures ANOVA				
F	2.57	1.50	1.87	1.11
d.f.	9,72	6,21	9,36	6,24
p	0.06	0.24	0.17	0.38

Numbers of sites in each data set and river are given in parentheses. Also shown are *F* statistics and *p* values for one-way repeated measures analysis of variance values to test for trends in O/E_{50} scores through time.

stream health assessment. The data from which our predictive model was developed, validated and tested comes from a region of comparatively high environmental variability due to the unpredictable nature of rainfall and river discharge (Pusey et al., 1993, 2000, 2004). Yet the model could provide reasonably accurate and precise predictions of species composition and appeared sensitive enough to distinguish sites impacted by human disturbance.

The reference condition approach used here required that strong relationships exist between

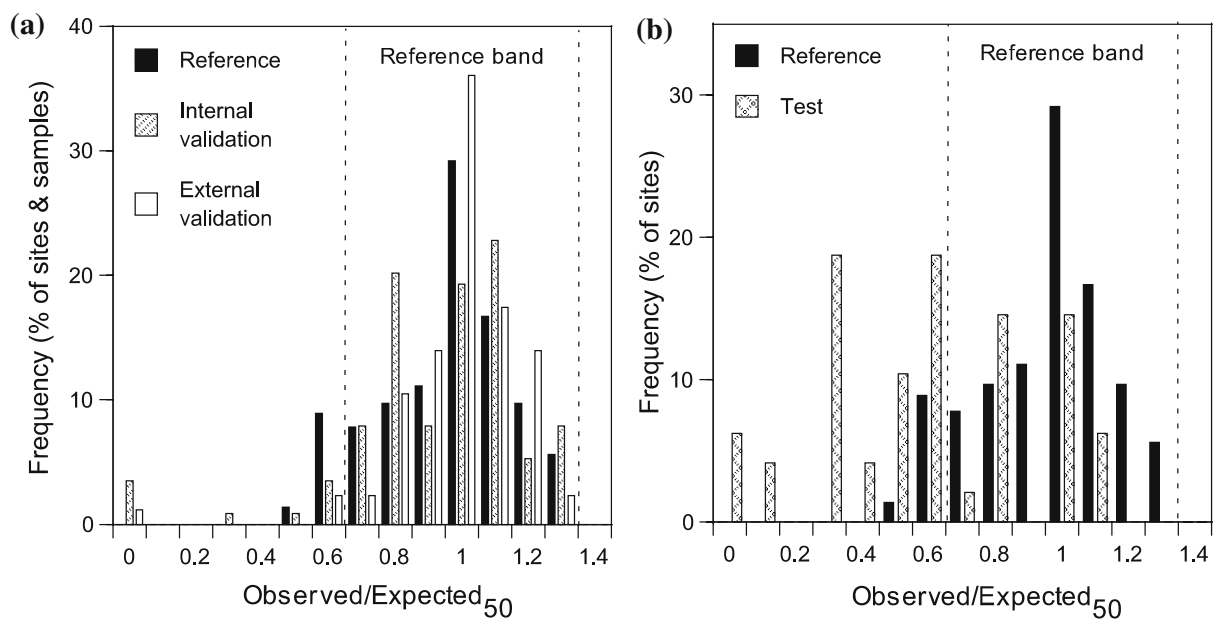

Figure 6. Frequency distributions of O/E_{50} ratios for (a) reference, internal validation and external validation sites and (b) reference and test sites. Vertical dashed lines indicated the width of the reference band.

Table 5. Principal components analysis of 16 disturbance variables from the 48 test sites in south-eastern Queensland

Variable	Principal component				
	1 (25.5%)	2 (16.6%)	3 (13.2%)	4 (12.1%)	5 (11.6%)
% catchment grazed	**0.83**	0.04	0.07	0.17	0.06
Temperature diel range	**0.70**	0.30	−0.21	−0.14	−0.26
pH	**0.69**	0.31	−0.15	0.02	−0.06
% catchment cleared	**0.68**	0.08	0.29	0.33	0.37
Conductivity	**0.57**	0.41	0.26	0.36	0.05
% aquatic macrophytes	0.03	**0.84**	0.06	−0.06	0.19
% filamentous algae	0.18	**0.76**	−0.12	−0.06	−0.04
Dissolved oxygen diel range	0.48	**0.69**	0.01	0.14	0.10
% riparian cover	−0.42	**−0.55**	−0.06	0.18	0.04
Total nitrogen	0.04	0.01	**0.95**	0.07	−0.02
Total phosphorus	−0.06	−0.03	**0.95**	−0.02	0.05
Turbidity	0.09	−0.18	−0.15	**0.80**	0.17
% mud	0.18	0.05	0.10	**0.75**	0.06
% catchment cropped	−0.11	0.48	0.30	**0.57**	−0.29
% catchment urban	−0.17	−0.06	0.25	0.25	**0.77**
% submerged terrestrial vegetation	0.09	0.21	−0.18	−0.05	**0.76**

The percentage variation explained by each component is given in parentheses and the highest variable loadings on each principal component are shown in bold type (from Kennard et al., 2005).

stream biota and environmental predictor variables least affected by human activity. Our predictive model indicated that spatial variation in freshwater fish assemblage composition in south-eastern Queensland streams can be related to a small set of variables describing catchment scale (elevation, and relative site position within the stream network) and local scale environmental features characterising the reference sites (wetted width, depth and water velocity) (see also Pusey et al., 1993, 2000). These potential 'landscape filters' (*sensu* Poff, 1997) are sufficiently correlated with fish assemblage composition that a predictive model could be developed to describe these relationships. The predictive capacity of our model would undoubtedly be improved by the inclusion of additional environmental predictor variables of potential ecological importance to fish in the region (e.g. variables describing hydrology, substrate composition and in-stream

Table 6. Summary of multiple regression model to predict variation in O/E_{50} scores at the 48 test sites according to variation in the disturbance gradient variables (principal components)

Principal component	Description	OE_{50} (%)
PC1	Intensive catchment land use (clearing and grazing) and degraded water quality (high diel temperature range, pH and conductivity)	27.0
PC2	Degraded riparian vegetation, aquatic plant infestation and high diel DO range	0
PC3	High nutrients	0
PC4	Intensive catchment land use (cropping), degraded habitat (muddy substrate) and high turbidity	23.3
PC5	Intensive catchment land use (urbanization) and degraded habitat (submerged terrestrial weeds)	9.4
	GLM R^2	59.7

The approximate model R^2 and the relative importance of each predictor variable fitted in the model (indicated by the percent of total variance explained) is given.

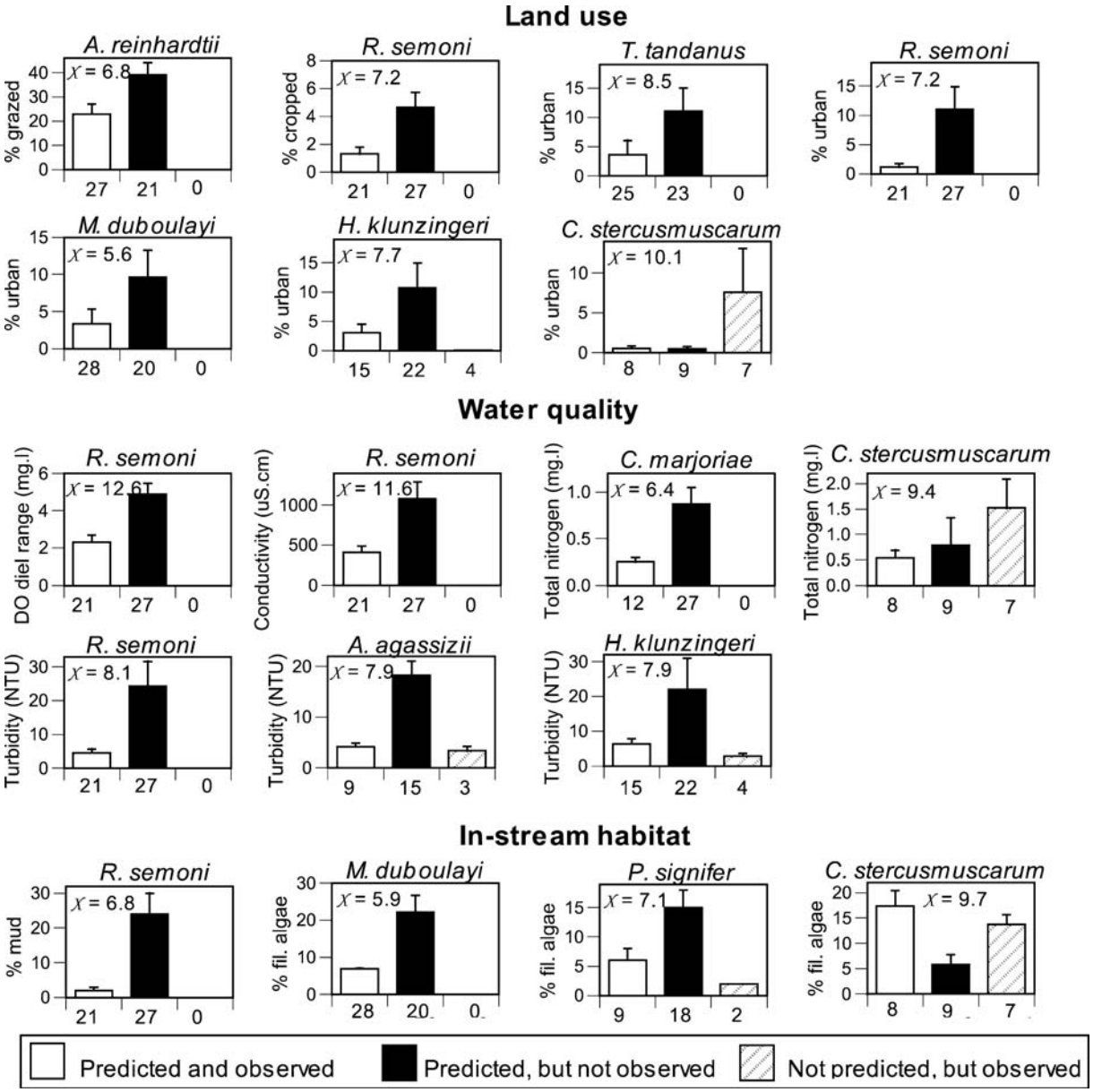

Figure 7. Difference in mean values (±SE) of disturbance variables significantly different at sites where each species was predicted (at the PO_{50} level) and observed to occur (open bars), sites where each species was predicted to occur but was not observed (closed bars), and sites where each species was not predicted to occur but was observed (hatched bars). Chi-square values for Kruskal Wallace tests are given for each comparison; all were significant at $p < 0.05$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn & Keough, 2002). Sample sizes for each site category are shown below the *x*-axis of each plot.

habitat structure). However, these environmental factors may also be influenced greatly by human activity and their use as predictor variables increases the potential for biased predictions, particularly if the models are to be used to predict species composition at test sites potentially impacted by anthropogenic flow regime changes or in-stream habitat modification. The scope of the predictive model could be improved by including additional reference sites that encompass a greater range of biological and environmental conditions in the south-eastern

Queensland region. In particular, reference sites on short coastal streams of the Noosa, Pine and South Coast drainage basins need to be sampled and incorporated into an updated version of the predictive model. We view the predictive models developed in the present study to be dynamic and that further model development be an iterative process whereby new sites are added to the reference site database as they become available and that models be updated periodically.

Overall, the model produced reasonably accurate and precise predictions of the number of species at the reference sites, although accuracy and precision varied with the choice of species probability of occurrence thresholds. Internal validation procedures revealed that the model tended to over-estimate the number of species expected at low diversity sites and underestimate for high diversity sites. Greater accuracy and precision in the match between observed and expected assemblages was obtained when rare species with low probabilities of occurrence were excluded from predictions using a probability of occurrence threshold >50%. This was confirmed by external validation of the model, where species predictions at PO_{50} closely matched those observed. These results support the conclusions of Hawkins et al. (2000) and Bailey et al. (2004) that omission of rare taxa can improve robustness of predictive models. Bailey et al. (2004) argued that the absence of taxa with low probability of occurrence at test sites is unlikely to convey meaningful information about the condition of that site, as they have a high probability of being absent by chance alone. However, the exclusion of rare species has potential to reduce the sensitivity of an assessment of the health of a site and may underestimate the difference between undisturbed and impacted sites (thereby increasing the chance of committing a type II error) (Cao et al., 1998, 2001). Rare taxa may be more vulnerable to disturbances (due to restricted distributions coupled with low abundances) (Cao & Williams, 1999; Cao et al., 2001), implying that examination of the presence or absence of a complement of rare taxa may provide further information as to the health of a site. Low overall taxon richness does have the potential to bias model predictions given that the failure to detect a single species during sampling could result in considerable reduction in the O/E score at a test site. Low numbers of species expected can also result in a low sensitivity of the model (i.e. low precision) to detect disturbance at mildly disturbed sites (Smith et al., 1999; Turak et al., 1999). In the present study, the total number of fish species available for prediction (24 species) and the number of species expected to occur at PO_{50} (average of six species), was less than half that typically available in applications of RIVPACS-style models based on aquatic macroinvertebrates, diatoms or habitat categories (e.g. Marchant et al., 1997; Chessman et al., 1999; Davies et al., 2000). Nevertheless, the precision of our model was comparable to outcomes from these studies (SD of reference site $O/E_{50} = 0.20$, width of reference band = 0.59). Although their model appeared less precise (SD of $O/E_0 = 0.45$), Joy & Death (2002) successfully developed a predictive model based on a total of only 13 fish species, with less than five species usually expected at PO_0, and concluded that the model was sufficiently sensitive for impacted sites to be detected. These authors suggested that sites containing few species resulted in unstable O/E ratios at PO > 50%. Our results appear contrary to this and clearly indicate that low numbers of species at a site can result in less reliable predictions at PO_0 and that the accuracy and precision of predictions is improved by eliminating species with a low probability of occurrence.

Strategies to maximise the number of species available and thereby improve predictive modelling capabilities include the pooling of reference site data from multiple habitats (Parsons & Norris, 1996) and/or from several seasonal sampling occasions (Furse et al., 1984; Simpson & Norris, 2000) in an attempt to account for species turnover across local spatial scales and between seasons. We minimised the potential for missing a species due to under-sampling by employing a robust standardised sampling regime designed to ensure that the majority of species present in a range of habitat types within a river reach were actually collected. The potential benefits of developing a model based on combined seasons data will be explored elsewhere.

Temporal variation in fish assemblage composition did not influence our ability to predict species composition through time. Sites did not appear to fluctuate concordantly in their O/E

scores based on common fish species. However, changes in site rankings through time are a fairly stringent test of temporal concordance (Barmuta et al., 2003) and for most sites, O/E_{50} scores for each sampling occasion remained within the reference band, indicating that temporal variation was not sufficiently great to reduce the confidence of the model predictions based on one season (winter) when applied to new sites and/or sampling occasions. Factors such as taxonomic richness (Micheli et al., 1999; Cottingham et al., 2001), taxonomic resolution (e.g. family versus species data, Metzeling et al., 2002), inclusion of rare species (Grossman et al., 1991, Robinson et al., 2000) and data type (e.g. abundance versus presence absence, Meffe & Minckley, 1987; Boulton et al., 1992; Humphrey et al., 2000; Oberdorff et al., 2001a; Metzeling et al., 2002; Paller, 2002; Scarsbrook, 2002) can affect impressions of the degree of temporal variability or persistence of biotic communities and can affect the precision of biotic assessments made on the basis of these data (Linke et al., 1999; Townsend & Riley 1999; Reece et al., 2001; Reynoldson et al., 2001; Metzeling et al., 2002; Barmuta et al., 2003). Our data based on species presence absence at probabilities of occurrence >50% was more robust to temporal variations as rare species were excluded from the predictions (i.e. while not presented here, O/E_0 scores fluctuated more through time than O/E_{50} scores).

Four sites in the Mary River were highly variable through time, with O/E_{50} scores falling below the reference band on several occasions (Fig. 5). These sites were located on tributary streams that ceased to flow for prolonged periods and either became small isolated pools, or completely dried out. We presume these extreme environmental disturbances exert strong controls on fish assemblages in the region, but that component fish species are sufficiently resilient to return to a pre-disturbance state once environmental conditions become more benign or resemble the pre-disturbance state. We interpret the rapid return of O/E scores to near unity following disturbance events as evidence of this (Fig. 5). A more comprehensive treatment of the role of environmental variability and extreme discharge events on the stability, persistence and resilience of fish assemblages will be published elsewhere.

Our model developed for sites sampled in one season only (winter), was able to accurately predict fish assemblage structure during other seasons, provided that they were not subject to unusually extreme environmental conditions (e.g. extended periods of low flow that restricted fish movement or resulted in habitat desiccation and local fish extinctions). To minimise the chances of committing a type I error (incorrectly diagnosing a site as disturbed), new sites should ideally be sampled within the same season as the reference sites used to construct the model, and sites affected by unusually or extreme environmental conditions should be excluded from the assessment. The long period of time (>3 years) between the sampling of test and reference sites in our study introduced a source of error that has potential to compromise the validity of our test site predictions. However, based on our evaluation of a limited number of sites tracked through time, our data did not reveal any strong annual trends in O/E scores, suggesting that any systematic biases accruing over time were relatively weak. Furthermore, O/E_{50} scores for the five internal validation sites sampled in spring 2000 were within the reference band, indicating that the reference model could accurately predict forward in time. A recommended strategy to avoid any systematic bias accruing from site differentiation through time has been to resample a subset of reference sites simultaneously with sampling of test sites. These reference site re-samples can then be incorporated into updated versions of the predictive model, (Reece et al., 2001; Reynoldson et al., 2001; Clarke et al., 2002; Barmuta et al., 2003). Wright (1995) and Barmuta et al. (2003) cautioned that sampling of reference sites that have recently experienced or are currently experiencing natural environmental extremes such as floods or droughts should be avoided as their inclusion may make the resulting model insensitive to detecting human impacts. The same principle should also apply to the sampling of test sites. Re-sampling a subset of reference sites over consecutive years could also provide an opportunity to detect any trends or other systematic changes in species composition related to long-term cyclic phenomena such as El-Nino cycles (Mol et al., 2000; Puckridge et al., 2000; Metzeling et al., 2002; Barmuta et al., 2003) or climate change (Meyer et al., 1999; Mingelbier et al., 2001).

Predictions of fish assemblage composition at the 48 test sites subject to known gradients of disturbance suggested that observed deviations from expected species composition may be an effective indicator of aquatic ecosystem health, as illustrated by the associations between anthropogenic disturbance variables and individual species presence or absence and summary O/E_{50} scores. Human impacts on local fish assemblages are likely to be scale dependent, and potentially affected by processes operating at both local scales (e.g. riparian and in-stream habitat degradation) and landscape scales (e.g. agricultural runoff from upstream areas and artificial barriers downstream) (Roth et al., 1996; Allan et al., 1997; Stauffer et al., 2000). The results of the present study add weight to this viewpoint, as fish assemblage O/E_{50} scores and individual species presence or absence were associated with disturbance variables describing surrounding catchment land use, water quality and in-stream habitat degradation.

As our test site data was collected on a single sampling occasion, we knew nothing about the magnitude of temporal variation in fish assemblages at these potentially disturbed sites relative to reference sites least affected by human activity. Several studies have shown that fish assemblages at anthropogenically disturbed sites are more variable though time than assemblages at undisturbed reference sites (Karr et al., 1987; Schlosser, 1990; Taylor et al., 1996). This may be related to greater variability in physical habitat structure at disturbed sites (e.g. Paller, 2002). Further investigation is required to evaluate levels of temporal variability in fish assemblages at sites subject to varying intensities of human disturbance, as this would provide useful information on the power and sensitivity of indicators based on these data. It is desirable that stream biomonitoring programs incorporate temporal assessments as changes in biotic assemblages over time that exceed the range of normal variability, together with the direction of those changes, can improve the confidence in a site assessment and indicate whether a site is recovering or deteriorating (Linke et al., 1999; Townsend & Riley; 1999; Paller, 2002).

We concur with Joy & Death (2000, 2002, 2003) that a multivariate predictive modelling approach based on accurately defining the reference condition for fish species composition can be used effectively for broad scale monitoring in catchments experiencing the common range of human disturbances (catchment land use and associated local riparian, in-stream habitat and water quality degradation). From such initial assessments of stream health it is possible to flag sites for more detailed evaluation and diagnosis of options for remediation. Our approach may not be sufficiently sensitive to use in situations requiring compliance monitoring, unless the targets for compliance are particular species presence/absence patterns at various spatial scales. We recommend the use of a wider suite of bioassessment tools to sharpen the evaluation of sites in relation to compliance targets and to provide broader evaluations of stream health based on fish. These could include indicators based on the relative abundance of alien species (e.g. Kennard et al., 2005), and many other attributes of fish assemblage structure and function (e.g. defined on the basis of habitat use, reproductive style, trophic position and environmental tolerances) (Karr et al., 1986; Fausch et al., 1990; Simon, 1999, 2003). The use of multivariate predictive models in river bioassessment has been criticised because of their ''inherent statistical complexity'' and a perceived difficulty in conveying outputs to managers and the public (Gerritsen, 1995; Fore et al., 1996). We suggest that the accuracy and precision of bioassessment results is of primary importance, irrespective of the complexity of the statistical procedures necessary to obtain them. Furthermore, we agree with those who suggest that the outputs from the multivariate predictive models (lists of species expected and observed and an overall summary of the match between the two lists – O/E) are conceptually simple methods for summarising the biotic assemblage at a given test site and the degree of departure from the expected condition and hence, by implication, ecosystem health. Provided the expected condition for both types of data can be accurately defined, the use of a combination of multivariate and multimetric approaches would be ideal as the two approaches convey different but complementary information about the status of the biota in question (Norris, 1995; Reynoldson et al., 1997; Johnson, 2000) and hence, the health of the aquatic ecosystem.

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References

Allan, J. D., D. L. Erikson & J. Fay, 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37: 149–161.

Angermeier, P. L. & I. J. Schlosser, 1989. Species-area relationships for stream fishes. Ecology 70: 1450–1462.

Angermeier, P. L. & M. A. Winston, 1998. Local vs regional influences on local diversity in stream fish communities of Virginia. Ecology 79: 911–927.

ANZECC & ARMCANZ, 2000. Australian and New Zealand Water Quality Guidelines. Australia and New Zealand Environment and Conservation Council & Agriculture and Resource Management Council of Australia and New Zealand, Canberra.

Bailey, R. C., R. H. Norris & T. B. Reynoldson, 2004. Bioasseessment of Freshwater Ecosystems Using the Reference Condition Approach. Kluwer Academic Publishers, Boston.

Barmuta, L. A., L. Emmerson & P. Otahal, 2003. AusRivAS Errors Analysis – Final Report for AusRivAs Toolbox Project TB1. National River Health Program & Land and Water Australia, Canberra.

Belbin, L., 1995. PATN – Pattern Analysis Package. CSIRO Division of Wildlife and Rangelands Research, Canberra.

Boulton, A. J., C. G. Peterson, N. B. Grimm & S. G. F. Fisher, 1992. Stability of an aquatic macroinvertebrate community in a multi-year hydrologic disturbance regime. Ecology 73: 2192–2207.

Bray, J. R. & J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349.

Bunn, S. E., 1995. Biological monitoring of water quality in Australia: Workshop summary and future directions. Australian Journal of Ecology 20: 220–227.

Cao, Y. & D. D. Williams, 1999. Rare species are important for bioassessment – reply to Marchant's comments. Limnology and Oceanography 43: 1841–1842.

Cao, Y., D. D. Williams & N. E. Williams, 1998. How important are rare species in aquatic community ecology and bioassessment? Limnology and Oceanography 43: 1403–1409.

Cao, Y., D. P. Larsen & R. St-J. Thorne, 2001. Rare species in multivariate analysis for bioassessment: some considerations. Journal of the North American Benthological Society 20: 144–153.

Chessman, B., I. Growns, J. Currey & N. Plunkett-Cole, 1999. Predicting diatom communities at the genus level for the rapid biological assessment of rivers. Freshwater Biology 41: 317–331.

Clarke, R. T., M. T. Furse, J. F. Wright & D. Moss, 1996. Derivation of a biological quality index for river sites: comparison of the observed with the expected fauna. Journal of Applied Statistics 23: 311–332.

Clarke, R. T., M. T. Furse, R. J. M. Gunn, J. M. Winder & D. Wright, 2002. Sampling variation in macroinvertebrate data and implications for river quality indices. Freshwater Biology 47: 1735–1751.

Cottingham, K. L., B. L. Brown & J. T. Lennon, 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4: 72–85.

Davies, P. E., 2000. Development of a national river bioassessment system (AUSRIVAS) in Australia. In Wright, J. F., D. W. Sutcliffe & M. T. Furse (eds), Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques. Freshwater Biological Association and Environment Agency, UK, 113–124.

Davies, N. M., R. H. Norris & M. C. Thoms, 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshwater Biology 45: 343–369.

Faith, D. P., P. R. Minchin & L. Belbin, 1987. Compositional dissimilarity as a robust measure of ecological distance: a theoretical model and computer simulations. Vegetatio 69: 57–68.

Fausch, K. D., J. Lyons, J. R. Karr & P. L. Angermeier, 1990. Fish communities as indicators of environmental degradation. American Fisheries Society Symposium 8: 123–144.

Fore, L. S., J. R. Karr & R. W. Wisseman, 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. Journal of the North American Benthological Society 15: 212–231.

Furse, M. T., D. Moss, J. F. Wright & P. D. Atmitage, 1982. The influence of seasonal and taxonomic factors on the ordination and classification of running-water sites in Great Britain and on the prediction of their macro-invertebrate communities. Freshwater Biology 14: 257–280.

Gerritsen, J., 1995. Additive biological indices for resource management. Journal of the North American Benthological Society 14: 451–457.

Grossman, G. D., J. F. Dowd & M. Crawford, 1991. Assemblage stability in stream fishes: a review. Environmental Management 14: 661–671.

Harris, J. H., 1995. The use of fish in ecological assessments. Australian Journal of Ecology 20: 65–80.

Harris, J. H. & R. Silveira, 1999. Large-scale assessments of river health using an Index of biotic integrity with low-diversity fish communities. Freshwater Biology 41: 235–252.

Hawkins, C. P., R. H. Norris, J. N. Hogue & J. W. Feminella, 2000. Development and evaluation of predictive models for measuring the biological integrity of streams. Ecological Applications 10: 1456–1477.

Hughes, R. M., 1995. Defining acceptable biological status by comparing with reference conditions. In Davis, W. S. & T. P. Simon (eds), Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. Lewis, Boca Raton, FL, 31–48.

Hughes, R. M. & T. Oberdorff, 1999. Applications of IBI concepts and metrics to waters outside the United States and Canada. In Simon, T. P. (ed.), Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press, Boca Raton, FL, 79–83.

Humphrey, C. L., A. W. Storey & L. Thurtell, 2000. AUSRIVAS: operator sample processing errors and temporal variability – implications for model sensitivity. In Wright, J. F., D. W. Sutcliffe & M. T. Furse (eds), Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques. Freshwater Biological Association and Environment Agency, UK, 143–163.

Jackson, D. A. & H. H. Harvey, 1989. Biogeographic associations in fish assemblages: local vs regional processes. Ecology 70: 1472–1484.

Johnson, R. K., 2000. RIVPACS and alternative statistical modelling techniques: accuracy and soundness of principles. In Wright, J. F., D. W. Sutcliffe, & M. T. Furse, (eds), Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques. Freshwater Biological Association and Environment Agency, UK, 323–332.

Joy, M. K. & R. G. Death, 2000. Development and application of a predictive model of riverine fish community assemblages in the Taranaki region of the North Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 34: 241–252.

Joy, M. K. & R. G. Death, 2002. Predictive modelling of freshwater fish as a biomonitoring tool in New Zealand. Freshwater Biology 47: 2261–2275.

Joy, M. K. & R. G. Death, 2003. Assessing biological integrity using freshwater fish and decapod habitat selection functions. Environmental Management 32: 747–459.

Karr, J. R., 1981. Assessment of biotic integrity using fish communities. Fisheries 6: 21–27.

Karr, J. R. & E. W. Chu, 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press, Washington, D.C.

Karr, J. R., P. R. Yant & K. D. Fausch, 1987. Spatial and temporal variability of the index of biotic integrity in three midwestern streams. Transactions of the American Fisheries Society 116: 1–11.

Karr, J. R., K D. Fausch, P. L. Angermeier, P. R. Yant & I. J. Schlosser, 1986. Assessing Biological Integrity in Running Waters: A Method and its Rationale (5th edn). Illinois Natural History Survey Special Publication, Champaign.

Kennard, M. J., A. H. Arthington, B. J. Pusey & B. D. Harch, 2005. Are alien fish a reliable indicator of river health? Freshwater Biology 50: 174–193.

Lake, P. S., 1995. Of floods and droughts: river and stream ecosystems of Australia. In Cushing, C. E., K. W. Cummins & G. W. Minshall (eds), Ecosystems of the World 22: River and Stream Ecosystems. Elsevier, New York, 659–694.

Linke, S., R. C. Bailey & J. Schwindt, 1999. Temporal variability of stream bioassessments using benthic macroinvertebrates. Freshwater Biology 42: 575–584.

McMahon, T. A., 1986. Hydrology and management of Australian streams. In Campbell, I. C. (ed.), Stream Protection – The Management of Rivers for In-stream Uses. Water Studies Centre, Chisholm Institute, Melbourne, 23–44.

Marchant, R. A., R. H. Hirst, R. Norris, L. Butcher, L. Metzeling & D. Tiller, 1997. Classification and prediction of macroinvertebrate assemblages from running waters in Victoria, Australia. Journal of the North American Benthological Society 16: 664–681.

Meffe, G. K. & W. L. Minckley, 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. American Midland Naturalist 117: 177–191.

Metzeling, L., D. Robinson, S. Perriss & R. Marchant, 2002. Temporal persistence of benthic macroinvertebrate communities in south-eastern Australian streams: taxonomic resolution and implications for the use of predictive models. Marine and Freshwater Research 53: 1223–1234.

Meyer, J. L., M. J. Sale, P. J. Mulholland & N. L. Poff, 1999. Impacts of climate change on aquatic ecosystem functioning and health. Journal of the American Water Resources Association 35: 1373–1386.

Micheli, F., K. Cottingham, J. Bascompte, O. Bjornstad, J. Eckert, J. Fischer, T. Keitt, B. Kendall, J. Klug & J. Rusak, 1999. The dual nature of community variability. Oikos 85: 161–169.

Mingelbier, M., F. Lecomte & J. J. Dodson, 2001. Climate change and abundance cycles of two sympatric populations of smelt (Osmerus mordax) in the middle estuary of the St Lawrence River, Canada. Canadian Journal of Fisheries and Aquatic Sciences 58: 2048–2058.

Mol, J. H., D. Resida, J. S. Ramlal & C. R. Becker, 2000. Effects of the El-Nino-related drought on freshwater and brackish-water fishes in Suriname, South America. Environmental Biology of Fishes 59: 429–440.

Moss, D., M. T. Furse, J. F. Wright & P. D. Armitage, 1987. The prediction of the macro-invertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshwater Biology 17: 41–52.

Murray Darling Basin Commission, 2004. Fish Theme Pilot Audit Technical Report – Sustainable Rivers Audit. MDBC Publication 06/04.

Newbury, R. W. & M. C. Gaboury, 1993. Stream Analysis and Fish Habitat Design: A Field Manual. Newbury Hydraulics Ltd, Gibson.

Norris, R. H., 1995. Biological monitoring: the dilemma of data analysis. Journal of the North American Benthological Society 14: 440–450.

Norris, R. H., I. Prosser, B. Young, P. Liston, N. Bauer, N. Davies, F. Dyer, S. Linke & M. Thoms, 2001. The assessment of River Conditions (ARC): an audit of the ecological condition of Australian rivers. http://www.nlwra.gov.au/.

Oberdorff, T., B. Hugueny & T. Vigeron, 2001a. Is assemblage variability related to environmental variability? An answer for riverine fish. Oikos 93: 419–428.

Oberdorff, T., D. Pont, B. Hugueny & D. Chessel, 2001b. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. Freshwater Biology 46: 399–415.

Paller, M. H., 2002. Temporal variability in fish assemblages from disturbed and undisturbed streams. Journal of Aquatic Ecosystem Stress and Recovery 9: 149–158.

Parsons, M. & R. H. Norris, 1996. The effects of habitat-specific sampling on biological assessment of water quality using a predictive model. Freshwater Biology 36: 419–434.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391–409.

Puckridge, J. T., K. F. Walker & J. F. Costelloe, 2000. Hydrological persistence and the ecology of dryland rivers. Regulated Rivers Research and Management 16: 385–402.

Puckridge, J. T., F. Sheldon, K. F. Walker & A. J. Boulton, 1998. Flow variability and the ecology of large rivers. Marine and Freshwater Research 49: 55–72.

Pusey, B. J., A. H. Arthington & M. G. Read, 1993. Spatial and temporal variation in fish assemblage structure in the Mary River, south-eastern Queensland: the influence of habitat structure. Environmental Biology of Fishes 37: 355–380.

Pusey, B. J., M. J. Kennard & A. H. Arthington, 2000. Discharge variability and the development of predictive models relating stream fish assemblage structure to habitat in north-eastern Australia. Ecology of Freshwater Fish 9: 30–50.

Pusey, B. J., M. J. Kennard & A. H. Arthington, 2004. Freshwater Fishes of North-Eastern Australia. CSIRO Publishing, Melbourne.

Pusey, B. J., M. J. Kennard, J. M. Arthur & A. H. Arthington, 1998. Quantitative sampling of stream fish assemblages: single- versus multiple pass electrofishing. Australian Journal of Ecology 23: 365–374.

Quinn, G. P. & M. J. Keough, 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Reece, P. F., T. B. Reynoldson, J. S. Richardson & D. M. Rosenberg, 2001. Implications of seasonal variation for biomonitoring with predictive models in the Fraser River catchment, British Colombia. Canadian Journal of Fisheries and Aquatic Sciences 58: 1411–1418.

Reynoldson, T. B., D. M. Rosenberg & V. H. Resh, 2001. Comparison of models predicting invertebrate assemblages for biomonitoring in the Fraser River catchment, British Colombia. Canadian Journal of Fisheries and Aquatic Sciences 58: 1395–1410.

Reynoldson, T. B., R. H. Norris, V. H. Resh, K. E. Day & D. M. Rosenberg, 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. Journal of the North American Benthological Society 16: 833–852.

Robinson, C. T., G. W. Minshall & T. V. Royer, 2000. Inter-annual patterns in macroinvertebrate communities of wilderness streams in Idaho, USA. Hydrobiologia 421: 187–198.

Roth, N. E., J. D. Allan & D. E. Erikson, 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141–156.

SAS Institute Inc., 1988. SAS/STAT User's Guide, Release 6.30 Edition. SAS Institute Inc, Cary, NC.

Scarsbrook, M. R., 2002. Persistence and stability of lotic macroinvertebrate communities in New Zealand. Freshwater Biology 47: 417–431.

Schlosser, I. J., 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. Environmental Management 14: 621–628.

Schlosser, I. J., 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704–712.

Schlosser, I. J., 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303: 71–81.

Schlosser, I. J. & P. L. Angermeier, 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17: 392–401.

Simon, T. P. (ed.), 1999. Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press New York.

Simon, T. P. (ed.), 2003. Biological Response Signatures: Indicator Patterns Using Aquatic Communities. CRC Press Boca Raton.

Simpson, J. & R. H. Norris, 2000. Biological assessment of water quality: development of AUSRIVAS models and outputs. In Wright J. F., D. W. Sutcliffe & M. T. Furse (eds), Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques. Freshwater Biological Association and Environment Agency, UK, 125–142.

Smith, M. J. & A. W. Storey (eds), 2001. Design and Implementation of Baseline Monitoring (DIBM3): Developing an Ecosystem Health Monitoring Program for Rivers and Streams in Southeast Queensland. Report to the South-East Queensland Regional Water Quality Management Strategy, Brisbane 416 pp.

Smith, M. J., W. R. Kay, D. H. D. Edwards, P. J. Papas, K. StJ. Richardson, J. C. Simpson, A. M Pinder, D. J. Cale, P. H. J. Horwitz, J. A. Davis, F. H. Yung, R. H. Norris & S. A. Halse, 1999. AusRivAS: using macroinvertebrates to assess ecological condition of rivers in Western Australia. Freshwater Biology 41: 269–282.

Statistical Sciences, 1999. S-PLUS, version 2000 for Windows. Mathsoft Inc, Seattle, WA.

Stauffer, J. C., R. M. Goldstein & R. M. Newman, 2000. Relationship of wooded riparian zones and runoff potential

to fish community composition in agricultural streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 307–316.

Tabachnik, B. G. & L. S. Fidell, 1989. Using Multivariate Statistics (2nd edn). Harper Collins Publishers, New York.

Taylor, C. M., M. R. Winston & W. J. Matthews, 1996. Temporal variation in tributary and mainstem fish assemblages in a Great Plains stream system. Copeia 1996: 280–289.

Townsend, C. R. & R. H. Riley, 1999. Assessment of river health: accounting for perturbation pathways in physical and ecological space. Freshwater Biology 41: 393–405.

Turak, E., L. K. Flack, R. H. Norris, J. Simpson & N. Waddell, 1999. Assessment of river condition at a large spatial scale using predictive models. Freshwater Biology 41: 283–298.

Unmack, P. J., 2001. Biogeography of Australian freshwater fishes. Journal of Biogeography 28: 1053–1089.

Williams, L. R., C. M. Taylor, M. L. Warren & J. A. Clingenpeel, 2003. Environmental variability, historical contingency, and the structure of regional fish and macroinvertebrate faunas in Ouachita Mountain stream systems. Environmental Biology of Fishes 67: 203–216.

Wright, J. F., 1995. Development and use of a system for predicting the macroinvertebrate fauna in flowing waters. Australian Journal of Ecology 20: 181–197.

Wright, J. F., D. Moss, P. D. Armitage & M. T. Furse, 1984. A preliminary classification of running water sites in Great Britain based on macroinvertebrate species and the prediction of community type using environmental data. Freshwater Biology 14: 221–256.

Zar, J. H., 1996. Biostatistical Analysis (3rd edn). Prentice-Hall International, Inc., New Jersey.