A Quantitative Basis for the Use of Fish as Indicators of River Health in Eastern Australia

A Quantitative Basis for the Use of Fish as Indicators of River Health in Eastern Australia

By

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Synopsis

In response to increasing community concern with declines in the ability of aquatic ecosystems to deliver critical goods, services and long-term benefits to human society, there is greater recognition of the need for quantitative procedures to assess aquatic ecosystem health and monitor biotic responses to remedial management. This thesis aims to evaluate the potential to incorporate attributes of freshwater fish assemblages into an ecosystem health monitoring program for wadeable rivers and streams in coastal catchments of south-eastern Queensland, Australia.

I identify five key requirements of a quantitative and defensible river health assessment program that need to be evaluated before indicators based on fish can be validly applied for river health assessment in the region. The five requirements are: 1) quantification of error associated with sampling fish; 2) assessment of natural ranges of spatial and temporal variation in fish assemblage attributes; 3) accurate definition of the reference condition expected for these attributes in the absence of human disturbance; 4) demonstrated relationships of the indicators with disturbance; and 5) evaluation of potentially important confounding environmental and biological factors. These are critical considerations for minimising the frequency of Type I errors (incorrectly classifying a site as impaired) and Type II errors (incorrectly classifying a site as unimpaired) and accurately assessing river health.

The ability to develop an efficient data sampling program without sacrificing accuracy and precision, and hence ability to detect changes through space and time, is a critical requirement of every river health assessment program. I demonstrated that accurate and precise reach-scale estimates of fish assemblage attributes, such as species richness, species composition and species relative abundances, could be obtained from multiple-pass electrofishing plus seine netting of three mesohabitat units and concluded that this was generally a more efficient sampling protocol than less intensive sampling over larger spatial scales. I demonstrated that relatively small differences (e.g. $< 20\%$) in these assemblage attributes could be detected with a high statistical power ($1-\beta > 0.95$) and that relatively few stream reaches (e.g. < 4) needed to be sampled to accurately estimate assemblage attributes within close proximity (e.g. 20% of the half width of the confidence interval) to the true population means.

Fish assemblage attributes that respond to anthropogenic disturbances but exhibit low natural temporal variability are potentially the most sensitive yet robust indicators of human impacts for use in bioassessment programs. I showed that some characteristics of fish assemblages (e.g. species richness, composition and to a lesser extent, species relative abundances) were generally highly stable through time, both seasonally and inter-annually. In contrast, fish assemblages occurring in streams with highly variable flow regimes were more variable. This variability appeared due to natural impacts associated with low flow disturbance. However, fish assemblages at these sites appeared resilient to these natural disturbances, provided that flow and habitat conditions resembled the pre-disturbance state.

A critical underpinning of bioassessment programs is the ability to accurately define attributes of the assemblage at a location that are expected in the absence of anthropogenic disturbance (i.e. defining the reference condition). I developed and validated a multivariate predictive model to define the reference condition for native fish species composition based on a large set of least-disturbed reference sites. I also compared four separate approaches to defining the reference condition for native species richness, a univariate biotic attribute underpinning many river health assessment programs.

I demonstrated in that spatial variation in these attributes of fish assemblages could be predicted using a small number of simple environmental variables, but that the accuracy of predictions varied with the method used. The multivariate 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. I showed that the predictive ability of the 'maximum species richness line' (MSRL), an approach commonly used for defining the reference condition for univariate attributes such as native species richness, is inherently compromised by the scoring procedure used and because it is limited to predicting variation in the dependent variable along a single environmental gradient (e.g. stream size). This resulted in substantially higher prediction error in comparison to three alternative regression methods, which incorporate single or multiple environmental variables as predictors. The MSRL approach led to an increased frequency of Type I errors for least-disturbed reference and

validation sites (i.e. incorrectly classing these sites as disturbed) and compromised the ability of the metric to accurately detect a disturbance 'signal' at the set of notionally disturbed test sites.

Assessment of the relationships of the fish indicators with human disturbance gradients indicated that streams affected by human activity due to catchment land use and associated local riparian, in-stream habitat and water quality degradation are more likely to be susceptible to invasion by alien fish species and display major differences in native fish assemblage composition and native species richness from that expected by comparison with similar reference areas minimally affected by human disturbances.

Provided that the key requirements of river health assessment identified in this thesis are satisfied, I conclude that indicators based on native fish assemblage composition, native species richness and alien fish species are potentially powerful indicators of human disturbance and can form the basis for a river health monitoring program in south-eastern Queensland and other similarly variable environments in Australia and elsewhere.

Declaration

I hereby declare that this work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the thesis itself.

Mark J. Kennard

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Chapter 1: General introduction

1.1. Background

1.1.1. Models of ecosystem structure and function

Growing concern about the globally pervasive impacts of human modifications to riverine landscapes (Benke 1990, Allan & Flecker 1993, Vitousek *et al.* 1997, Jackson *et al.* 2001, Malmqvist & Rundle 2002), has led to increasing recognition of the need for quantitative procedures for assessing aquatic ecosystem 'health' and monitoring biotic responses to remedial management. Natural functioning aquatic ecosystems have important intrinsic values and also provide many goods, services and long-term benefits to human society (Costanza *et al*. 1997, Baron *et al*. 2002), hence their protection, remediation and restoration is of critical importance.

Rivers and streams are influenced by the landscapes through which they flow (Hynes 1975, Vannote *et al.* 1980), a fundamental link recognised in many of the conceptual models describing the structure and functioning of natural river systems developed over the past 25 years or more. Early concepts such the River Continuum Concept (RCC, Vannote *et al.* 1980) and its corollaries, for example nutrient spiralling (Elwood *et al.* 1983) and the role of stream hydraulics (Statzner & Higler 1986), and subsequent developments including the Flood-Pulse Concept (Junk *et al.* 1989) and the Riverine Productivity Model (Thorp & Delong 1994), tend to emphasise linear (i.e. longitudinal and lateral) relationships between physical and biological processes in rivers. However, others have suggested that lotic systems should be viewed as being organised within a nested hierarchy, functioning at a variety of spatial and temporal scales (e.g. Frissell *et al.* 1986, Amorous *et al.* 1987, Pringle *et al.* 1988, Johnson *et al*. 1995, Fausch *et al.* 2002). The integration of hierarchical models with concepts of patch dynamics (White & Pickett 1985, Pringle *et al.* 1988, Townsend 1989) and the role of disturbance (Resh *et al.* 1988) has led to further insights into the relative importance of physical and biological processes and the role of natural spatial and temporal variation in driving aquatic ecosystem structure and function (Fig. 1.1).

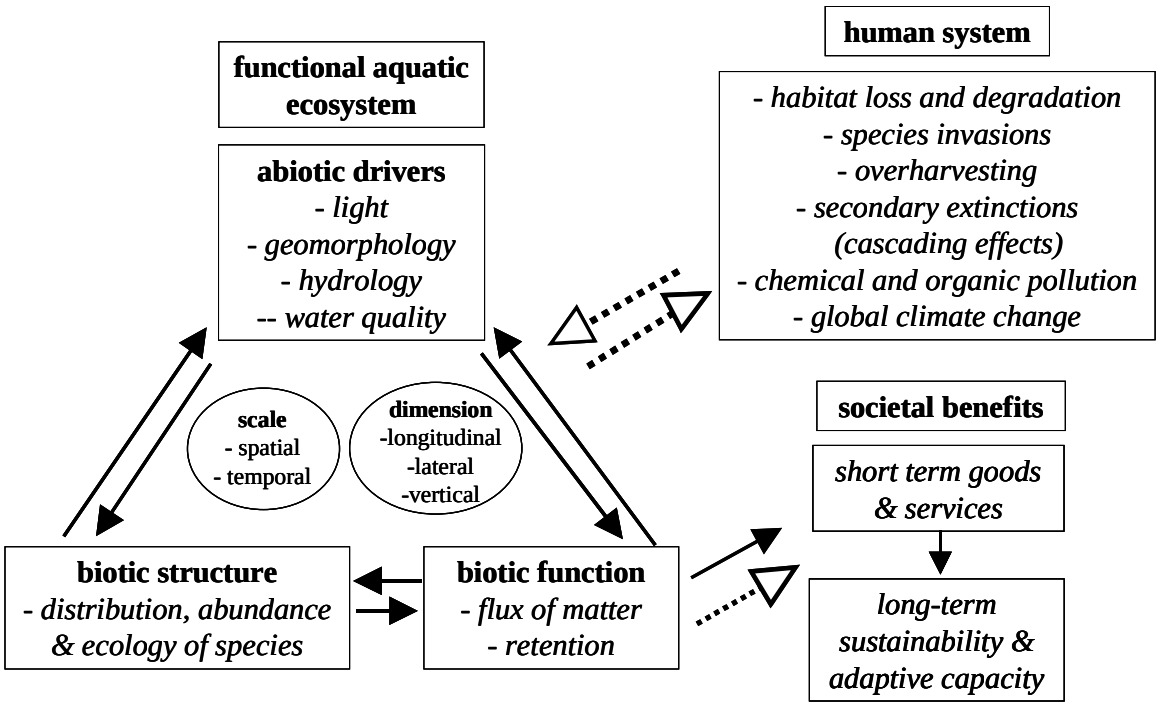

Figure 1.1. Simplified conceptual model of linkages between abiotic drivers and biotic responses in functional aquatic ecosystems that deliver goods, services and long-term benefits for human society (linkages shown with dark solid arrows). Human disturbances impact natural aquatic ecosystems and hence affect the societal benefits they provide (linkages shown with dashed open arrows). The nature and strength of these relationships is contingent on the spatial and temporal scale of examination. Figure modified from Lorenz *et al.* (1997) and Baron *et al.* (2002), using information sourced from Allan & Flecker (1993).

Of overriding importance are large scale physical factors such as geomorphology and climate which define higher levels of organisation of the physical (e.g. catchment boundaries, river morphologies, flow regimes and water quality) or biological (e.g. species pools and floral and faunal distributions) aspects of the river-floodplain ecosystem (i.e. the concept of landscape filters, Smith & Powell 1971, Poff 1997) (Fig. 1.1). These higher levels of organisation, in turn, contain lower levels of organisation (e.g. microhabitat attributes and biotic communities) and ecosystem function (e.g. flux and retention of organic matter) that may be determined by smaller scale processes (e.g. flow characteristics and species interactions) (Johnson *et al.* 1995). Undoubtedly, combinations of regional and local abiotic and biotic factors are responsible for structuring local ecosystem structure and function (e.g. Angermeier and Winston 1998) and impressions of their relative importance may be dependent upon the scale at which these mechanisms are examined (Jackson *et al.* 2001).

These concepts are potentially useful for understanding mechanistic pathways for the impacts of human disturbances on river ecosystems (Lorenz *et al*. 1997). Unfortunately however, many of the linkages in natural river ecosystems portrayed in Figure 1.1 are poorly understood, poorly validated, and remain largely descriptive hypotheses rather than predictive or quantitative models. Furthermore, except in broad terms, they do not provide predictions of the effects of human disturbances, or candidate physical, chemical and biological indicators that environmental managers can use to assess ecological health, or mechanisms by which management or rehabilitation of rivers may be effectively undertaken (Walker 1993, Johnson *et al.* 1995, Ward *et al*. 2001).

1.1.2. Human impacts on aquatic ecosystems

A range of human disturbances can function individually or interact to directly and/or indirectly affect functional aquatic ecosystems and hence the goods, services and long-term benefits they provide for human society (Allan (2004), Baron *et al.* (2004) and Figure 1.1). Soule (1991) described a "sinister sextet" of the major sources of global species loss in general, which Allan & Flecker (1993) adapted to identify six major threats to biodiversity in flowing river systems. These include:

1. Habitat loss and degradation caused by water infrastructure projects, land transformations and agriculture that cause modifications to hydrology, connectivity, riparian-aquatic linkages and in-stream habitat integrity;
2. Species invasions;
3. Overharvesting;
4. Secondary extinctions due to cascading effects;
5. Chemical and organic pollution; and
6. Global climate change.

Allan (2004) emphasised the importance of land use impacts associated with agriculture, extractive industries and urbanisation. He highlighted six primary sources of impact on aquatic structure and function: sedimentation; nutrient enrichment; contaminant pollution; hydrologic alteration; riparian clearing/canopy opening; and loss of large woody debris (Allan 2004). Evaluating the importance and mechanisms of impact on aquatic ecosystems is hampered by the current limitations in our understanding of relationships between natural environmental drivers and ecosystem

responses. Progress requires studies in regions with a representative suite of undisturbed rivers in which such relationships can be quantitatively examined and can serve as benchmarks for assessing human impacts (Ward *et al.* 2001, Chessman & Royal 2004). Unfortunately, such areas are becoming increasingly scarce. Another problem with detecting and diagnosing sources of impacts of human disturbance on aquatic ecosystems or defining the magnitude of the problem, has been historical imprecision and/or disagreement in what exactly is the demonstrable evidence of human impacts and what are the targets for a healthy ecosystem against which impacts are to be assessed.

1.1.3. Assessment of aquatic ecosystem 'health'

The status of aquatic ecosystems and their response to human impacts are commonly described using terms such as condition, biotic or ecological integrity, or health (Karr 1999, Norris & Thoms 1999, Allan 2004). Implicit in these concepts is the reference to some pre-defined state. The state may include the natural or inferred-natural condition prior to human impact, or a condition determined by community expectations, values and uses of the aquatic ecosystem (Norris & Thoms 1999). Perhaps as a consequence of this, there has been considerable debate among scientists and managers as to the meaning of terms such as condition, integrity and health, and their value in conveying to the community important principles about the impacts of human disturbances on aquatic ecosystems (Calow 1992, Suter 1993, Wicklum & Davies 1995, Westra 1996, Boulton 1999, Karr 1999, Norris & Thoms 1999). Frey (1977, p.128, cited in Norris & Hawkins 2000) defined biotic integrity as "the capability of supporting and maintaining a balanced, integrated, adaptive community or organisms having a composition and diversity comparable to the natural habitats of the region". Definitions of ecosystem health are based on parallels with human health and emphasise principles of ecosystem organisation, resilience and vigour, as well as the absence of signs of ecosystem stress (Rapport 1995, Rapport *et al.* 1998). The incorporation of a human dimension in which humans value rivers and the goods and services they provide for a range of needs and uses, and where unhealthy rivers satisfy only a subset of these, is critical (Karr 1996, Meyer 1997). Although many have argued that an analogy between human health and ecosystem health oversimplifies a complex issue (see Boulton 1999), incorporating principles of ecological integrity (maintaining ecosystem structure and function) and human values (what society values in the ecosystem) into the definition of river health

may provide impetus for advances in aquatic ecology, more effective and sustainable management of aquatic ecosystems, and broader acceptance of management goals and activities by the community (Karr 1996, 1999, Meyer 1997, Boulton 1999).

1.1.4. Indicators of ecosystem health

A range of methodologies based on the use of indicators of the physical, chemical, biological (structural) and functional (process) characteristics of ecosystems has been developed for assessment, diagnosis and prognosis of ecosystem health (Norris & Thoms 1999, Gergel *et al*. 2002, Niemi & McDonald 2004). The choice of physical, chemical or biological indicator depends largely on the reasons for undertaking the work or the type of anthropogenic impact to be assessed. A wide range of aquatic organisms has been used including algae, macrophytes, macroinvertebrates and fish (Norris and Norris 1995). More recently, indicators of ecosystem processes (e.g. benthic metabolism) have been used (e.g. Bunn 1995, Bunn *et al*. 1999, Bunn & Davies 2000). Indicators are useful tools because, ideally, they have an observable measurable quantity with significance beyond what is actually being measured (Lorenz *et al*. 1997). However, indicators are, by definition, suggestive of some unmeasurable condition and have been criticised on this basis (e.g. Suter 2001). Desirable qualities of river health indicators include accuracy, sensitivity, precision, rapidity, robustness, proven worth, cost effectiveness, simplicity and/or clarity of outputs. However, many of these features may be in mutual conflict (e.g. the robustness of an indicator *versus* its sensitivity) thus there must be some direct trade-off between these desirable characteristics (Fairweather 1999). Ultimately, indicators should be widely applicable, simple to interpret and easy to communicate (Fairweather 1999).

Cairns (1995) suggested that suitable indicators of aquatic ecosystem condition should: be based on ecological knowledge and conceptual models of ecosystems; incorporate elements of biological structure, composition and function; be useful in waters other than those in which they have been developed; be diagnostic, heuristic or both; and have sufficiently small sampling and annual variability to be responsive to marked differences or changes in habitat quality or disturbance levels.

Fish have been advocated as useful indicators of biotic integrity or river health (e.g. Fausch *et al*. 1990, Harris 1995, Paller *et al*. 1996, Simon 1999, Karr & Chu 1999) because:

1. they are almost ubiquitous components of aquatic ecosystems;
2. they are relatively long-lived and mobile and therefore reflect conditions over broad spatial and temporal scales;
3. local assemblages generally include a range of species representing a variety of trophic levels and therefore integrate effects from lower trophic levels;
4. fish are at the top of the aquatic food web and are consumed by humans, making them important for assessing contamination;
5. environmental and life history requirements are comparatively well understood; and
6. they are relatively easy to collect, identify and subsequently release unharmed.

However, freshwater fish present some potential problems as indicators (Berkman *et al.* 1986) because:

1. quantitative samples are difficult to obtain;
2. species distributions and abundances may vary between regions or drainages due to factors other than disturbance;
3. site by site differences may be difficult to interpret due to spatial and temporal variation in species composition and abundance;
4. fish are mobile and thus may avoid areas of stress; and
5. hypotheses concerning likely responses of indicators of fish assemblage structure and function to specific disturbance types are not well developed or explicitly stated.

The relative mobility of many fishes also highlights the potential for impacts occurring outside the scale of investigation to bias assessments at smaller spatial scales. The longevity of some species of fishes can also lead to circumstances where their absence may reflect impacts occurring several years to decades previously (Schlosser 1990). Also, because fish integrate effects from lower trophic levels, by the time effects are visible in fish communities, the ecological health of lower trophic levels may be irreparably damaged. In addition, because of their mobility, the presence of species

indicates suitable conditions (*viz*. water quality and habitat), whereas the absence of a particular species does not necessarily reflect the converse. Nevertheless, freshwater fishes are used widely as indicator organisms (Harris 1995, Simon 1999) and are the focus of this thesis.

1.1.5. Approaches to ecosystem health assessment using biota

A critical underpinning of ecosystem health indicators is the ability to accurately define the expected condition for those attributes upon which the indicators are based. This requires that natural spatial and temporal variation in the attributes, driven by variation in environmental conditions, can be accounted for to the extent that impacts of human-induced disturbance can be accurately assessed (Resh & Rosenberg 1989, Grossman *et al.* 1990). Most approaches to assessing ecosystem health using ecological indicators specifically incorporate the concept of reference to the natural state as a mechanism to assess whether a location is impacted or not (Norris 1995, Reynoldson *et al.* 1997). The attributes of the reference condition are usually derived from surveys of "undisturbed" or "least-disturbed" systems. Such surveys need to be extensive so as to incorporate spatial and temporal variation in the physical and biological characteristics of aquatic systems. The actual description of the characteristics of natural systems may also be problematic in landscapes that have already been substantially altered by anthropogenic activities and for which little historical information exists.

There are two principal methods for river health assessment using the reference condition concept: multivariate predictive models of biotic community composition (e.g. Wright 1995, Clarke *et al*. 1996, Simpson & Norris 2000, Oberdorff *et al*. 2001) and of summary attributes of community structure and function (e.g. Index of Biotic Integrity – IBI, Karr 1981, Karr *et al*. 1986). Multivariate predictive models of biotic structure 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. Predictive models are developed that enable site-specific predictions of biotic 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. An evaluation of the biological integrity of the site is obtained by comparing the expected fauna at a new site, with that observed. 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). The development of multivariate predictive models of fish assemblage composition and their utility in stream bioassessment programs in Australia has received little attention. However, fish-based predictive modelling methods have been demonstrated to provide a sensitive tool for biomonitoring river health in Europe (Oberdorff *et al*. 2001) and New Zealand (Joy & Death 2000, 2002, 2003).

The other common approach to bioassessment based on the reference condition concept has been to relate changes in summary attributes or 'metrics' that describe aspects of biotic assemblage structure and function to environmental stress. Summary metrics have been advocated as an effective means of encapsulating the complexity of natural communities sufficiently to assess the types and strengths of human impacts and to communicate results of studies to others (e.g. environmental managers) (Karr *et al*. 1986, Fausch *et al*. 1990, Karr & Chu 1999, Barbour *et al*. 1995, Simon 1999). Individual summary metrics based on species richness and composition, trophic composition and individual abundance and condition are usually combined into a 'multimetric' index (Barbour *et al*. 1995) for the assessment of aquatic systems. The multimetric approach was first developed for fish (the Index of Biotic Integrity - IBI, Karr 1981) has subsequently been adapted for macroinvertebrates and applied in a range of aquatic ecosystems throughout the world. Like multivariate predictive models, multimetric methods are referential in their approach, however the methods used for defining the expected conditions in the absence of human disturbance differs markedly in that they do not generally employ multivariate statistical models for this purpose. Indeed, it is this conceptual simplicity in defining the reference condition that is commonly regarded as one of the method's strengths (Karr & Chu 1999). Harris (1995) suggested that multimetric methods such as the IBI are potentially applicable to stream health assessment in Australia and, to this end, the IBI has been tested and applied in several rivers of southern Australia (Harris & Silveira 1999, Murray Darling Basin Commission 2004).

There has been extensive debate on the respective merits of the predictive modelling and multimetric approaches (e.g. Suter 1993, Norris 1995, Reynoldson *et al*. 1997, Karr 1999, Karr & Chu 1999, Norris & Thoms, 1999, Karr & Chu 2000, Norris & Hawkins 2000). Much of this difference of opinion appears to have arisen from fundamental differences in philosophical approaches to river health assessment and perhaps also due to misconceptions and misrepresentations of what the two approaches aim to achieve and how they differ (see Norris & Hawkins 2000).

The central goal of bioassessment is to decide whether a site exposed to anthropogenic stress is impaired while minimising Type I errors (incorrectly classifying a site as impaired) and Type II errors (incorrectly classifying a site as unimpaired) (Bailey *et al*. 1998, Linke *et al*. 1999). Irrespective of the approach used, both multivariate and multimetric methods have several key requirements that should be satisfied before they can be applied validly and quantitatively for river health assessment in a given river or region, while simultaneously minimising Type I and Type II errors. These requirements include (but are not limited to):

1. the ability to collect raw biological data in a standardised fashion and with sufficient accuracy and precision such that it truly represents the locality in question and is directly comparable with other locations;
2. assessment of the natural ranges in spatial and temporal variation of the biological attributes in question and the drivers of this variation;
3. the ability to accurately define the reference condition for biological attributes expected in the absence of anthropogenic stress based on relationships between natural environmental drivers and biotic patterns, such that human disturbance-induced changes can be quantified using biological indicators;
4. the sensitivity and demonstrated ability of the chosen indictors to reflect/respond to human disturbance (irrespective of the methods used to define their expected state in the absence of human stress); and
5. the relative importance of potentially confounding environmental and biological factors in interpreting spatial and temporal variation in biological attributes, such that the accuracy and sensitivity of the indicators to human disturbances can be assessed.

Satisfying these requirements can provide a quantitative basis for the use of fish as indicators of river health that is not only rigorous and scientifically defensible, but more importantly, is crucial to justify management interventions and acceptance by the community.

1.2. Aims and structure of thesis

This thesis aims to evaluate the assumptions and requirements listed above to assess whether referential approaches to bioassessment using fish can be incorporated into an ecosystem health monitoring program for wadeable rivers and streams in coastal catchments of south-eastern Queensland, Australia. There are substantial challenges to developing such a program in this region including: the relatively high environmental variability in river flow regimes; substantial and diverse existing human disturbances; low diversity and (arguably) an ecologically generalist fish fauna in comparison to elsewhere (Harris 1995); a lack of understanding of the expected responses of individual fish species to the common human impacts; and a lack of established or rigorously validated protocols for using fish as indicators of river health in south-eastern Queensland, or Australia in general. I will argue that these challenges are not insurmountable and that once the assumptions and requirements of bioassessment programs are satisfied, bioassessment methods based on fish are applicable to south-eastern Queensland and elsewhere.

The thesis is structured as follows: Chapter 2 describes the location of the study region in south-eastern Queensland and presents a brief summary of the climate, hydrology, land use and human impacts, and data sets used in the thesis. The methodology used for sampling of fish and habitat characteristics is described in Chapter 3. In this chapter, I use a set of least-disturbed sites to compare the accuracy, precision and efficiency of two fish sampling methods (single pass electrofishing or multiple pass electrofishing plus seine netting) to estimate stream fish assemblage attributes at two spatial scales (within discrete mesohabitat units and within stream reaches consisting of multiple mesohabitat units). I examine the extent to which the efficiency of each sampling method may be influenced by interspecific variation in fish behaviour and habitat use, and spatial variation in environmental conditions. My ultimate goal is to evaluate how changes in sampling effort (within and among mesohabitat units) influence the

accuracy, precision and efficiency of fish assemblage estimates, depending on the fish sampling method employed.

Chapter 4 examines the influence of natural hydrologic disturbances (due to extreme high and low flow events) on the stability, persistence and resilience of stream fishes at least-disturbed sites in the study area. Conclusions about the magnitude and drivers of temporal variation in biotic assemblages are dependent on many factors including the manner in which assemblage variation is described, the role of rare species and sampling error, and the potentially confounding relationships of environmental variability gradients with other natural environmental and biological gradients. In this chapter, and also in Chapter 5, I specifically address the implications of natural environmental and biological variability for river health assessment, particularly with respect to the ability to accurately and precisely define the reference condition, such that human disturbance signals can be detected.

In Chapter 5, I construct a multivariate predictive model of native fish assemblage composition based on relationships with a small number of catchment scale and local scale environmental features. I address the question of whether accurate and precise multivariate predictive models can be constructed in a region with highly variable and unpredictable flow regimes. The model is constructed using a set of least-disturbed reference sites sampled on one occasion during one season. I evaluate the effect of low species richness on model performance and validate the predictive capacity of the model using two further sets of temporally sampled data from reference sites in two rivers. Here, I address an assumption common to many bioassessment programs of whether the reference communities from which predictions are derived are stable through time, and therefore whether valid comparisons can be made with test sites often sampled years afterwards (Barmuta *et al*. 2003). In this chapter, I also describe the application of the model to evaluate the sensitivity of fish assemblage composition and individual species as indicators of human disturbance at a set of independent test sites sampled along known gradients of human disturbance brought about by land use pressures. I use a set of independent measures of anthropogenic disturbance to describe this gradient of human impact and describe the methodology for doing so.

In Chapter 6, I critically evaluate some of the assumptions underlying the approach for defining the reference condition for summary biotic metrics commonly used in the

Index of Biotic Integrity (Karr & Chu 1999). I examine whether stratification by a single environmental descriptor (e.g. catchment area) and the use of a scoring system based on deviations from a maximum expected condition, is appropriate for defining the reference condition for a fish assemblage metric (native species richness). Native species richness is a commonly used measure of the general ecological condition of aquatic ecosystems and several species richness metrics are important components of the IBI, generally (but not always) being expected to decline with increasing environmental stress (Harris 1995, Oberdorff *et al*. 2001, 2002). I compare the predictive accuracy of the IBI approach with three regression-based methods that use a range of local and landscape variables as predictors of species richness. I develop and validate predictive models based on a set of least-disturbed reference sites and use the models to predict species richness at a set of test sites impacted to varying degrees by human disturbance. I also compare the frequency of classification errors from each method against set biocriteria and evaluate the ability of metrics derived from each method to accurately reflect the human disturbance gradient at the test sites.

Chapter 7 describes an evaluation of another commonly used indictor of river health, namely the presence and abundance of alien fish (i.e. those species introduced from other countries). The ability of many introduced fish species to thrive in degraded aquatic habitats, and their potential to impact on aquatic ecosystem structure and function, suggest that they may represent both a symptom and a cause of declines in river health and the integrity of native aquatic communities. The varying sensitivities of many commonly introduced fish species to degraded stream conditions, the mechanism and reason for their introduction and the differential susceptibility of local stream habitats to invasion due to the environmental and biological characteristics of the receiving water body, are all confounding factors that may obscure the interpretation of patterns of introduced fish species distribution and abundance and therefore their reliability as indicators of river health. In this chapter, I examine relationships of alien fish species distributions and indices of abundance and biomass with the natural environmental features, the biotic characteristics of the local native fish assemblages and indicators of anthropogenic disturbance at a large number of sites subject to varying sources and intensities of human impact.

Chapter 8 summarises the major findings of the thesis, highlights the implications of this research for the development of a river health monitoring program using fish in

south-eastern Queensland, Australia, and identifies areas of future research that would further strengthen such a monitoring program.

Chapter 2: Study area

2.1. Location

The study area was confined to coastal catchments of south-eastern Queensland, Australia (Fig. 2.1), an area identified as constituting a single biogeographic province based on freshwater fish distributions (Unmack 2001, Pusey *et al.* 2004). Detailed descriptions of the region and the characteristics of the study rivers are given in Pusey *et al*. (1993, 1998a, 2004) and Mackay *et al.* (2003). Prior to European settlement, the region was dominated by wet and dry sclerophyll forests with substantial areas of sub-tropical rainforest and coastal 'wallum' *(Banksia* heathlands).

Rivers and streams in the region generally have well-defined riffle-run-pool sequences in the mid- to upper reaches of the catchments. Lowland main-channel areas are characterised by long, deep, and slow-flowing reaches with sandy substrates that are interspersed with bedrock controls and large riffles. In rivers and streams least affected by human activity, water clarity is usually high (for more details on the physicochemical characteristics of the study sites, refer to Chapters 3 and 5).

2.2. Climate and hydrology

The climate of the south-eastern Queensland region is transitional between subtropical and temperate (Bridgewater 1987). Patterns of temperature, typified by that recorded at Gympie in the Mary River basin, and Beaudesert in the Logan-Albert River basin, are strongly seasonal (Pusey *et al.* 2004). Mean monthly thermal maxima and mean monthly minima vary by about 10^{o}C and 15^{o}C, respectively, throughout the year (Fig. 2.2). The pattern of rainfall is strongly influenced by the summer monsoon but also frequently by the northward extension of temperate weather systems (Pusey et al. 1993, 2004).

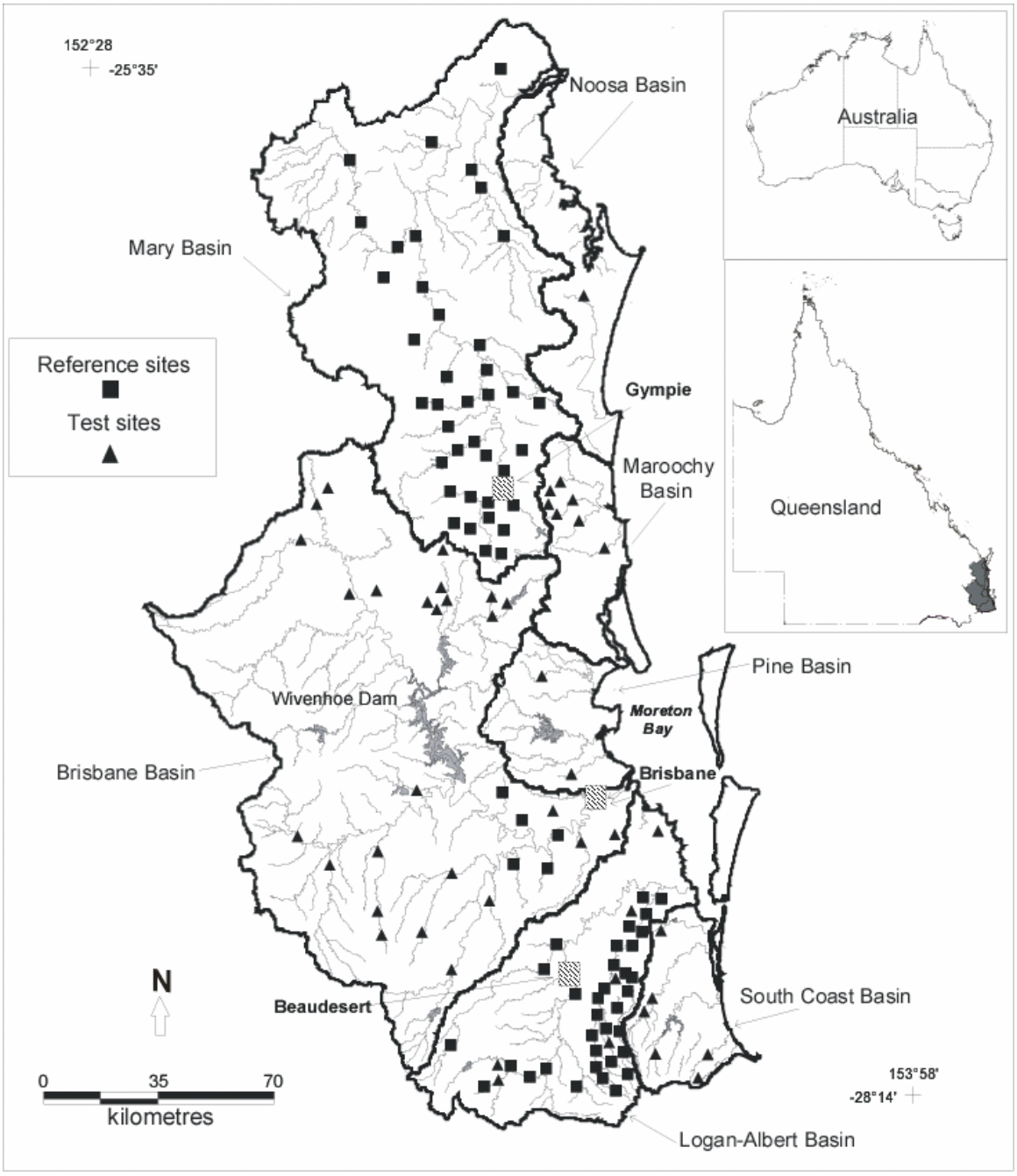

Figure 2.1. Map of study area showing location of reference sites and test sites in river basins of south-eastern Queensland (Note: some sites located close together overlay each other and hence may not be visible on map). Major impoundments and place names mentioned in the text are also depicted. The insets show the location of the study area in Queensland, Australia.

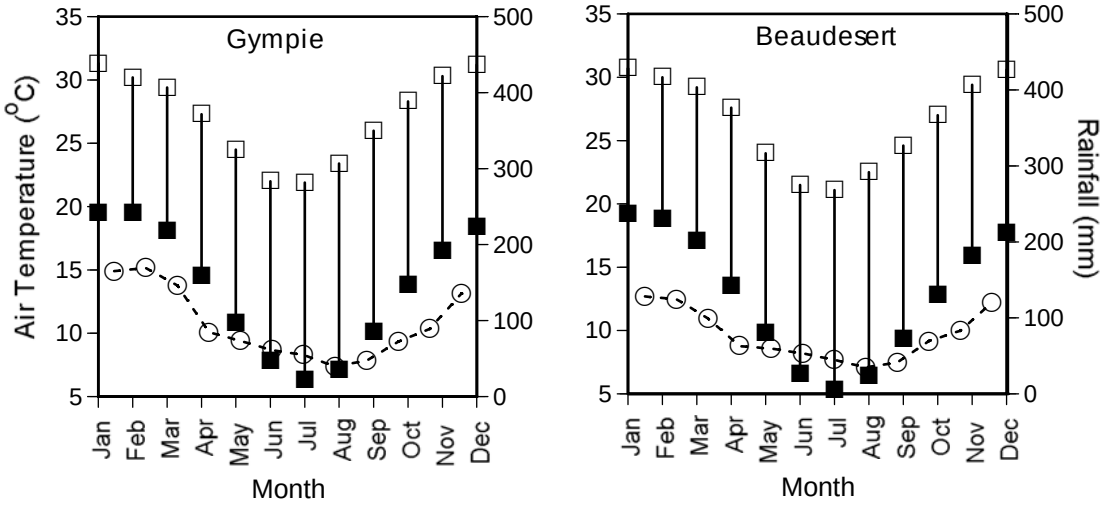

Figure 2.2. Plots of mean daily minimum temperature (closed squares), mean daily maximum temperature (open squares) and mean monthly rainfall (open circles) for each month at Gympie (central Mary River basin) and Beaudesert (central Logan-Albert River basin), south-eastern Queensland. Data record length was >80 years for both locations. Data source: Queensland Bureau of Meteorology, figure modified from Pusey *et al.* (2004).

The majority of rainfall and streamflow in the region occurs in the Austral summer and early autumn months of January to March, often followed by a second minor discharge peak in autumn and early winter (between April and June) (Figs. 2.2, 2.3). The incidence and magnitude of these secondary peaks in flow is quite unpredictable, as are summer wet season flows, and thus rivers of this region tend to show high annual CV values (100% or greater) (Pusey *et al.* 2000). River discharge is highly variable, both intra- and inter-annually in comparison to other regions of eastern Australia and elsewhere (see Pusey *et al.* 1993, 2000, 2004). Discharge variability is highest during the summer months (mean coefficients of variation of daily discharge for each month usually greater than 120%, Chapter 4) and flows during mid-winter and spring are usually low and stable (Fig. 2.3, Chapter 4). High flows (floods) can occur at any of year but are most common during summer and autumn (January to April). Extended periods of low flows can also occur at any time of year, but are most common during spring and summer (September to December). Many tributary streams in the region may cease to flow for extended periods, during which time longitudinal connectivity is lost as streams often recede to a series of isolated pools interspersed by extensive areas of dry stream bed (Pusey *et al.* 1993, 2000, 2004, Chapter 4). A full description of the long-term flow regime for two of the study rivers in south-eastern Queensland, and the hydrological characteristics during the study period, is given in Chapter 4.

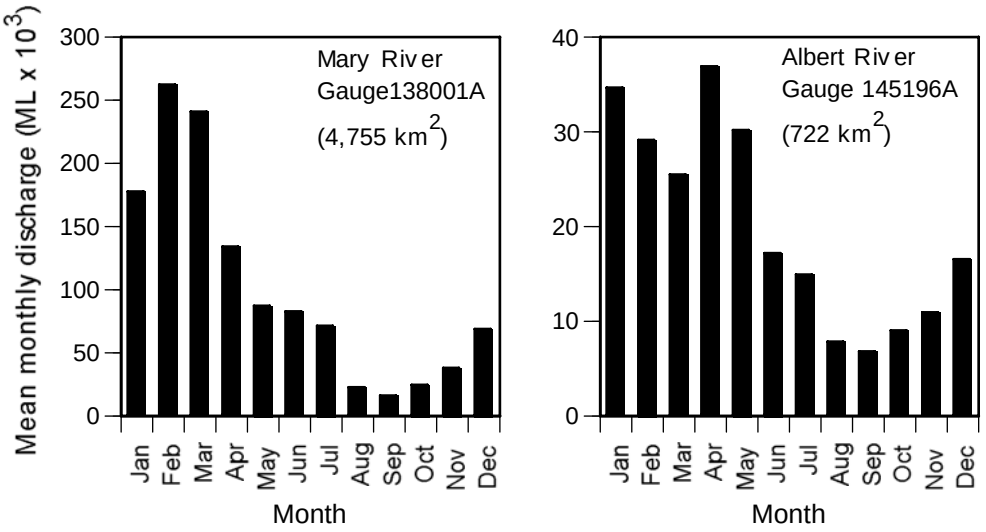

Figure 2.3. Variation in mean total monthly discharge for gauging stations in the lower Mary River and lower Albert River, south-eastern Queensland. The catchment area (km^2) upstream of each gauging station is given in parentheses. Data record length was >20 years for each gauge. Data source: Queensland Department of Natural Resources and Mines, figure modified from Pusey *et al.* (2004).

2.3. Land use and human impacts

Human land use practices associated with extensive land clearing, cattle grazing, agricultural cropping and large urban and industrial development, have led to substantial degradation of local riparian, in-stream habitat and water quality conditions in many streams and rivers of the south-eastern Queensland region (Smith & Storey, 2001, Chapter 5). In addition, the Brisbane River, the largest river basin in the region, is regulated by a large dam and some of the smaller streams and rivers contain barriers to fish movements caused by smaller dams and weirs (Kennard *et al*. 2000, Kennard 2004, Kennard 2005). The Mary and Logan-Albert River catchments, the focus of much of the work presented in this thesis, still retain large areas that are minimally disturbed by human activity and both rivers are largely unregulated. However, several impoundments (small dams and weirs) exist on some tributary streams and water extraction occurs for irrigation, stock, domestic and urban water supply purposes (Pusey et al. 1993; Brizga et al. 2004; Brizga 2005). Further details on the land use impacts in the south-eastern Queensland study region are presented in Chapters 5, 6 and 7.

2.4. Data sets

A data set comprising fish and habitat samples at 82 reference sites (least-affected by human activity) was used to evaluate sampling protocols (Chapter 3), examine temporal variability of fish assemblages (Chapter 4) and develop predictive models (Chapters 5 and 6). The majority of reference sites were located in the Mary, and Albert Rivers, with smaller numbers of sites situated in the Brisbane and Logan Rivers (Fig. 2.1). 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. Sampling during each season was usually restricted to a six week temporal 'window'. I avoided sampling immediately after high flow events and on occasions when high flows occurred during the sampling window, I waited at least two weeks until flows had subsided and fish sampling could be conducted efficiently. I undertook all fish and habitat sampling as part of several research projects while employed at Griffith University. All field sampling was undertaken with the help of one or two field assistants.

Reference sites in each river were selected to represent the best condition available, whilst simultaneously ensuring that such sites were arrayed sufficiently widely throughout each catchment to encompass as much of the natural biological and environmental variation as possible (Fig. 2.1). I considered these sites to be minimally disturbed using criteria proposed by Hughes (1995) (e.g. undisturbed riparian vegetation, bank and channel structure in natural condition, natural hydrograph). Site selection was constrained by sampling methodology (backpack electrofishing, Chapter 4) 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).

Forty-eight test sites from six river basins in south-eastern Queensland (Fig. 2.1) were selected to test the predictive models and to examine whether differences in observed *versus* predicted fish assemblage attributes (Chapters 5 and 6) and the presence and abundance of alien fish species (Chapter 7) were related to known gradients in human

disturbance. The major sources of human impacts at these sites resulted from catchment land use (mostly catchment clearing, cropping, grazing and urbanisation) and associated local riparian, in-stream habitat and water quality degradation. Test sites ranged from minimally disturbed to highly impacted (see Chapters 5, 6 and 7 for further description). Test sites were sampled once between September and October 2000. Three of the original reference sites in the Mary River and two sites in the Albert River were also sampled again during September 2000 to examine the temporal concordance of fish assemblages between the reference site (1994 – 1997) and test site (2000) sampling periods (Chapter 5).

The spatial scale of sampling is described in detail in Chapter 3, as are methods used for sampling fish and habitat. Methods used to characterise the disturbance gradient at test sites, including a set of independent measures of human disturbance, are described in Chapter 5.

Chapter 3: Estimating local stream fish assemblage attributes: sampling effort and efficiency at two spatial scales

3.1. Synopsis

Optimal sampling designs for environmental monitoring and assessment programs are those that simultaneously maximise accuracy, precision and sensitivity, and minimise resource use. In this chapter I compare the accuracy, precision and relative efficiency of single pass electrofishing and multiple pass electrofishing plus seine netting at two spatial scales (within discrete mesohabitat units and within stream reaches consisting of multiple mesohabitat units). My results demonstrate that multiple-pass back-pack electrofishing plus supplementary seine netting provide more accurate and precise estimates of fish species richness, assemblage composition and species relative abundances in comparison to single-pass electrofishing alone, and that intensive sampling of three mesohabitat units (equivalent to a riffle-run-pool sequence) is a more efficient sampling strategy to estimate reach-scale assemblage attributes than less intensive sampling over larger spatial scales. This sampling protocol was sufficiently sensitive that relatively small differences in assemblage attributes (e.g. < 20%) could be detected with a high statistical power ($1-\beta > 0.95$) and that relatively few stream reaches (e.g. < 4) need be sampled to accurately estimate assemblage attributes within close proximity to the true population means. I conclude that the intensive sampling strategy described here is suitable for monitoring programs that aim to detect spatial and temporal variation in reach-scale fish assemblage attributes that underpin indicators of river health, or to monitor the ecological outcomes of stream rehabilitation projects.

This Chapter forms the basis of the following journal manuscript:

Kennard, M.J., Pusey, B.J., Harch, B.H., Dore, E. & Arthington, A.H. (In review). Estimating local stream fish assemblage attributes: sampling effort and efficiency at two spatial scales. *Marine and Freshwater Research*.

3.2. Introduction

Accurately estimating biotic assemblage attributes such as species richness, species composition and species relative abundances is a fundamental requirement of environmental monitoring and assessment programs. The precision of these estimates influences the ability to detect meaningful differences in assemblage attributes through time and space. Maximising accuracy and precision is frequently constrained by sampling effort, which in turn is often limited by available funds and resources. The minimum sampling effort required is that which provides the necessary information to achieve the goal of a sampling program, and depends on such factors as the species and attributes of interest, the required accuracy and precision, and the efficiency of the sampling protocol (Sheldon 1984a, Andrew & Mapstone 1987, Bohlin *et al*. 1989, Norris *et al.* 1992, Maher *et al*. 1994, Angermeier & Smogor 1995). Ultimately, the best sampling program is one that simultaneously maximises accuracy, precision and sensitivity, and minimises resource use. The increasing focus on the management of Australian inland waters to sustain human needs as well as simultaneous maintenance of natural biodiversity and ecosystem processes requires that programs designed to monitor or assess ecosystem health are appropriate to the task. Freshwater fish are frequently advocated as appropriate target organisms in such programs, yet little information exists on the effort required to quantify relevant attributes of fish assemblages in the context of such programs.

Pusey *et al.* (1998a) evaluated the accuracy of single- versus multiple-pass electrofishing plus seine netting in two eastern Queensland river basins. They concluded that multiple-pass electrofishing and supplementary seine netting yielded significantly more accurate estimates of fish species richness, abundance, species composition and assemblage structure within single mesohabitat units (i.e. riffles, runs or pools) than a single electrofishing pass. This study was concerned with sampling effort at small spatial scales and did not directly examine the relative accuracy and precision of single-pass electrofishing and multiple pass electrofishing over larger spatial scales (i.e. multiple mesohabitat units within a stream reach). Furthermore, Pusey *et al*. (1998a) did not fully examine the biological and environmental factors potentially influencing sampling efficiency at these spatial scales.

Fish sampling strategies for bioassessment programs are typically undertaken at the reach scale to encompass the presumed home ranges of the major species and thus maximise estimates of local fish species richness. Failure to detect species during sampling has the potential to bias bioassessments and could result in considerable deviations in expected and observed assemblages and a low sensitivity to detect meaningful changes in space or time (Maher *et al.* 1994, Growns *et al.* 1996, Paller *et al.* 1996, Chapters 5 and 6). This may be particularly important for Australian streams, where local fish species diversity may often be comparatively low (Harris 1995, Harris and Silveira 1999). Sampling relatively short sections of stream using intensive sampling may be insufficient to estimate reach-scale assemblage attributes, because insufficient micro- and mesohabitat configurations that support different species and varying numbers of individuals may be encountered. Bioassessment programs or biodiversity surveys have frequently used low intensity sampling (e.g. using single pass electrofishing) over comparatively longer stream reaches to ensure larger numbers of habitat configurations (and presumably the species they support) are sampled (Lyons, 1992, Pusey & Kennard 1996, Harris & Gehrke 1997, Gehrke *et al*. 1999, Mitro & Zale 2000, Gehrke & Harris 2001, Murray-Darling Basin Commission 2004). Increasing sampling intensity within a stream reach (e.g. by increasing the number of electrofishing passes or using multiple sampling methods) should increase the accuracy and precision of estimates of assemblage attributes without increasing the number of replicates (number of mesohabitat units), but it is not clear that the increased statistical power to detect a hypothesised effect is worth the additional time (and cost) required to undertake more intensive sampling (Andrew & Mapstone 1987, Paller 1995a, b).

Accurate and precise estimation of fish assemblage attributes can be influenced by a range of biological, environmental and technical factors (Regis *et al*. 1981, Bohlin *et al*. 1989, Zalewski & Cowx 1989). Species (and individuals of different sizes) vary in their susceptibility to being captured by electrofishing. Variation in galvanotaxic and galvanonarcotic responses of fish are widely documented and have been attributed to such factors as variation in physiology, size, behaviour and microhabitat use (Larimore 1961, Boccardy & Cooper 1963, Mahon 1980, Mahon & Balon 1980, Balayev 1981, Wiley & Tsau 1983, Koehn & McKenzie 1985, Onorato *et al*. 1998). Electrofishing efficiency can also vary with factors such as water conductivity (Hill & Willis 1994, Pusey *et al.* 1998a), temperature (Regis *et al*. 1981), stream width (Kennedy & Strange 1981, Meador *et al*. 2003a), stream depth (Paller 1995a), habitat structure (Peterson *et*

al. 2004) and disturbance and fright bias (Temple *et al*. 1998). These issues may have major implications for the optimum design of sampling programs that aim to provide accurate, precise yet efficient estimates of fish assemblage attributes. For example, a possible consequence of interspecific variation in capture efficiency is that a single electrofishing pass will overestimate the abundance of those species most susceptible to electrofishing or that are present in the highest abundances, and possibly fail to detect or underestimate the abundance of some hard to catch or uncommon species, irrespective of the length of stream (and number of habitat configurations) sampled.

In this chapter I compare the accuracy, precision and efficiency of two fish sampling methods (single pass electrofishing or multiple pass electrofishing plus seine netting) to estimate stream fish assemblage attributes at two spatial scales (within discrete mesohabitat units and within stream reaches consisting of multiple mesohabitat units). I examine the extent to which the efficiency of each sampling method was influenced by interspecific variation in fish behaviour and habitat use, and spatial variation in environmental conditions. My ultimate goal is to evaluate how changes in sampling effort (within and among mesohabitat units) influence the accuracy, precision and hence efficiency of fish assemblage estimates, depending on the fish sampling method employed.

3.3. Methods

3.3.1. Study area and sampling sites

The data used in this chapter was confined to sites sampled in the Mary River and Albert River (Fig. 3.1). The Mary and Albert River basins drain to the eastern coast of Australia, are bounded to the west by extensions of the Great Dividing Range and are comparatively small in size (9,400 km^2 and 1,195 km^2, respectively). Streams in the Mary and Albert River basins generally have well-defined riffle-run-pool sequences and stream reaches selected for sampling were arrayed widely throughout each catchment (Fig. 3.1). Reaches chosen for study were least affected by human activity, and riparian and in-stream habitat was generally minimally disturbed.

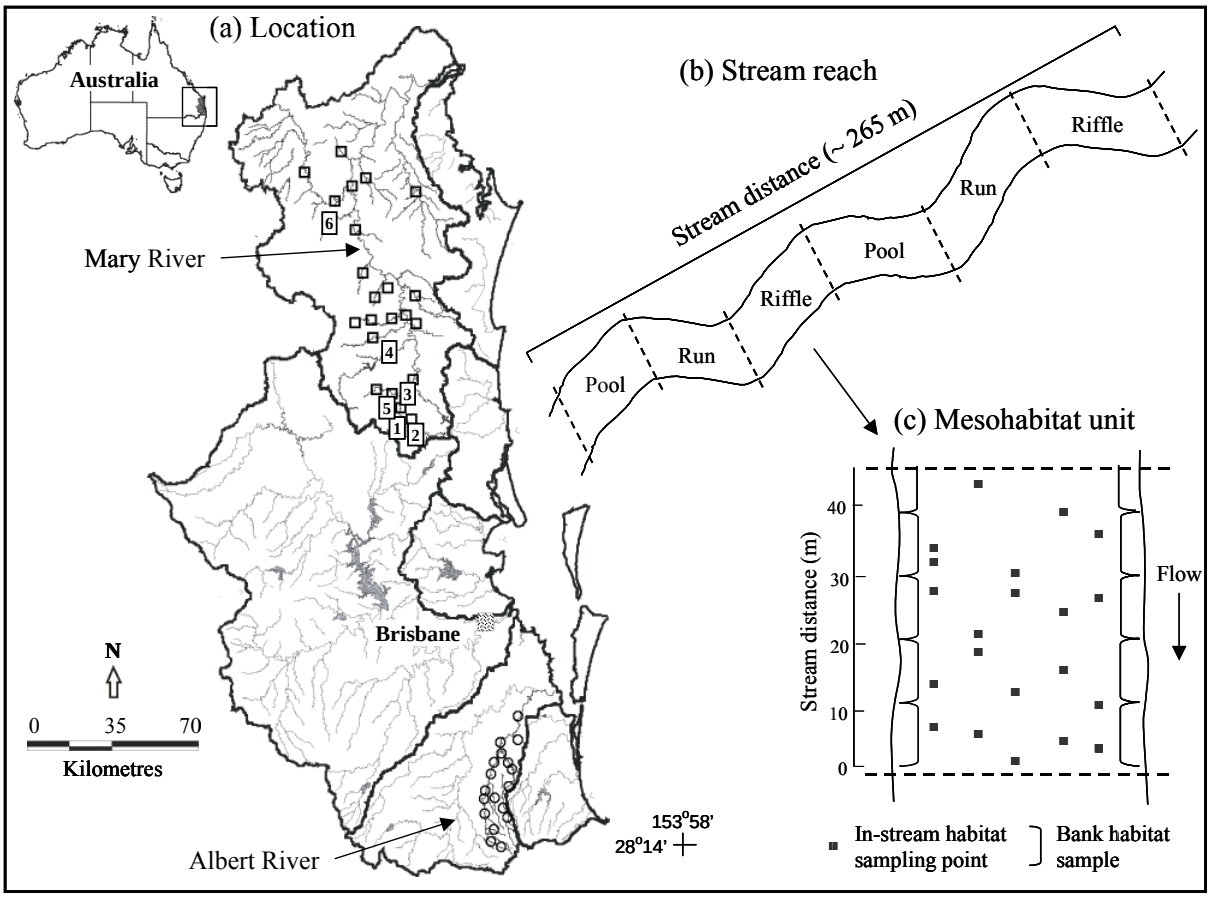

Figure 3.1. Spatial scale of sampling in the Mary River and Albert River in south-eastern Queensland, Australia. (a) Location of stream reaches where sampling of mesohabitat units was undertaken. (b) The subset of stream reaches where extended sampling of multiple (six) mesohabitat units was undertaken in the Mary River is depicted in (a) by numbered squares. (c) Sampling points within each mesohabitat unit where measurements of in-stream and bank habitat were taken.

I evaluated fish sampling effort and efficiency *within individual mesohabitat units* (i.e. riffles, runs and pools) using data collected from 72 mesohabitat samples in the Mary and Albert River basins. Between one and three mesohabitats were sampled at each of 46 locations situated on third to seventh order streams and rivers (as estimated from 1:100,000 topographic maps) in these river basins. Mesohabitats were sampled once between June and August 1995. I chose the winter sampling period when hydrological conditions were characterised by low and relatively stable flows (Pusey *et al*. 1993, 2000, 2004), but there was sufficient flow to allow fish unrestricted longitudinal movement among mesohabitats and river reaches. Mesohabitats sampled in each river were generally similar in size and encompassed the same range of in-stream habitat conditions. On average, mesohabitats were 38.0 m long and 9.4 m wide (equivalent to 4.0 mean stream widths, hereafter MSW), 312 m^2 in area and 0.38 m deep (Table 3.1).

Water clarity and water conductivity were usually high in both rivers (mean turbidity 3.5 NTU, mean conductivity 393 $\mu s.cm^{-1}$).

Table 3.1. Summary (means, standard deviations and ranges) of physical characteristics and water quality parameters in mesohabitats sampled in the Mary and Albert Rivers (n = 72 samples).

	Mean (± SD)	Range
Physical characteristics		
Site length (m)	38.0 ± 11.9	16.0 – 65.0
Wetted width (m)	9.4 ± 7.6	1.9 – 40.0
Mean depth (m)	0.38 ± 0.21	0.11 – 0.89
Site area (m^2) (site length * mean wetted width)	312.7 ± 223.0	46.4 – 1215.0
Site volume (m^3) (site area * mean depth)	144.6 ± 166.0	9.0 – 891.9
Mean velocity ($m.sec^{-1}$)	0.15 ± 0.17	0 – 0.74
Water quality		
Turbidity (NTU)	3.5 ± 3.6	0.9 – 29.0
Conductivity ($\mu S.cm^{-1}$)	392.7 ± 308.5	50.4 – 1153.2
Temperature (^oC)	16.7 ± 3.2	8.4 – 22.3

I evaluated fish sampling effort and efficiency *within stream reaches* (i.e. over multiple mesohabitat units) at a subset of six stream reaches located in the mid and upper portions of the Mary River catchment (situated on third to sixth order streams, Fig. 3.1). These sites were sampled in January and February of 2003. Within each of the six stream reaches, I sampled a series of six contiguous mesohabitat units, 44.5 m long, 8.7 m wide and 5.1 MSW on average. This equated to total stream reach lengths of about 265 m or 30 MSW on average. Hereafter, I refer to reach length in terms of number of mesohabitat units and number of mean stream widths (MSW) as this allows comparison between different stream reaches and with studies undertaken elsewhere.

3.3.2. Fish sampling procedures

Fish assemblages at each site were intensively sampled using the procedures detailed in Pusey *et al*. (1998a) and are similar to those used by other researchers (e.g. Martin-Smith 1998, Erős and Grossman 2005). Sampling was conducted using a back-pack DC electrofishing unit (Smith-Root Mk 12 POW) with a standard Smith-Root anode (25 cm diameter ring attached to a 2 m pole) and cathode (3.2 m wire cable). The electrofisher was typically operated at 300-400 V, 70 Hz frequency and 4 ms pulse width as this output was the most effective for collecting a wide range of fish species within different habitat types in south-eastern Queensland rivers and streams. A small net (9 mm stretched mesh) was attached to the anode ring as this markedly improved fish capture

efficiency (particularly within undercut banks), whilst also minimising the duration of electroshocking required to collect fish (M. J. Kennard, personal observation). I was particularly judicious in the use of the electrofisher as I was concerned with the potential for electrofishing-induced injuries to fish resulting from extended or repeated exposure to the electric current, and so attempted to collect fish immediately at, or below, their immobilization threshold (Holliman & Reynolds 2003).

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 operator and one or two dip-netters then commenced electrofishing from the downstream end of the site and, using short, intermittent pulses, moved upstream in a zig-zag fashion, attempting to ensure that all of the enclosed area was electrofished once. Most fish species (excluding anguillid eels) collected in this study rarely displayed galvanotaxic responses to electroshocking (i.e. fish usually did not swim, or could not be drawn, towards the anode ring) but rather became immobilised on the stream bottom or swam erratically and so required vigorous and rapid sweepings of the anode pole net and the assistance of dip-netters. Upon capture, fish were identified to species level, counted, recorded on pre-prepared datasheets, removed from the stream and placed in 70 L containers. This procedure was considered to represent a single electrofishing pass. All subsequent electrofishing passes continued in the same manner until few or no more fish were caught (i.e. usually less than 25% of the total collected on the previous pass, Peterson *et al.* 2004). Following electrofishing, a seine net was pulled through each site where possible to catch any fish missed by the electrofisher. A maximum of five electrofishing passes and two seine hauls were required to collect the majority of fish present. Visual observation and occasional snorkelling surveys aided in this determination. Native fish were released back into the stream once the block nets were in position and ready for sampling in the next mesohabitat unit. Alien fish were euthanased (using benzocaine - MS222), and not returned to the water (in accordance with the Queensland Fisheries Act, 1994). The elapsed time and the actual electrofisher 'power on' time were recorded upon completion of each electrofishing pass to measure sampling effort. The duration of each seine net haul (and fish processing) was usually about 10 minutes.

3.3.3. Habitat sampling procedures

Habitat variables were estimated for each mesohabitat according to a standard protocol described in Pusey *et al*. (2004). Wetted stream width, mean water velocity and water depth were measured at a series of points located randomly throughout the site. In general, this scheme resulted in 20 replicate measures for each parameter at each site, which equated to an average of seven habitat samples per mean stream width. Proportional substrate composition was estimated for one square metre around each survey point and allocated to each of seven substrate classes according to a modified Wentworth scale. The substrate classes were: mud (< 0.06 mm), sand (0.06 – 2 mm), fine gravel (2 – 16 mm), coarse gravel (16 – 64 mm), cobbles (64 – 128 mm), rocks (> 128 mm) and bedrock. The abundance of submerged microhabitat structures (aquatic macrophytes, filamentous algae, submerged vegetation (mainly grasses), emergent vegetation, submerged overhanging vegetation (tree branches), leaf litter, large (> 15 cm minimum stem diameter) and small (1 – 15 cm diameter) woody debris were also estimated at each survey point. As many of these microhabitat structures were concentrated along the stream margins, I estimated the lineal extent (proportion of wetted perimeter) of these structures, in addition to the proportion of undercut banks and root masses, using multiple transect segments along each bank. For every 10 meters of stream traversed, bank habitat was assessed out to a distance of 1 m from the bank, at an average sampling intensity of two samples per mean stream width. Average values (wetted width, depth and velocity), or average proportion of mean wetted site area (substrate composition and microhabitat structures) or stream bank (microhabitat structures including undercut banks and root masses) were then calculated for each site. Ambient water quality conditions (Table 3.1) were characterised by the mean of three replicate measurements for each parameter taken at each site and sampling occasion. For subsequent comparative analyses, I objectively defined mesohabitat types (riffles, runs or pools) on the basis of the velocity to depth ratio of each mesohabitat sampled (Newbury & Gaboury 1993, Orth 1995). I assigned those mesohabitats with velocity/depth ratios in the upper third of the distribution of all mesohabitats sampled as riffles (v/d ratios > 0.98, n = 25 samples), mesohabitats within the lower third of the distribution were designated pools (v/d < 0.03, n = 24 samples) and those in the middle third of the distribution were designated runs (v/d = 0.03 – 0.98, n = 23 samples).

3.3.4. Data analysis

3.3.4.1. Sampling effort and efficiency within mesohabitat units

I evaluated sampling efficiency using fish data summarised in four ways: total fish species richness, total fish abundance, species composition (presence/absence) and species relative abundances. The total number of species and individuals collected after all electrofishing passes plus additional seine netting, were taken to represent the total fish assemblage present within each site (N_T). The cumulative total species richness and total abundance collected up to pass *i* was represented by N_i. The contribution of each cumulative pass was standardised by the total (N_i/N_T) and expressed as a percentage. The contribution of seine netting to N_T was similarly standardised. Multivariate comparisons of fish species composition and species relative abundance data sampled on each electrofishing pass was performed by calculating the Bray-Curtis similarity between the fish assemblage sampled on each successive cumulative pass N_i and the total fish assemblage N_T (i.e. N_i versus N_T). The Bray-Curtis measure is widely used in ecological studies and is regarded as an effective measure of ecological association (Faith *et al*. 1987, Legendre & Legendre 1998).

I used two-way repeated measures analysis of variance (ANOVA) to examine whether successive electrofishing passes contributed significant new information to the estimation of total species richness, total abundance, species composition and species relative abundances, and whether sampling efficiency varied between mesohabitat types (riffles, runs and pools). In this analysis I used sites as subjects, mesohabitat type as a treatment and tested the within-subject effect of electrofishing pass. Orthogonal contrasts between the *n*th level cumulative pass and the total collected by electrofishing were performed for all significant within-subject effects of electrofishing pass and for significant pass-by-mesohabitat type interactions. Variation in the relative efficiency of single pass electrofishing between mesohabitat types was evaluated using a single contrast between data collected on the first pass (P_1) in each mesohabitat type relative to N_T. Variation in relative efficiency of seine netting (after completion of all electrofishing passes) between mesohabitat types was evaluated using a one-way ANOVA. Initial analysis of the relationship between variances and means indicated heterogenous variances so all standardised cumulative catch data were log (x+1) transformed prior to analysis. Relationships between electrofishing sampling effort (as

summarised by the total time spent electrofishing and total 'power on' time), site dimensions (site length, area and volume) and site biological characteristics (total fish species richness and total fish abundance) were evaluated using Spearman's rank correlation. Variation in sampling effort and biological characteristics between mesohabitat types was assessed using one-way ANOVA (data were log (x+1) transformed prior to analysis).

The mean probability of detecting a species at a site or mean probability of estimating their true relative abundances (as defined by multiple-pass electrofishing plus seine netting) were used as measures of sampling efficiency by single pass electrofishing. Interspecific variation in sampling efficiency was tested using 1-way analysis of variance. I also examined whether variation in sampling efficiency was related to individual species' behaviour and microhabitat use by grouping species according to whether they were benthic, pelagic or usually inhabited beds of submerged vegetation (species behavioural designations were based on information provided in Pusey *et al.* (2004) and unpublished observations, Table 3.2). One-way ANOVA was used to test whether sampling efficiency by single pass electrofishing differed among species behavioural groups and post-hoc comparisons were tested using Least Significant Difference (LSD) tests. Similar one-way ANOVA and LSD tests were used to examine whether sampling efficiency of seine netting varied between species behavioural types.

Table 3.2. Characteristics of fish species collected from mesohabitats in the Mary River and Albert River. Maximum sizes (cm standard length) are those commonly attained by each species in south-eastern Queensland and behavioural designations refer to those species that are benthic (B), pelagic (P) or frequently inhabit submerged vegetation (SV) (Pusey *et al*. 2004, M. J. Kennard, unpublished data). The relative abundance and frequency of occurrence of each species are expressed as percentages of the total number of fishes collected and mesohabitats sampled (n = 18,341 individual and 72 samples, respectively). Native fish families are arranged in approximate phylogenetic order (after Pusey *et al.* 2004) and alien species are denoted by *. All fish illustrations by B.J. Pusey except *C. carpio* (Pedro T. Escudero, Mindanao State University, Philippines) and *G. holbrooki* and *X. helleri* (sourced from www.dpi.qld.gov.au/extra/aquaticinvaders).

Species	Size (cm)	Behaviour	Relative abundance (%)	Freq. of occurrence (%)
Anguillidae				
Anguilla reinhardtii	100	B	4.68	84.99
A. australis	50	B	0.08	4.02
Plotosidae				
Tandanus tandanus	50	B	1.73	71.85
Neosilurus hyrtlii	30	B	0.05	3.49
Retropinnidae				
Retropinna semoni	6	P	16.09	71.85
Atherinidae				
Craterocephalus marjoriae	5	P	12.59	66.76
C. stercusmuscarum	5	P	3.15	28.42
Melanotaeniidae				
Melanotaenia duboulayi	6	P	12.42	75.60
Pseudomugilidae				
Psuedomugil signifer	3	SV	20.29	72.39
Scorpaenidae				
Notesthes robusta	20	B	0.03	3.22
Chandidae				
Ambassis agassizii	5	SV	3.48	35.66
Ambassis marianus	6	SV	0.49	3.22
Therapontidae				
Leiopotherapon unicolor	15	P	0.43	17.96
Apogonidae				
Glossamia aprion	9	SV	0.68	13.14
Eleotridae				
Gobiomorphus australis	12	B	1.00	11.26
Gobiomorphus coxii	12	B	0.04	2.95
Hypseleotris compressa	7	B	1.14	12.60
H. galii	4	B	5.27	48.26
H. klunzingeri	4	B	6.12	45.84
Mogurnda adspersa	8	B	1.32	29.76
Philypnodon sp.	4	B	0.51	23.32
P. grandiceps	7	B	0.62	23.59
Cyprinidae				
Cyprinus carpio *	40	P	0.07	6.17
Poeciliidae				
Gambusia holbrooki *	4	SV	4.85	34.85
Xiphophorus helleri *	6	SV	2.87	14.48

3.3.4.2. Sampling effort and efficiency at the stream reach scale

I examined changes in reach-scale estimates of total species richness, species composition and species relative abundances with increasing numbers of mesohabitats (and hence length of stream sampled) and compared these estimates using data collected from single pass electrofishing and multiple pass electrofishing (three passes only) plus seine netting (one seine haul per mesohabitat) at six stream reaches in the Mary River. I incrementally constructed hypothetical series of mesohabitat units using a boot-strapped resampling approach similar to that employed by Angermeier and Smogor (1995). One, then two, then three (etc.) individual mesohabitats were randomly selected (with replacement) up to the maximum of six mesohabitats actually sampled in each stream reach. For each increment of sampling effort (one mesohabitat unit) data were pooled and fish species richness, species composition and species relative abundances calculated. The total number of species and individuals collected after multiple pass electrofishing plus seine netting of all six mesohabitat units in a stream reach was taken to represent the total fish assemblage present within each stream reach ($N_{T\ reach}$). The cumulative total species richness collected up to mesohabitat i was represented by $N_{i\ reach}$. The contribution of each cumulative set of mesohabitat samples was standardised by the total ($N_{i\ reach}/N_{T\ reach}$) and expressed as a percentage. Calculations of $N_{i\ reach}/N_{T\ reach}$ were undertaken separately for data collected by single pass electrofishing and by multiple pass electrofishing plus seine netting. Multivariate comparisons of fish species composition and species relative abundance data sampled from each cumulative set of mesohabitats was performed by calculating the Bray-Curtis similarity between the fish assemblage from each successive set of mesohabitats sampled $N_{i\ reach}$ and the total fish assemblage $N_{T\ reach}$ (i.e. $N_{i\ reach}$ versus $N_{T\ reach}$). These calculations were also undertaken separately for each fish sampling method. For each fish assemblage attribute (species richness, species composition and species relative abundance) and fish sampling method, I ran the randomised resampling procedure 1000 times, calculated $N_{i\ reach}/N_{T\ reach}$ or $N_{i\ reach}$ versus $N_{T\ reach}$ for each resample and calculated the mean and standard deviation (SD) for each level of sampling effort (number of mesohabitats).

Changes in the accuracy (proximity of an estimate to the true value) of estimates of species richness, species composition and species relative abundance with each cumulative number of mesohabitats sampled was calculated as the mean (± SD) percentage of total fish species richness (from all six mesohabitats) or mean (± SD)

Bray Curtis similarity with total species composition and species relative abundance, respectively. Changes in precision (degree of variation in the estimate) for each cumulative number of mesohabitats sampled was represented by the coefficient of variation (mean/SD) for each fish assemblage attribute (following Kritzer *et al*. 2001). I examined relationships between sampling effort within stream reaches (i.e. number of mesohabitat units sampled) and statistical power (1-β) to detect a 20% decrease in the mean (effect size - δ) for fish assemblage data collected by both single pass electrofishing and multiple-pass electrofishing plus seine netting. For each level of sampling effort (number of mesohabitats) within stream reaches, I used the pooled mean and standard deviation from all stream reaches for power calculations and set the Type I error rate (α) to 0.05. I substituted a range of values of δ (10 to 100% in increments of 10) in these analyses but report only for δ = 20% as the trends for each fish sampling method with increasing numbers of mesohabitat samples were similar for each level of 1-β and δ. I also calculated the sample sizes (i.e. number of stream reaches) required to achieve a half width of the confidence interval (Zar 1996) within specified percentages (10 to 100% in increments of 10) of the estimated true population mean for each fish assemblage data set sampled using single pass electrofishing and multiple pass electrofishing plus seine netting. For these analyses I used a one-sample test based on the pooled mean and standard deviation from all stream reaches and report only for fish assemblage estimates based on sampling of three mesohabitat units per stream reach as trends for each fish sampling method were similar with each level of within-reach sampling effort (i.e. number of mesohabitat samples).

To establish whether rates of changes in fish assemblage attributes along stream reaches were associated with longitudinal variation in habitat structure, I examined rates of longitudinal accumulation of microhabitat configurations (i.e. particular combinations of depth, velocity, substrate, in-stream microhabitat structures and bank microhabitat structures) along stream reaches. Raw habitat data from the random point measurements (described in the section on habitat sampling methods) were condensed into five categories each of depth (0.01 – 0.25, 0.26 – 0.50, 0.51 – 0.75, 0.76 – 1.0 and > 1.0 m) and velocity (0.01 – 0.25, 0.26 – 0.50, 0.51 – 0.75, 0.76 – 1.0 and > 1.0 $m.sec^{-1}$). Seven substrate categories, 10 in-stream habitat categories and eight bank microhabitat categories were also recognised (described earlier). The occurrence of these unique habitat categories was treated similarly to the longitudinal accumulation of fish species (described earlier). The cumulative number of habitat categories was estimated for each

of 1000 resamples of incrementally increasing numbers of individual random point measurements within each stream reach and expressed as a percentage of the total number of habitat categories within each stream reach. For each level of sampling effort (number of random point measurements) the mean and standard deviation of the 1000 resamples were calculated. I performed three separate analyses: one based on the longitudinal accumulation of depth, velocity and substrate categories, one based on the accumulation of in-stream microhabitat categories and one based on the accumulation of bank microhabitat categories. Repeated measures analysis of variance was performed using the SPSS statistical software package (SPSS 1999) and all other analyses were preformed using S-PLUS 2000 (Statistical Sciences 1999).

3.4. Results

3.4.1. Sampling effort and efficiency within mesohabitat units

The total time taken to sample discrete mesohabitat units using an electrofisher averaged 50 minutes; this equated to about 900 seconds electrofisher power on time (Fig. 2). The relative time spent on each electrofishing pass was similar for both measures of sampling duration (Fig. 2). Approximately 50% of the total sampling time was spent on the first pass and 95% of the total sampling time was spent on the first three passes. There were significant differences ($P < 0.05$) in the average time taken to electrofish different mesohabitat types (Fig. 3.2), with riffles being sampled more rapidly on average than runs or pools ($F = 3.81$ and $F = 4.78$ for 1-way ANOVAs of between-mesohabitat type comparisons of mean total time and power on time, respectively). Both total time spent electrofishing, and time spent on the first electrofishing pass, were positively correlated (though often only weakly) with the size of the study sites (stream length, area and volume) and the total number of individuals present, but not with variables describing the physical characteristics or water quality of the study sites (Table 3.3). Riffles, runs and pools differed significantly in the mean total number of species and total number of individuals ($P < 0.01$), with pools containing the highest number of species and individuals on average ($F = 6.13$ and $F = 4.92$ for 1-way ANOVAs of between-mesohabitat type comparisons of mean species richness and mean total abundance, respectively) (Fig. 3.3).

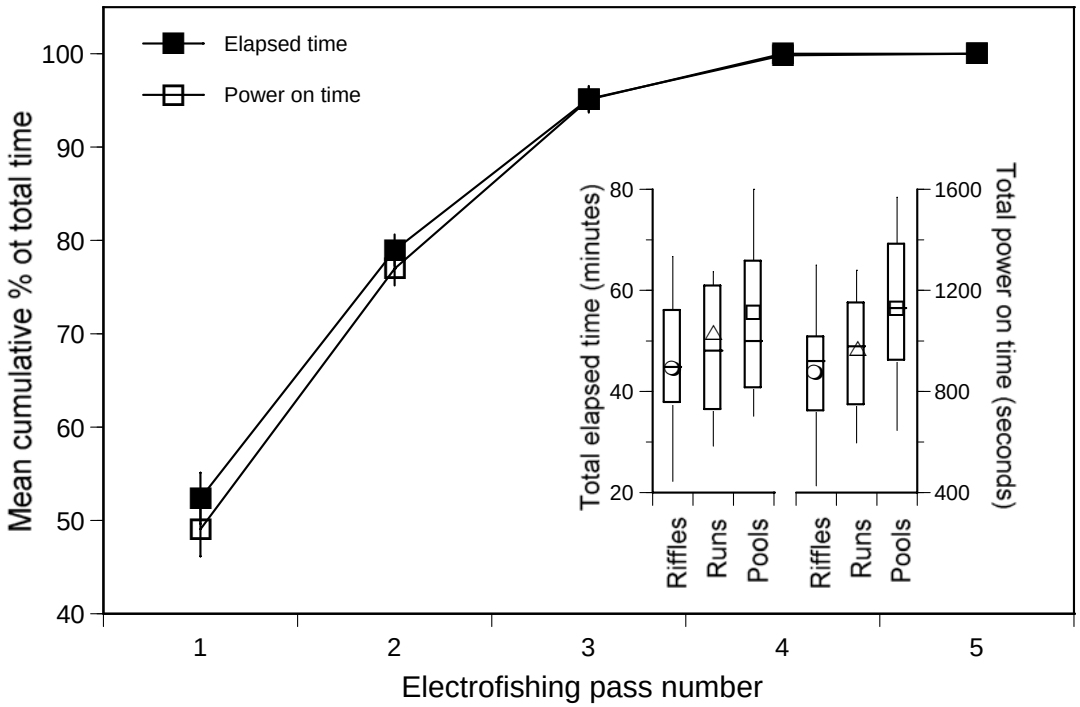

Figure 3.2. Mean (± SE) cumulative percent of total sampling duration (elapsed time and electrofisher power on time) spent on each consecutive electrofishing pass at individual mesohabitat units in the Mary and Albert Rivers. Inset box plots show the variation in total elapsed time and power on time spent sampling individual mesohabitat types. The lines at the top, middle and bottom of each box represent the 75th percentile, median and 25th percentile, respectively. Upper and lower bars represent 90th and 10th percentiles and mean values are represented by squares.

Up to 85 % of the total number of species present were usually collected from a single electrofishing pass and on average, seine netting accounted for less than about 5 % of the total number of species (Fig. 3.3). Less than 45% of the total number of individuals was collected on the first electrofishing pass and seine netting accounted for between 10 and 30% of individuals. Comparatively more sampling effort (electrofishing passes and seine netting) was required to accurately estimate species relative abundance than species composition, and this was consistent across mesohabitat types (Fig. 3.3). Repeated measures ANOVA revealed a significant main effect of electrofishing pass for analyses of total species richness, total abundance, species composition and species relative abundance data sets ($P < 0.001$), and significant cumulative pass-by-mesohabitat type interactions for analyses of total abundance and species relative abundance data sets (Table 3.4, Fig 3.3). Contrasts between the *n*th cumulative pass and the total assemblage estimated by electrofishing indicated that for each fish assemblage data set, the first three passes contributed significantly to estimates of total fish assemblage attributes ($P < 0.001$) but that the remaining electrofishing passes added no significant new information (Table 3.4, Fig. 3.3).

Table 3.3. Spearman's rank correlation coefficients between measures of sampling effort (total time spent sampling and percentage of total time spent sampling on electrofishing pass 1) and physical, chemical and biological attributes of the study sites. All mesohabitat samples were included in analyses (n = 72 samples). Correlation coefficients shown in bold are significant at $P < 0.05$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn & Keough, 2002).

	Sampling effort			
	Total elapsed time	Total power on time	Pass 1 % total elapsed time	Pass 1 % total power on time
Sampling effort				
Total elapsed time				
Total power on time	**0.80**			
Pass 1 % total elapsed time	**0.66**	**0.59**		
Pass 1 % total power on time	**0.49**	**0.66**	**0.80**	
Site dimensions				
Site length	0.26	0.27	0.22	0.27
Site area	0.35	**0.56**	**0.41**	**0.56**
Site volume	0.21	**0.52**	**0.39**	**0.56**
Site physical characteristics				
Mean wetted width	0.07	0.34	0.23	**0.48**
Mean velocity	0.12	0.36	0.33	0.38
Mean depth	-0.13	-0.16	-0.28	-0.21
Site water quality				
Turbidity	0.30	0.33	0.25	0.28
Conductivity	0.01	-0.15	0.03	0.06
Temperature	-0.32	-0.23	-0.02	0.04
Site biological characteristics				
Total species richness	0.29	0.22	0.15	0.27
Total abundance	**0.66**	**0.56**	0.32	**0.41**

Electrofishing efficiency (estimates of fish assemblage attributes using data collected on the first pass) differed significantly between mesohabitat types (Table 3.4) for estimation of total abundance and species relative abundances, with pools being sampled less efficiently than runs or riffles (Fig. 3.3). Electrofishing efficiency was not strongly correlated with parameters describing the physical, chemical or biological characteristics of the study sites (only one of 52 correlations significant at $P < 0.05$, results not shown). Significant differences between mesohabitat types in seine netting efficiency (after completion of all electrofishing passes) existed for all fish assemblage data sets (one-way ANOVA's, $P < 0.01$ for each data set), with seine netting contributing significantly more information in pools compared with other mesohabitat types (Fig. 3.3). Seine net efficiency was higher in pools because these mesohabitats contained relatively more pelagic fish than runs or riffles (Fig. 3.4 and next section).

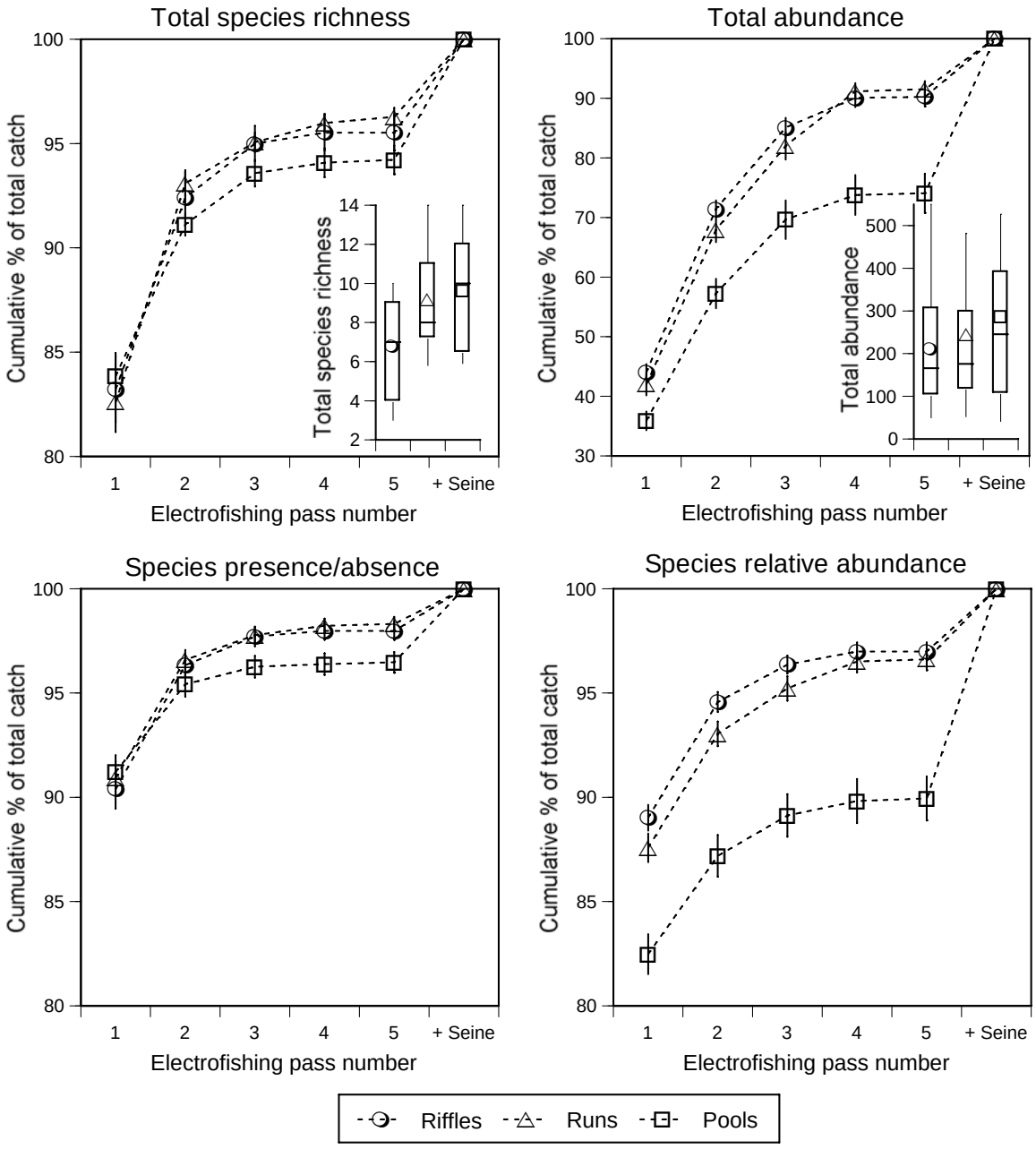

Figure 3.3. Changes in estimates of fish species richness, total abundance, species presence/absence and species relative abundance with increasing sampling effort within riffles (circles), runs (triangles) and pools (squares). For total species richness and total abundance, the data represents the sequential increase in mean (± SE) cumulative percentage of the total catch collected by each electrofishing pass and supplementary seine-netting. Inset box plots show the variation in total species richness and total abundance collected within each mesohabitat type. For species composition and species relative abundance, the data represents the mean (± SE) Bray-Curtis similarity between each cumulative pass and the total assemblage (derived from all electrofishing passes plus seine-netting).

Table 3.4. *F* values (Wilks Lambda) and their associated significance levels for repeated measures Analysis of Variance of within-mesohabitat type (cumulative passes) and between-mesohabitat type variation in log(X+1) transformed estimates of within-mesohabitat total species richness, total abundance, species presence/absence and species relative abundances. See text for explanation of contrasts.

		Total species richness		**Total abundance**		**Species presence/absence**		**Species relative abundance**	
Source of variance	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat	2	0.69	0.501	14.61	<0.001	0.42	0.619	21.93	<0.001
Site (Habitat)	69								
Pass	4	96.71	<0.001	454.66	<0.001	75.35	<0.001	200.35	<0.001
Pass X Habitat (Error 1)	8	1.09	0.375	5.83	<0.001	1.03	0.417	4.11	<0.001
Contrast 1 (electrofishing efficiency)									
Pass 1 (between Habitats)	2	0.20	0.821	4.12	0.011	0.27	0.762	15.07	<0.001
Contrast group 2									
P1 *vs* P5	1	312.82	<0.001		<0.001	267.46	<0.001		<0.001
P2 *vs* P5	1	77.24	<0.001		<0.001	67.68	<0.001		<0.001
P3 *vs* P5	1	20.40	<0.001		<0.001	19.61	<0.001		<0.001
P4 *vs* P5	1	3.77	0.056		>0.05	3.91	0.052		>0.05
Pass X Site (Habitat) (Error 2)	65								

3.4.2. Interspecific variation in sampling efficiency and mesohabitat use

Significant interspecific differences in the probability of detecting a species at a site ($F = 11.02$, $P < 0.001$) or the probability of estimating their abundance ($F = 75.75$, $P < 0.001$) using single pass electrofishing were detected (Fig. 3.4a). Variation in sampling efficiency between mesohabitat types appears related to interspecific variation in fish behaviour (and hence probability of capture) and mesohabitat use. Grouped by behavioural type, single pass-electrofishing detected the presence of benthic species and species inhabiting submerged vegetation with similar efficiency (mean percentage of samples = 86.1 % ± 0.1 SE and 87.0 % ± 0.1 SE, respectively), but mean sampling efficiency of pelagic species (79.8 % ± 0.1 SE) was significantly lower (post-hoc LSD comparisons between pelagic species and other species behavioural types significant at $P < 0.001$). A greater percentage of the total number of individuals from benthic species was caught on the first pass (mean 57.1 % ± 0.9 SE) than pelagic species (34.0 % ± 1.0 SE) or species in submerged vegetation (43.7 % ± 1.2 SE) (all post-hoc LSD comparisons between behavioural types significant at $P < 0.001$). In addition, several species (e.g. *Pseudomugil signifer, Gambusia holbrooki, Melanotaenia duboulayi,*

Craterocephalus marjoriae, C. stercusmuscarum, Retropinna semoni and *Cyprinus carpio*) were caught in similar or greater abundances in the subsequent electrofishing passes than on the first pass (Fig. 3.4a), despite sampling effort (duration) being similar between the first pass and the sum of subsequent passes (Fig. 3.2).

After multiple electrofishing passes many individuals of pelagic, small-bodied schooling species (e.g. *M. duboulayi, C. marjoriae, C. stercusmuscarum* and *R. semoni*) still avoided capture, as did those that became trapped or remain hidden amongst submerged vegetation (e.g. *Ambassis agassizii, A. marianus* and *Glossamia aprion*) (Fig. 3.4a). These cryptic, trapped or fast-swimming individuals were more effectively sampled using supplementary seine netting ($F = 133.47$, $P < 0.001$, all post-hoc comparisons between behavioural types significant at $P < 0.001$). Substantial variation in species composition and abundance of riffle fauna was evident compared with runs and pools (Fig. 3.4b). Riffles were dominated by a subset of species including *Gobiomorphus coxii, Anguilla australis, R. semoni, A. marianus* and *A. reinhardtii*. The remaining species were more common in runs and pools.

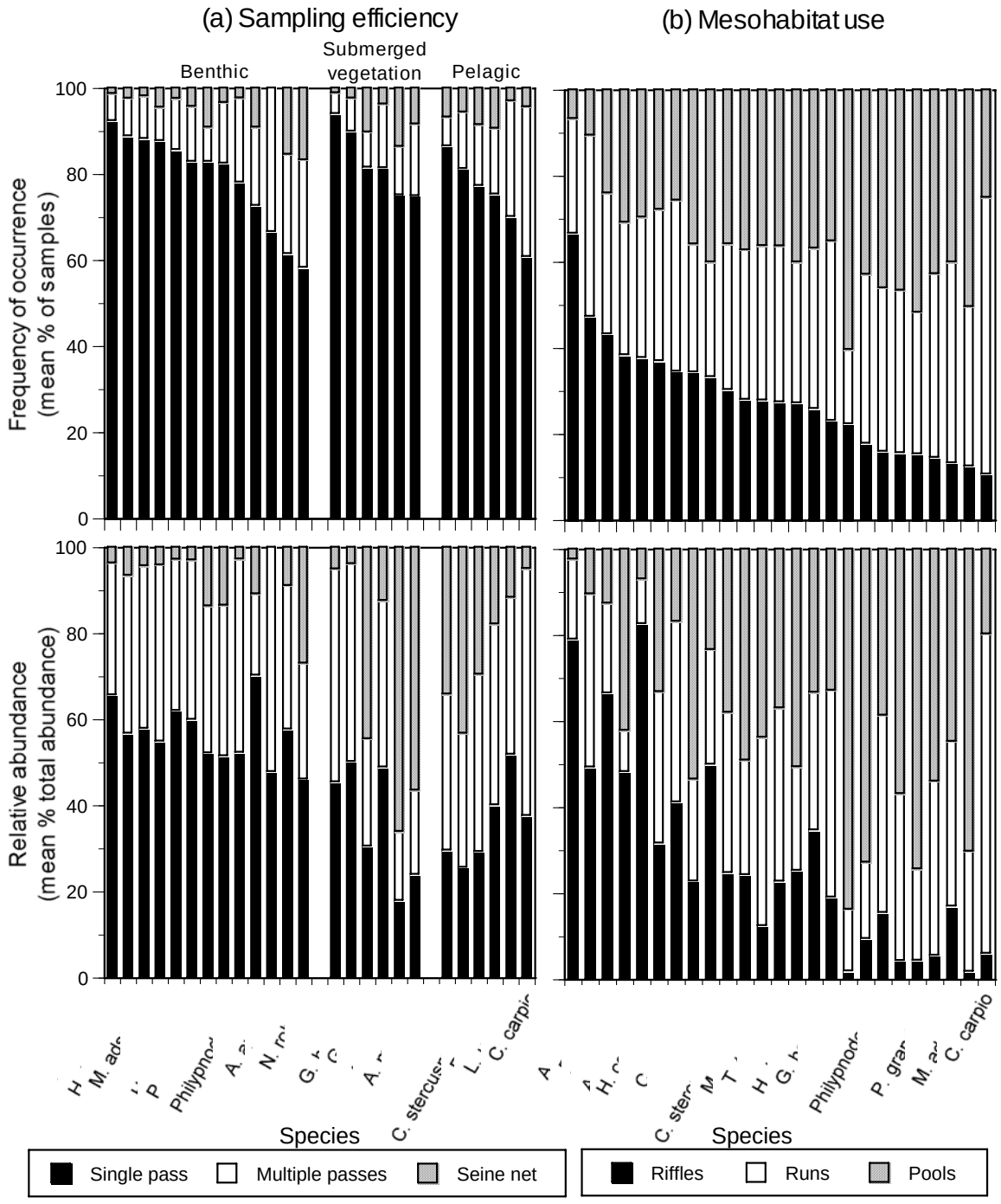

Figure 3.4. Intserspecific variation in (a) sampling efficiency and (b) mesohabitat use. Sampling efficiency is defined as the probability of capture (as assessed by mean frequency of occurrence in mesohabitat samples) and percentage of total catch (mean relative abundance) for each species (grouped by behavioural type) sampled by single pass electrofishing, multiple pass electrofishing and supplementary seine netting. Mesohabitat use is indicated by the mean frequency of occurrence and mean relative abundance of each species occurring in riffles, runs or pools. Sample sizes for each species (number of individuals or number of mesohabitats) can be calculated using the data presented in Table 3.2).

3.4.3. Sampling effort and efficiency at the stream reach scale

Total species richness in the six focus stream reaches in the Mary River ranged between 9 and 15 (mean = 12 ± 1 SD) and total fish abundance ranged between 671 and 891 individuals (mean = 758 ± 40 SD). At the stream reach-scale, single pass electrofishing tended to over-estimate the abundance of some numerically common or easily sampled species (e.g. *P. signifer*, *G. holbrooki, Hypseleotris galii* and *A. reinhardtii*) and underestimate the abundance of some numerically rare or difficult to catch species (e.g. *M. duboulayi*, *A. agassizii*, *C. marjoriae* and *C. stercusmuscarum*) in comparison to multiple pass electrofishing plus seine netting. Furthermore, single pass electrofishing tended to underestimate the frequency of occurrence of all species (Fig. 3.5).

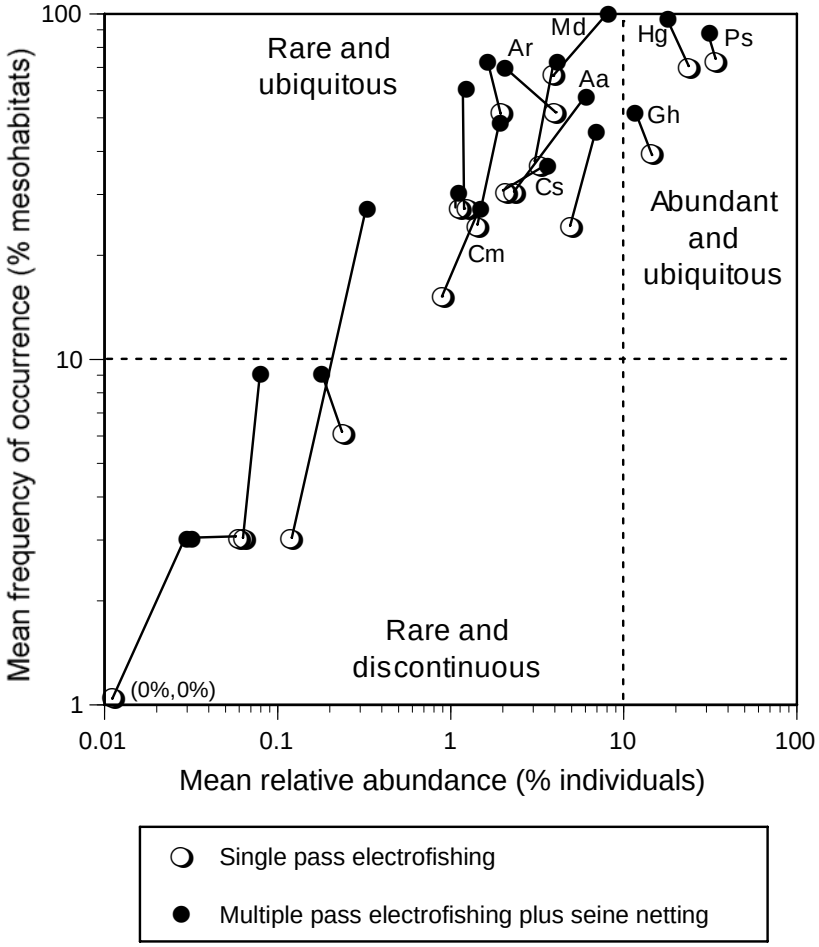

Figure 3.5. Fish species relative abundance (percentage of total abundance) versus frequency of occurrence (percentage of mesohabitats occupied) averaged across the six Mary River stream reaches sampled. Each point represents one species sampled using single pass electrofishing or multiple pass electrofishing plus seine netting (species discussed in the text are denoted by the first letter of the genus and species, respectively). Data are plotted on log scale. Rare species are defined as forming less than 10% of total abundance and discontinuous species are defined as occurring in less than 10% of mesohabitats (averaged across stream reaches).

At each stream reach, the cumulative number of species collected initially increased rapidly with increasing sampling distance, irrespective of sampling method, however cumulative numbers of species sampled using multiple pass electrofishing plus seine netting reached asymptotes earlier than those sampled using single pass electrofishing (Fig. 3.6). Curves based on cumulative numbers of species sampled using single pass electrofishing failed to reach an asymptote in most stream reaches and total numbers of species sampled (after six mesohabitats) were often much lower than the true number of species present (as determined from multiple pass electrofishing plus seine netting). Sampling in stream reaches with relative high total species richness tended to accumulate species more slowly than sampling in stream reaches with fewer species (Fig. 3.6).

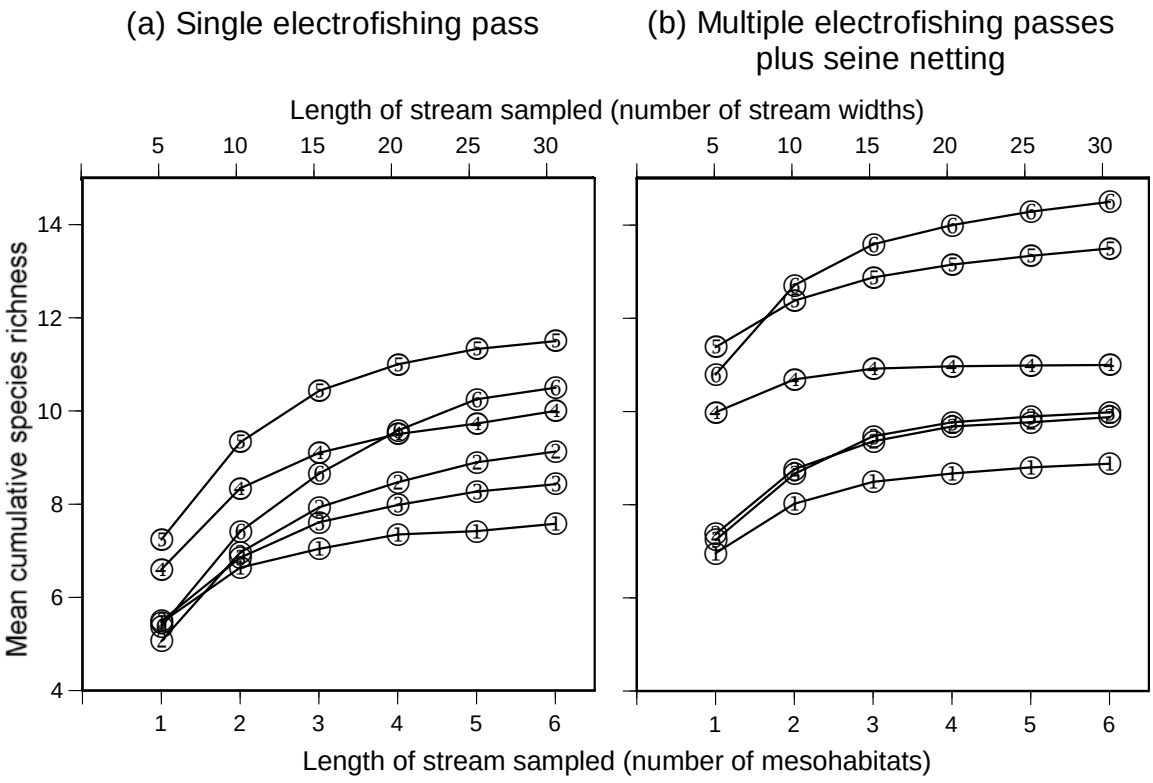

Figure 3.6. Mean cumulative species richness versus length of stream sampled using (a) single-pass electrofishing and (b) multiple-pass electrofishing plus seine netting in each of the six stream reaches. Reach numbers match those given in Figure 3.1. Estimates of mean species richness for each sampling interval (cumulative number of mesohabitats) were based on 1000 bootstrapped randomisations that incrementally constructed hypothetical series of mesohabitat units. For clarity, standard deviations are not shown.

The accuracy and precision of reach-scale estimates of total species richness, species composition and species relative abundances increased with increasing stream length and hence number of mesohabitat units sampled (using both sampling methods) (Fig. 3.7). For a given level of sampling effort (number of mesohabitats), the accuracy and precision of estimates of fish assemblage attributes were lower for single pass electrofishing in comparison to multiple pass electrofishing plus seine netting (Fig. 3.7). For example, single pass electrofishing of three mesohabitats equivalent to 15 MSWs resulted in estimates of mean accuracy for the three fish assemblage attributes between 75% and 85% and estimates of precision between 0.10 and 0.16 (Fig. 3.7a). Multiple pass electrofishing plus seine netting of three mesohabitats resulted in comparably higher levels of accuracy and precision of these attributes (accuracy = 86% – 97% and precision = 0.04 – 0.09) (Fig. 3.7b). To gain equivalent levels of accuracy and precision, at least double the length of stream needed to be sampled by single pass electrofishing than by more intensive sampling using multiple pass electrofishing plus seine netting. To estimate total species richness and species composition with an accuracy of 90% and precision of 0.1, sampling of three to six mesohabitats was required using single pass electrofishing versus between one and three mesohabitats using more intensive fish sampling (Fig. 3.7). Even after sampling of six mesohabitats, species relative abundances could not be estimated to this level of accuracy and precision using single pass electrofishing.

Estimates of species composition were comparatively more accurate and precise, for a given number of mesohabitat samples, than estimates of total species richness and species relative abundance (Fig. 3.7b). The majority of species were numerically rare (i.e. 16 of 19 species formed less than 10% of the total abundance) but ubiquitous (i.e. usually present in two or more mesohabitats per stream reach on average, Fig. 3.5) and hence it took comparably less sampling effort to detect the presence of a species in a stream reach and therefore to accurately and precisely estimate species composition than it did to estimate their relative abundances (which varied markedly between mesohabitat types, see Fig. 3.4). Because estimates of total species richness give equal weighting to discontinuous and ubiquitous species, accumulations of species are strongly influenced by discontinuously distributed (i.e. patchy) species. This led to less precise estimates of total species richness in comparison to multivariate estimates of fish assemblage composition, which were less sensitive to patchily distributed species.

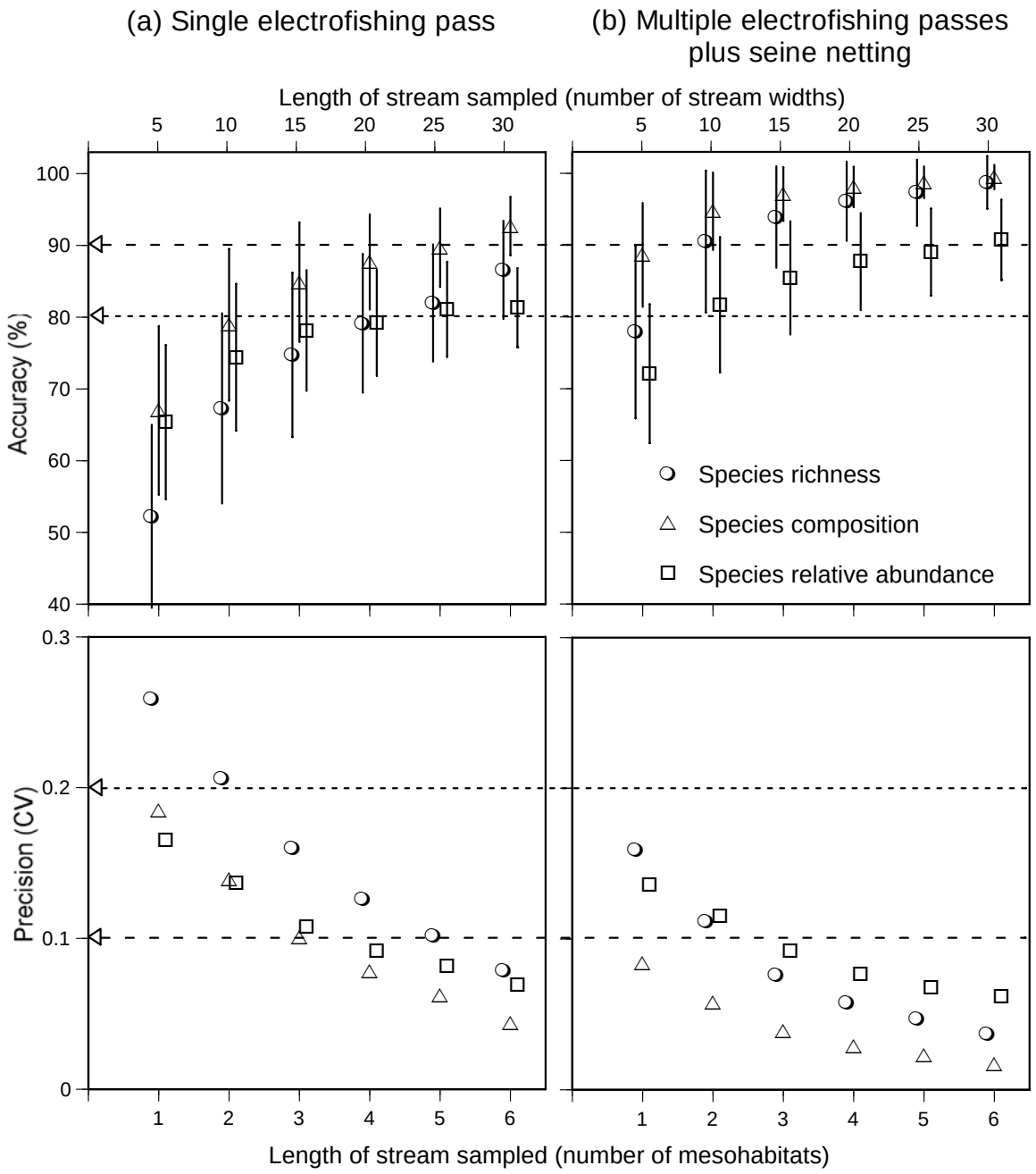

Figure 3.7. Change in average sampling accuracy (± SD) and average precision versus length of stream sampled using (a) single-pass electrofishing and (b) multiple-pass electrofishing plus seine netting to estimate total fish species richness (circles), species composition (triangles) and species relative abundance (squares). Accuracy for each cumulative number of mesohabitats sampled is represented by the mean (± SD) percentage of total fish species richness (closed circles) or mean (± SD) Bray Curtis similarity with total species composition (closed squares) and species relative abundance (closed triangles), respectively. Precision for each cumulative number of mesohabitats sampled is represented by the coefficient of variation (mean/SD). Estimates of accuracy and precision were based on 1000 bootstrapped randomisations that incrementally constructed hypothetical series of mesohabitat units. Results are averaged across six sampled stream reaches in the Mary River.

For an equivalent level of sampling effort (number of mesohabitats), the power to detect a 20% decrease in the mean of estimates of fish assemblage attributes was higher for multiple pass electrofishing plus seine netting in comparison to single pass electrofishing (Fig. 3.8a). Sampling of three mesohabitats yielded a power (1-β) greater than 0.95 using multiple pass electrofishing plus seine netting whereas sampling of six mesohabitat units was required to achieve comparable levels of power using single pass electrofishing. Multiple pass electrofishing plus seine netting of three mesohabitat units also yielded more precise estimates of fish assemblage attributes and so fewer stream reaches needed to be sampled to achieve a half width of the confidence interval within given percentages of the true population mean (Fig. 3.8b). For example, sampling of three to four stream reaches was required to achieve a half width of the confidence interval within 20% of the mean for each fish assemblage attribute in comparison to between five and eight stream reaches using single pass electrofishing.

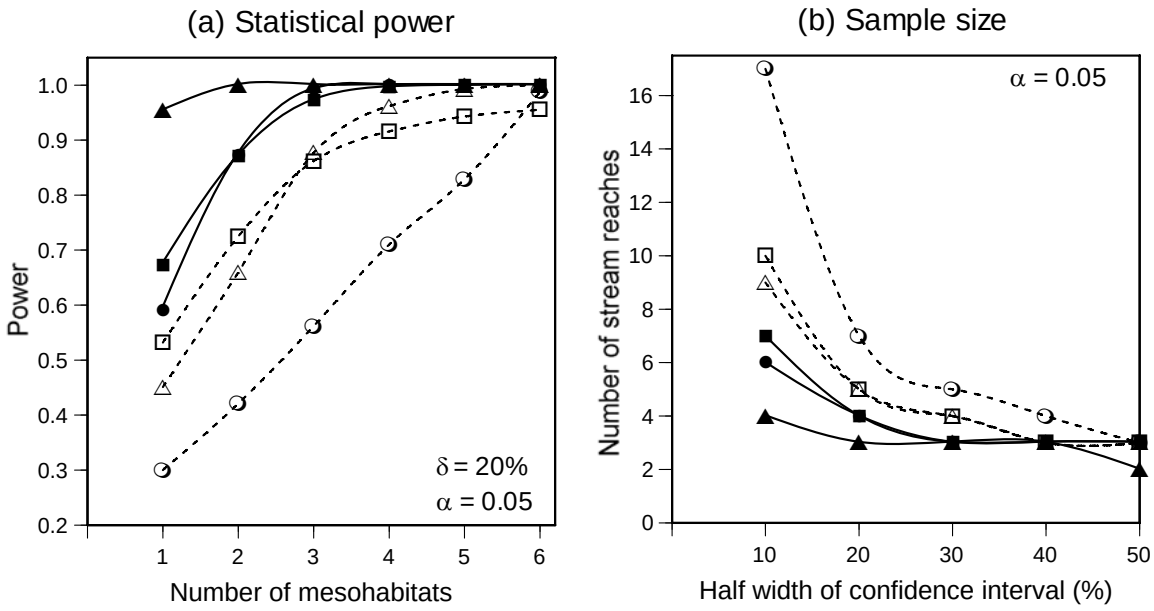

Figure 3.8. (a) The power (1-β) of different fish sampling methods to detect a 20% decrease (δ) in estimates of total species richness (circles), species composition (triangles) and species relative abundance (squares), with increasing number of mesohabitats sampled (α = 0.05). (b) The number of stream reaches required (based on sampling of three mesohabitats per reach) to achieve a half width of the confidence interval within given percentages of the true population mean for total species richness, species composition and species relative abundance (α = 0.05). Data from single pass electrofishing is shown with open symbols and dashed lines, data from multiple-pass electrofishing plus seine netting is shown with closed symbols and solid lines.

The relative efficiency (i.e. the time spent sampling versus number of mesohabitats required to achieve a given level of accuracy and precision) of each fish sampling method varied with the fish assemblage attribute of interest and the desired level of accuracy or precision (Table 3.5). For a given mesohabitat unit sampled, intensive sampling using multiple-pass electrofishing and seine netting took, on average, more than twice the amount of time to sample as single-pass electrofishing. However, single-pass electrofishing was always less efficient (as indicated by efficiency ratios < 1) than multiple pass electrofishing plus seine netting in accurately (i.e. 80% or 90%) estimating total species richness, species composition and species relative abundance (Table 3.5). Single-pass electrofishing was apparently sometimes more efficient (efficiency ratios > 1) than multiple pass electrofishing plus seine netting in precisely estimating fish assemblage attributes (Table 3.5).

3.4.4. Accumulation of habitat

The rate of accumulation of in-stream habitat characteristics with increasing stream distance (Fig. 3.9) was similar to average accumulation rates of fish assemblage attributes sampled by multiple pass electrofishing plus seine netting (Fig 3.7b). The mean percentage of physical habitat categories (depth, velocity and substrate) present in a river reach increased with increasing sampling distance (Fig. 3.9). After sampling 10 MSW, around 90% of the total physical habitat categories present had been encountered. Approximately 90% of bank microhabitat types had been sampled after less than 10 MSWs and about 80% of total in-stream microhabitat types were represented. Addition of new habitat types occurred relatively slowly after 15 MSWs of stream length had been sampled. The lower relative accuracy of in-stream microhabitat categories is indicative of generally more sparse distribution of these microhabitat types than those of bank and physical variables (Fig. 3.9), suggesting that a greater length of stream needed to be sampled before they were fully represented.

Table 3.5. Relative sampling efficiency (efficiency ratio) of single pass electrofishing versus multiple pass electrofishing plus seine netting to achieve a desired accuracy (80% and 90%) and precision (0.2 and 0.1) in estimating total species richness, species composition and species relative abundance in a river reach. The number of mesohabitat units required to achieve the prescribed accuracy and precision levels were obtained from Figure 3.7. Total mean sampling duration was estimated by multiplying the number of mesohabitat units by the sampling time required by a two or three person crew to collect, identify and enumerate fish using single pass electrofishing (mean 23 minutes per mesohabitat) or multiple (three) pass electrofishing (mean 45 minutes) plus seine netting (estimated as 10 minutes per site). Efficiency ratios were calculated by dividing the total mean sampling duration of single pass electofishing by the duration of multiple pass electrofishing plus seine netting. Note that single pass electrofishing did not estimate species richness or relative abundance to an accuracy of 90% after the maximum of 6 sampled mesohabitats (Fig. 3.7a) so efficiency ratios could not be calculated.

	Number of mesohabitats required		Total mean sampling duration		Efficiency ratio	
Accuracy =	**>80%**	**>90%**	**>80%**	**>90%**	**>80%**	**>90%**
Species richness						
Single pass	5	>6	115	–	0.96	–
Multiple passes + seine netting	2	2	110	110		
Species composition						
Single pass	3	5	69	115	0.80	0.48
Multiple passes + seine netting	1	1	55	55		
Species relative abundance						
Single pass	5	>6	115	–	0.96	–
Multiple passes + seine netting	2	5	110	275		
Precision =	**<0.2**	**<0.1**	**<0.2**	**<0.1**	**<0.2**	**<0.1**
Species richness						
Single pass	3	5	69	115	0.80	1.43
Multiple passes + seine netting	1	3	55	165		
Species composition						
Single pass	1	3	23	69	2.39	0.80
Multiple passes + seine netting	1	1	55	55		
Species relative abundance						
Single pass	1	4	23	92	2.39	1.79
Multiple passes + seine netting	1	3	55	165		

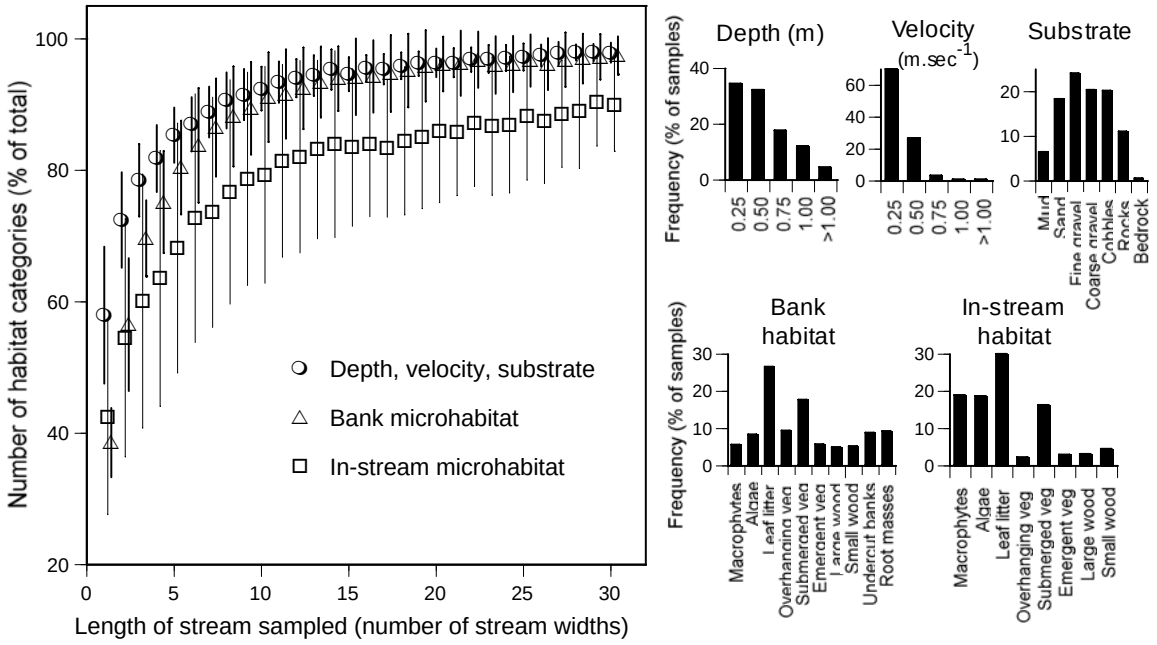

Figure 3.9. Cumulative increases in the mean percentage (± SD) of the total number of habitat types encountered in stream reaches versus length of stream sampled (expressed as number of mean stream widths). Separate curves are shown for depth, velocity and substrate categories, and for bank microhabitat and in-stream microhabitat categories. Means were generated using 1000 bootstrapped randomisations that incrementally constructed hypothetical combinations of habitat categories from observed samples and averaged over the six stream reaches. Frequency histograms of the number of habitat sampling points within each habitat category used in the analyses are also shown.

3.5. Discussion

The results of the present study confirm the earlier findings of Pusey *et al.* (1998a) that intensive sampling is required to estimate fish assemblage attributes within discrete mesohabitats. These findings are consistent over the three geomorphologically dissimilar river basins examined (Johnstone River, Mary River and Albert River), which vary in local fish species richness, composition and abundance. Evaluation of the accuracy and precision of single pass versus multiple pass electrofishing as performed in this study and in Pusey *et al*. (1998a) relied on the assumption that the estimate of the 'true' fish assemblage based on multiple pass electrofishing plus seine netting was accurate, particularly in terms of species abundances. Although maximum likelihood estimation methods are available to estimate species total population sizes based on removal sampling (e.g. Zippin 1956, Otis *et al*. 1978), these methods have several restrictive assumptions that are often violated (Riley & Fausch 1992, Riley *et al*. 1993, Peterson *et al.* 2004) and can result in overestimates of species capture efficiencies and

underestimates of fish population sizes (Peterson *et al*. 2004). The main goal of this chapter was to develop a sampling program able to monitor and compare variation in fish assemblage attributes (e.g. species richness, species composition and relative abundances), and not necessarily to estimate absolute population sizes.

Changes in catchability of some fish species exposed to an electrical current during previous electrofishing passes (Cross & Stott 1975, Riley *et al.* 1993, Bohlin *et al.* 1989, Mesa & Schreck 1989, Peterson *et al.* 2004) has the potential to bias estimates of fish species relative abundances based on multiple pass electrofishing. Reductions in galvanotaxic responses of fish with increases in the number of times an individual has been shocked reportedly contributes to reductions in catchability of some cyprinids, salmonids and anguillids (Chmielewski *et al.* 1973, Cross & Stott 1975), with the refractory period in cyprinids thought to last between three and 24 hours (Cross & Stott 1975). The extent to which species collected in this study experienced a refractory effect from repeated electroshocking is unknown. If some species were less catchable on subsequent electrofishing passes, it is possible that my estimates of species relative abundances from a single pass were more accurate than estimates from multiple electrofishing passes plus seine netting. However, my data do not support this for several reasons. Galvanotaxic responses to electroshocking for all species collected in this study (with the usual exception of *Anguilla* spp.) were rarely observed (i.e. fish usually did not swim, or could not be drawn, towards the anode ring). The usual response by most fish was immobilisation on the stream bottom or erratic swimming behaviour (but rarely towards the anode) requiring vigorous and rapid sweepings of the anode pole net and the assistance of dip-netters to capture these fish. Moreover, several species were caught in similar or greater abundances in the subsequent electrofishing passes than on the first pass, despite sampling effort being similar between the first pass and the sum of subsequent passes, suggesting that fish were not necessarily less catchable after being electroshocked.

Reductions in capture efficiency with each electrofishing pass may also arise because fish avoid capture by concealment in areas that are difficult to sample (e.g. coarse substrates, aquatic macrophyte beds and undercut banks), or by actively swimming to avoid the anode (Peterson *et al*. 2004). Fishes that are already concealed within such microhabitat refuges may however, require repeated electroshocking episodes before they emerge from cover and can be captured. I have regularly observed this

phenomenon with large species such as plotosids (*Tandanus tandanus* and *Neosilurus hyrtlii*), anguillids (*A. reinhardtii* and *A. australis*) and some eleotrids (e.g. *Philypnodon grandiceps*) which commonly take refuge in deep undercut banks (Pusey *et al*. 2004) and often only emerge from these areas after repeated shocking over several electrofishing passes. This study did clearly show however, that species differed in their susceptibility to capture by electrofishing (Fig. 3.4). This effect should yield estimates of species relative abundances biased towards those most easily caught by electrofishing (primarily benthic species and some small-bodied species commonly found in submerged marginal vegetation). My results also indicated that multiple-pass electrofishing underestimated abundances of some species that were more efficiently sampled using seine netting. The only means of evaluating the adequacy of an abundance estimation technique is to compare the estimates with known or unbiased estimates of fish abundance (e.g. by tagging and stocking a known number of fish in an enclosed area and counting the recapture of tagged fish on each pass) (Peterson *et al*. 2004). These issues require further research, however, I conclude that intensive sampling using dual gear (multiple pass electrofishing plus seine netting) should minimise the negative bias of my estimates of species abundances in comparison to single pass electrofishing alone, and that the standardisation of sampling effort enabled valid comparison of fish catch data among sites.

Repeated electroshocking episodes undoubtedly increase the potential to injure fish (see Nielsen (1998) and Carline (2004) for recent reviews). Sampling-induced mortality has obvious negative implications for bioassessment programs that aim to evaluate temporal variation in fish assemblages by repeated sampling at a study site, or studies in rivers where rare or endangered fish species that are of high conservation significance are frequently encountered. There is little quantitative data on immediate or longer-term injury or mortality rates of Australian fish species due to electroshocking. Barker *et al.* (2002) reported that only a very small percentage of fish suffered injuries and that the incidence of injury was much less than that caused by more conventional survey capture methods. My own experience supports this and suggests that short-term mortality rates for a range of fish species, in a range of eastern Queensland rivers, are generally less than 5% (Pusey *et al.* 1998a, M.J. Kennard, unpublished observations).

The site dimensions (length, area and volume) and number of species and individuals influenced the amount of time that had to be spent sampling each site, with larger sites

taking longer to sample. However, variation in the physical characteristics of sites did not appear to affect electrofishing efficiency. The range of variation in the physico-chemical conditions across the sites sampled in the present study (e.g. relatively high conductivity, low turbidity and depth usually less than 1 m) was not such that they would be expected to influence efficiency. Sampling efficiency did vary with mesohabitat type, presumably due to variation in species composition and relative abundances between riffles, runs and pools, and variation in the catchability of these species using electrofishing and seine netting.

This study showed that accurate estimates of assemblage attributes at the reach scale could be obtained from intensive sampling using multiple pass electrofishing plus seine netting of three mesohabitat units equivalent to 15 MSWs (accuracy of species richness, species composition and relative abundances 94%, 97% and 86%, respectively). Perhaps not surprisingly, this spatial scale corresponded to the point at which longitudinal accumulations of most habitat configurations present within stream reaches had also stabilised (Fig. 3.9). This length of stream is generally within the lower end of the range of stream lengths recommended for sampling of fish assemblages in similar studies conducted in North American streams and elsewhere (e.g. Kennedy & Strange 1981, Lyons 1992, Hill & Willis 1994, Angermeier & Smogor 1995, Paller 1995a, Simonson & Lyons 1995, Mitro & Zale 2000, Patton *et al*. 2000, Cao *et al*. 2001, Daulwater & Pert 2003). For example, Angermeier and Smogor (1995) reported that between five and 14 mesohabitats (equivalent to 15 – 67 MSWs) yielded accurate (90%) estimates of species richness and species relative abundances using two-pass electric seining. Lyons (1992) recommended a minimum of 35 stream widths be sampled using single pass electrofishing to estimate asymptotic species richness (although shorter distance were required at some sites). Patton *et al*. (2000) reported that an average of 22 MSWs was required to sample 90% of species using single pass electrofishing and 38 MSWs using single-haul seine netting. This study also showed that multiple pass electrofishing plus seine netting was generally a more efficient sampling strategy (in terms of time and effort) than single pass electrofishing. In contrast, Paller (1995a, b) concluded that accurate and precise estimates of total species richness and abundance were more efficiently obtained by sampling larger areas of stream with a single electrofishing pass than by more intensive multiple-pass electrofishing of smaller sampling areas. Mitro and Zale (2000) reported that increased precision in estimates of single-species abundances could be obtained by sampling more

habitat units with single-pass electrofishing then fewer habitat units with multiple-pass electrofishing.

It is difficult to compare estimates of sampling effort and efficiency among studies and between geographic regions, and many factors can lead to different conclusions regarding optimum sampling protocols. These factors include the objectives of the study, the assemblage attributes of interest, variation in local species diversity, habitat specificity and patchiness in species distributions, physicochemical characteristics and location of the study sites in the stream network, size of the sampling units, intensity of sampling, effectiveness of sampling gear, and experience and proficiency of the sampling crews (Bohlin *et al.* 1989, Angermeier & Smogor, 1995, Paller 1995a, b, Paller *et al.* 1996, Pusey *et al.* 1998a, Mitro & Zale 2000, Meador & McIntyre 2003, Meador *et al*. 2003a, this study). In streams with very high species diversity and substantial differences between species in microhabitat use and habitat specificity, as may be the case for some North American streams, long lengths of stream may need to be sampled in order to collect the majority of species present within the reach. However, streams of south-eastern Queensland, and southern Australia in general, are not especially species-rich, nor is microhabitat specialisation so pronounced (Pusey *et al.* 2004) as to result in profound compositional changes with varying micro- or mesohabitat structure (c.f. ubiquitous distribution of many species depicted in Figure 3.5). In contrast, rivers and streams in the Wet Tropics region of northern Queensland are characterised by a high number of species, many of which are comparatively rare (Pusey & Kennard 1996, Pusey *et al.* 2004), and so comparatively greater sampling effort may be required to describe reach-scale assemblage attributes in this region.

A major objective of this chapter was to evaluate the accuracy, precision and efficiency of fish sampling protocols to estimate reach-scale fish assemblage attributes in wadeable streams and rivers for potential use for an ecosystem health ambient monitoring program in south-eastern Queensland. This chapter has shown that for fish assemblage attributes such as species richness, species composition and species relative abundances, accurate, precise and efficient estimates can be obtained from multiple-pass electrofishing plus seine netting of three mesohabitat units. Furthermore, sampling at this intensity and spatial scale protocol yielded fish assemblage data that was sufficiently accurate and precise that relatively small differences in assemblage attributes (e.g. $< 20\%$) could be detected with a high statistical power ($1\text{-}\beta > 0.95$).

Furthermore, relatively few stream reaches (e.g. < 4) needed to be sampled to accurately estimate assemblage attributes within close proximity (e.g. 20% of the half width of the confidence interval) to the true population means. Using the fish sampling protocol recommended in this chapter, an experienced field team of two or three people can sample an average of 1.5 sites per day (although this estimate obviously depends on the number of fish present at a site and the spatial distribution of sites in a river or region). Given that laboratory processing time of fish samples is minimal (i.e. fish are usually identified and enumerated in the field), this estimate compares well with the sampling and raw data processing times required for other river health indicators such as benthic macro-invertebrates, and ecosystem processes (see Smith & Storey 2001). The fish sampling protocol should therefore be suitable and cost-effective for monitoring programs that aim to detect important spatial and temporal variation in fish assemblage attributes, discern changes in response to new anthropogenic stressors, or monitor the ecological outcomes of stream rehabilitation projects (e.g. based on flow or habitat restoration). Further, the results of this chapter show that an intensive sampling program (i.e. multiple electrofishing passes over a small number of mesohabitats) would provide better estimates of local species richness for studies aimed at defining spatial variation in biodiversity (e.g. inventories for biodiversity conservation planning) than would single pass electrofishing, while simultaneously providing accurate and precise quantification of other assemblage attributes that may be applicable to a range of other future management objectives.

Chapter 4: Stability, persistence and resilience of freshwater fish assemblages across gradients of flow and habitat variability

4.1. Synopsis

The flow regimes of many Australian rivers are highly variable by world standards and those of south-eastern Queensland are no exception. In rivers of this region, low flows are unpredictable in incidence and duration and high flows may occur at any time of year. However, discharge also varies spatially within these rivers, with many major tributaries prone to frequent periods of extended zero flows, whereas others have highly constant baseflows. As consequence, channel hydraulics and hence the availability of aquatic habitat is similarly variable in timing, duration and extent. Temporal and spatial variation in flow regime and habitat structure is likely to have an important influence on fish assemblage dynamics in these rivers. In the context of assessing the potential for developing a river health monitoring program based on fish assemblages in a hydrologically variable environment, this chapter examines the role that environmental variability and hydrologic disturbance has on fish assemblage stability, persistence and resilience of attributes of fish assemblages in the Mary and Albert Rivers, south-eastern Queensland. Fish assemblage attributes that respond to anthropogenic disturbances but exhibit low natural temporal variability are potentially the most sensitive yet robust indicators of human impacts for use in bioassessment programs. Quantitative fish and habitat data were collected from 27 locations sampled seasonally over four years. A set of hydrologic and hydraulic variables was used to describe temporal variability in environmental characteristics of the study sites over this period and nine indices were used to describe intra- and inter-annual variation in attributes of the fish assemblages at each site. The results of this study indicate that fish assemblages were generally highly persistent and some attributes of fish assemblages (e.g. species richness, species composition and to a lesser extent, species relative abundances) were highly stable through time, both on an intra-annual and inter-annual basis, at the majority of sites examined. Such attributes therefore make ideal candidates for bioassessment indicators. In contrast, fish assemblages occurring in streams with highly variable flow regimes were more variable. This variability appeared due to natural impacts associated with low flow disturbance. However, fish assemblages at these sites appeared resilient to these natural disturbances, provided that flow and habitat conditions resembled the pre-disturbance state. In the context of designing temporal sampling strategies for stream

bioassessment programs, I conclude that sampling during spring and summer, when extreme natural environmental disturbances due to low flows or floods are more likely, may make the detection of changes in fish assemblages due to anthropogenic impacts more difficult. In contrast, sampling during winter should minimise the chances of natural disturbances causing changes in fish assemblages that may be difficult to quantify and maximises the potential to accurately define the reference condition expected in the absence of anthropogenic disturbance.

4.2. Introduction

Populations and assemblages of stream fishes may be influenced by a variety of physical and biological processes including landscape and local habitat features, physico-chemical conditions, resource availability, biotic interactions between species, spatial and temporal variation in recruitment and colonisation, environmental disturbance, or some combination of the above (Resh *et al*. 1988, Grossman *et al.* 1990, Schlosser 1995, Poff 1997, Matthews & Marsh-Matthews 2000, Jackson *et al.* 2001). The relative importance of these factors and has led to a divergence of views as to the stochastic versus deterministic control of freshwater fish assemblages (e.g. Grossman *et al.* 1982, Yant *et al.* 1984, Moyle & Vondracek 1985).

Numerous studies have shown that landscape scale factors (e.g. catchment size and position in the stream network) and local scale habitat characteristics (e.g. depth, water velocity and substrate composition) are important determinants of local variation in fish species composition, abundance and biomass (Gorman & Karr 1978, Meffe & Sheldon 1988, Jackson & Harvey 1989; Schlosser 1982, 1985, 1987, 1995, Schlosser & Angermeier 1995, Poff 1997, Angermeier & Winston 1998, Matthews 1998, Pusey *et al.* 1993, 1995, 2000). The results of field surveys before and after natural physical disturbance such as floods and droughts have demonstrated major changes in habitat and fish populations, potentially indicative of low resistance of fish assemblages to extreme environmental disturbances (Matthews 1986, Meffe & Minckley 1987, Stock & Schlosser 1991, Pusey *et al.* 1993, Matthews & Marsh-Matthews, 2003). However, experimental removal of target fish taxa (Gunning & Berra 1968, 1969) or of entire assemblages from habitat patches (Meffe & Sheldon 1988, 1990), without the potentially confounding influence of alteration to the physical nature of the habitat, has also yielded insights into the regulation of stream fish assemblages, indicating that fish populations and assemblages in defaunated reaches can recover to pre-manipulation levels. A strong resilience to disturbance is implied by these studies and may arise from high dispersal rates and recolonisation potential coupled with strict habitat requirements, as evidence by strong relationships between fish assemblages and habitat. Meffe and Sheldon (1998, 1990) argued that such observations collectively suggest that fish assemblages may be largely deterministic systems highly predictable from habitat structure.

This premise forms the basis of many environmental management strategies and philosophy. Examples include the allocation and determination of environmental flows (Gore & Nestler 1988, Arthington *et al.* 1992, Arthington & Pusey 2003) as well as bioassessment programs designed to evaluate river health or biotic integrity based on attributes of biotic assemblages (Wright *et al.* 2000, Karr *et al.* 1986, Karr & Chu 1999). A critical underpinning of bioassessment programs in particular, is the ability to accurately define attributes of the assemblage that are expected in the absence of anthropogenic disturbance (i.e. defining the reference condition – Reynoldson *et al.* 1997, Chapter 1). This requires that natural spatial and temporal variation in assemblages driven by variation in environmental conditions can be accounted for, to the extent that impacts of human-induced disturbance can be accurately assessed (Resh & Rosenberg 1989, Grossman *et al.* 1990, Chapter 1). 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). Temporal variation of fish assemblages can be observed at intra-annual (i.e. daily, monthly, seasonal) and inter-annual time scales and impressions of temporal variability of biota may differ according to whether or not sampling regimes are synchronised with temporal cycles of species composition and abundance (Taylor *et al*. 1996, Paller 2002). In sites with variable hydrological regimes and disturbance histories, substantially different conclusions from bioassessment of a site could be drawn from different years or times of year, even if data were collected identically on each sampling occasion and there was no change in human disturbance (Wilcox *et al*. 2002).

In this chapter I examine the influence of hydrologic disturbances (due to extreme high and low flow events) on the stability, persistence and resilience of stream fishes in south-eastern Queensland, a region of Australia characterised by highly variable and unpredictable flow regimes. Temporal variation in the discharge regime of rivers in this region, particularly in terms of the magnitude, timing, frequency and duration of flow events, is likely to influence variation in disturbance regimes, aquatic habitat connectivity, overall habitat availability and variation in attributes of habitat structure that may provide refuge, spawning sites or food resources. Hydrological disturbances also influence the constancy of species composition and the stability of population

abundances and biomass due to variation in resistance of individual species and life stages to stressful conditions. In addition, extreme discharge events drive the frequency and spatial extent of local colonisation and extinction events. Figure 4.1 depicts a conceptual model of potential hydrological mechanisms determining variation in fish assemblages through time in south-eastern Queensland rivers and streams.

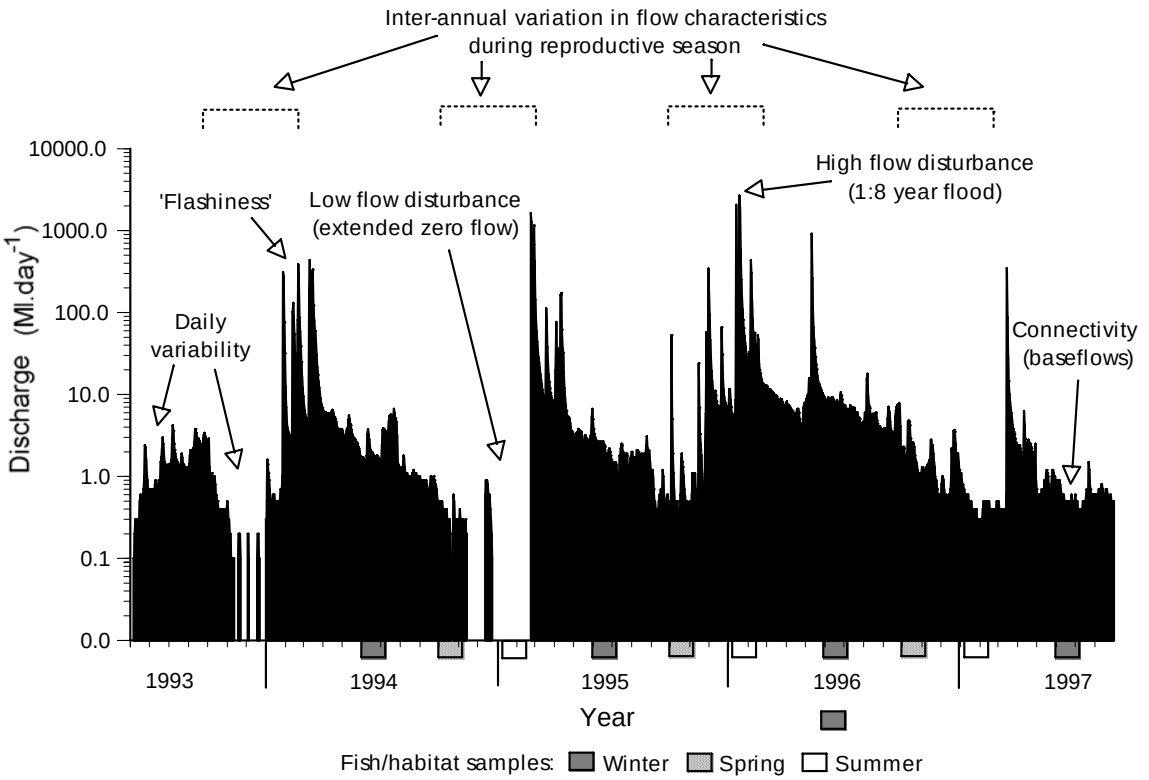

Figure 4.1. Variation in daily river discharge (Ml.day^{-1}) for Glastonbury Creek in the Mary River basin (see Figure 4.2 for location) during the period leading up to and including the study period. Arrows highlight key aspects of the flow regime of potential ecological importance for fish, and hypothesised to cause temporal variation in species composition, abundance and biomass. Also shown are the timing of fish and habitat surveys undertaken in winter, spring and summer between 1994 and 1997.

Extreme high flows may cause habitat rearrangement and physical flushing of fish downstream (Lake 2000, Pearsons *et al.* 1992). Extended periods of low flow can result in loss of longitudinal connectivity and isolation of fish in residual pools (Lake 2000, 2003, Magoulick & Kobza 2003, Matthews & Marsh-Matthews 2003). Fish may consequently be subjected to a deterioration of water quality as water levels subside (e.g. elevated temperature and salinity, low dissolved oxygen) and this also increases the potential for biotic interactions because of reduce habitat volume (e.g. competition for diminishing resources or decreased availability of refuges from avian and fish

predators) (Zaret & Rand 1971, Kushlan 1976, Mittelbach 1986, Mittelbach & Chesson 1987, Pusey & Bradshaw 1996). Ultimately, habitat desiccation and local species extinctions can occur (Lake 2000, 2003, Matthews & Marsh-Matthews 2003). Temporal variation in fish assemblages may also be associated with hydrologic conditions during the spawning season. For example, many fish species in south-eastern Queensland spawn during the period September to March (Pusey *et al.* 2004) and spawning and recruitment success of individual species may be related to the relative magnitude, timing and variability of flow events during this period (Pusey *et al.* 2004). I hypothesise that intra- and inter annual variation in these hydrologic factors are of importance to fish in terms of the temporal stability of species abundance and biomass, species persistence, and assemblage resilience to disturbance (Fig. 4.1).

In the context of assessing the potential for development of a stream health monitoring program based on fish assemblages in a hydrologically variable environment, I investigate relationships between descriptors of environmental variability and indices of fish assemblage variability. I hypothesise that if fish assemblages are resistant to environmental disturbance then summaries of fish assemblage variability over time would not be related to measures of hydrological and hydraulic variability (i.e. fish assemblages should fluctuate independently of environmental disturbance) over the same period. Alternatively, low resistance to disturbance would be indicated by comparatively greater variability in fish assemblage attributes at sites subject to frequent and/or intense disturbance. I also examine whether any relationships detected between environmental variability and fish assemblage variability are a consequence of relationships with other landscape environmental gradients or biological factors. For example, hydrologic and hydraulic habitat attributes vary with upstream catchment size, relative position in the stream network, elevation and other landscape factors (Frissell *et al*. 1986) and so the relative degree of environmental variability (and biological variability) may also be expected to vary along these landscape gradients (Horwitz 1987, Schlosser 1982). Fish assemblage attributes also vary across these natural landscape gradients (Sheldon 1968, Chapter 5, Chapter 6) potentially confounding my ability to discern relationships between environmental variability and fish assemblage variability. The total number of species, total number of individuals or total biomass of fish may also mediate or influence the degree of variability in fish assemblages and so may confound spatial patterns in the relationships between environmental variability and fish assemblage variability. Sites containing fish assemblages with high numbers of

species and individuals may be less susceptible to environmental disturbances, and hence be less temporally variable than sites with few fish, which may be more susceptible to local extinction under environmental stress (see also Tilman *et al.* 1998). I also examine whether the inclusion of rare or uncommon species influences descriptions of fish assemblage variability. Rare taxa may be more vulnerable to disturbances (due to restricted distributions coupled with low abundances) and hence may be more prone to local extinctions and/or greater temporal fluctuations than common or abundant species (Grossman *et al.* 1990, Cao and Williams 1999, Cao *et al.* 2001). Finally, I determine the resilience of fish assemblages (i.e. the ability to recover from disturbance) by comparing annual variation fish of assemblages that experienced within-year disturbance events. To this end, I examine the notion that fish assemblages should be consistent across years if environmental conditions returned to pre-disturbance state.

4.3. Methods

4.3.1. Hydrology and sampling sites

The data used in this chapter was confined to sites sampled in the Mary River and Albert River (Fig. 4.2). The majority of streamflow in these rivers occurs in the summer months of January to March, often followed by a second minor peak in discharge in autumn and early winter (between April and June) (Fig. 4.3a). The incidence and magnitude of these secondary peaks in flows is quite unpredictable, as are summer wet season flows, and thus rivers of this region tend to show high annual CV values (100% or greater) (Pusey *et al.* 2000). River discharge is highly variable, both intra- and inter-annually in comparison to other regions of eastern Australia and elsewhere (see Pusey *et al.* 1993, 2000, 2004). Discharge variability is highest during the summer months (mean coefficients of variation of daily discharge for each month usually greater than 120%, Fig. 3b) and flows during mid-winter and spring are usually low and stable (Fig. 4.3a, b). High flows (floods) can occur at any of year but are most common during summer and autumn (Fig. 4.3c). Extended periods of low flows can also occur at any time of year, but are most common during spring and summer (Fig. 4.3d). Some tributaries may cease to flow for extended periods, during which time longitudinal connectivity is lost as streams often recede to a series of isolated pools

interspersed by extensive areas of dry stream bed (Pusey *et al.* 1993; 2000; 2004; this chapter).

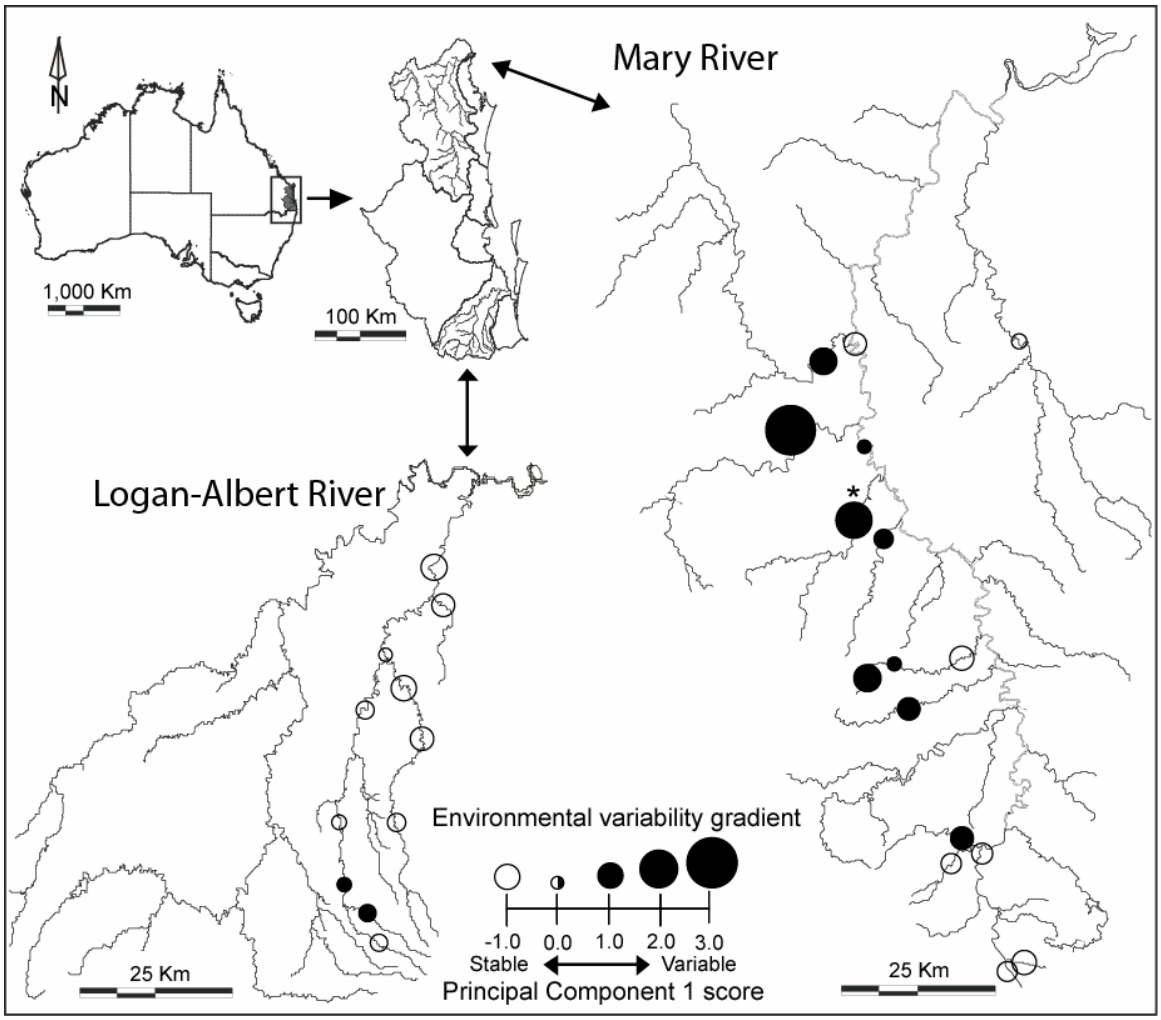

Figure 4.2. Location of the study sites (depicted by circles) in the Mary and Logan-Albert River basins in south-eastern Queensland, Australia. Site symbols are colour-coded and sized according to a gradient of relative hydrologic and hydraulic variability determined by a principal components analysis (see Table 4.1 and Figure 4.4). Negative loadings on the first principal component (depicted by larger open circles) indicate increasingly stable environmental conditions, positive loadings (larger closed circles) indicate increasingly variable environmental conditions. Glastonbury Creek, the site used to depict flow regime variation in Figure 4.1, is marked with *.

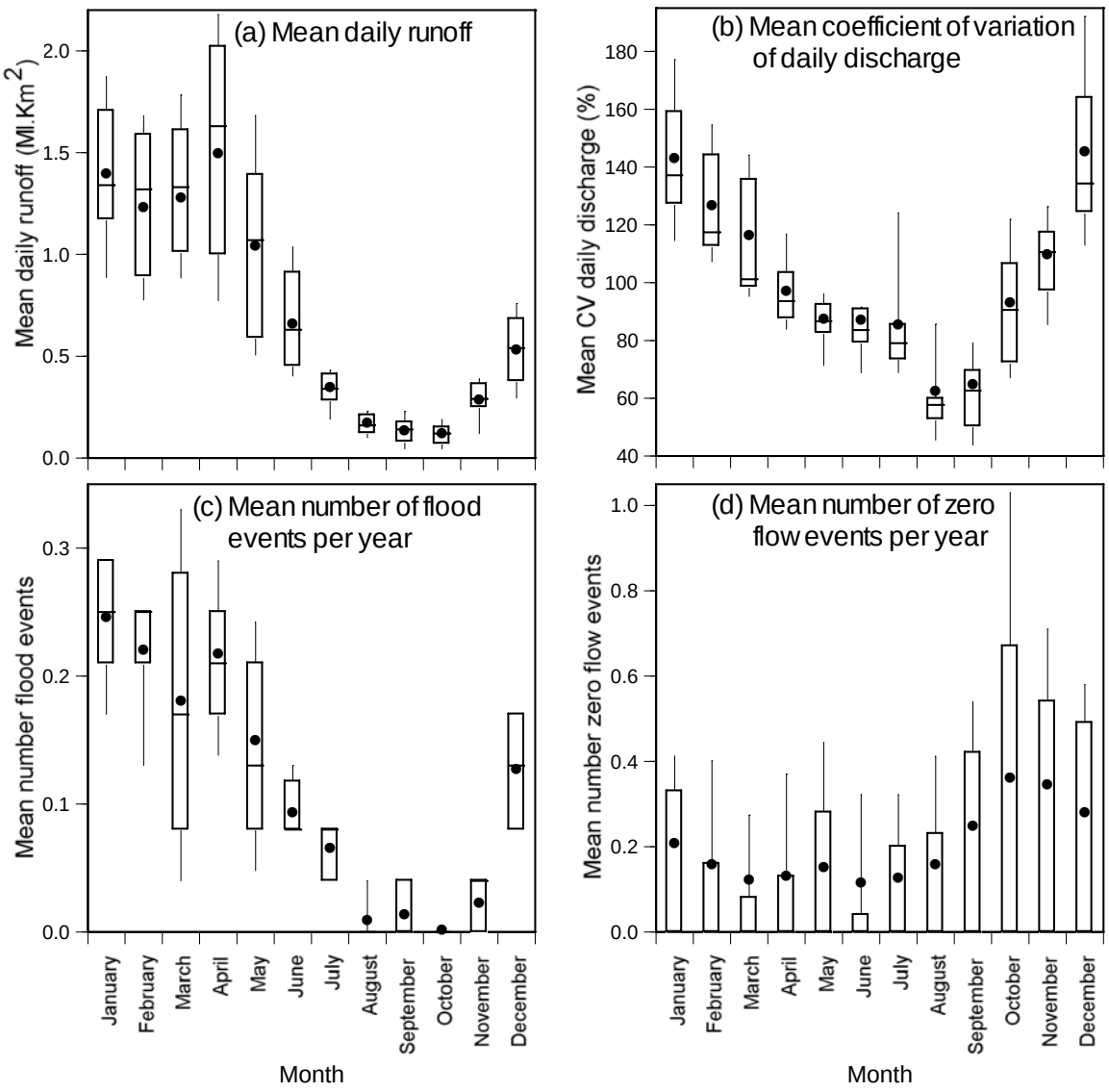

Figure 4.3. Box plots showing spatial variation in mean monthly discharge characteristics at 16 sites in the Mary River and 11 sites in the Albert River over a 25 year period (1st January 1974 – 31st December 1998). The plots show (a) mean daily runoff (Ml.Km^2), (b) mean coefficient of variation of daily discharge (%), (c) mean number of flood events per year (flood events > 1.67 year annual return interval) and (d) mean number of zero flow events per year. The lines at the top, middle and bottom of each box represent the 75th percentile, median and 25th percentile, respectively. Upper and lower bars represent 90th and 10th percentiles and means are represented by symbols.

Twenty-seven study sites in the Mary and Albert Rivers were used for examination in this chapter. The study sites were arrayed widely throughout each catchment (Fig. 4.2) to encompass as much of the natural biological and environmental variation as possible and considered to be least-disturbed (i.e. minimally disturbed riparian vegetation, bank and channel structure in natural condition, natural hydrograph, *sensu* Hughes (1995)). Fourteen of the sixteen sites in the Mary River were sampled seasonally (winter, spring and summer) on 10 occasions (between winter 1994 and winter 1997, Fig. 4.1), the remaining two sites were not sampled on the first occasion, but were sampled with a similar frequency as the other Mary River sites thereafter (total of 158 site-by-sampling occasion combinations). Eleven sites in the Albert River were sampled initially in winter 1994 and thereafter seasonally from winter 1995 to winter 1997 (a total of seven sampling occasions). Gear failure prevented sampling of six Albert River sites during spring 1996 (total of 82 site-by-sampling occasion combinations). Sampling on each occasion was usually restricted to a six week temporal 'window', during which time all sites in both rivers were sampled. I avoided sampling immediately after high flow events and on occasions when high flows occurred during the sampling window, I waited at least two weeks until flows had subsided and fish sampling could be conducted efficiently. The four-year sampling period encompassed a wide range of hydrological conditions: some streams in both catchments experienced several discharge extremes including an 8-year annual return interval flood in January 1996 and some streams in the Mary River experienced the longest period of zero flows on record.

4.3.2. Fish sampling procedures

Fish assemblages were sampled in accordance with the protocol recommended in Chapter 3 and that was consistent among sites and sampling occasions. Sites were between 70 and 80 m of stream length, usually constituting an entire meander wavelength or one riffle–run–pool sequence (Newbury & Gaboury, 1993). 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. Fish assemblages were intensively sampled using multiple-pass electrofishing (Smith-Root model 12B Backpack Electrofisher) and seine netting (11 mm stretched-mesh) until few or no further fish were collected following the protocol described and evaluated in Chapter 3. All fish collected were identified to species, counted, measured (standard length to the nearest mm) and native fish were returned alive to the point of capture.

The weight of each fish was estimated by reference to published relationships between body length and mass for each species (Pusey *et al.* 2004). From these data, I estimated species composition, abundances and biomass for each site and sampling occasion. The length of each site was fixed for the duration of the study period such that data collected from each temporal sample was directly comparable among occasions. Abundance and biomass data were standardised by site length to unsure that valid spatial comparisons could be undertaken. Note that I did not use site surface area to standardise fish catch data, as this measure of site size (and hence sample effort) varied substantially with flow variation and would have confounded my attempts to determine the effects of this environmental variability on fish populations described in terms of abundance and biomass.

4.3.3. Choice of environmental variables

I selected a set of hydrologic and hydraulic variables to describe the environmental characteristics of the study sites. I hypothesised that spatial and temporal variation in these variables may represent important drivers of, or correlates with, variation in fish species distributions, abundance and biomass in south-eastern Queensland rivers and streams. The total number of variables was limited to a subset hypothesised to be of greatest ecological relevance after examination of a correlation matrix of a larger number of candidate variables and reference to other research undertaken in the region (Pusey *et al.* 1993; 2000; 2004).

Three landscape scale variables and five local scale variables were used to describe the environmental characteristics of the study sites and were estimated according to a standard protocol described in Pusey *et al*. (2004) (Table 4.1). Landscape variables (catchment area upstream of site, distance from stream source and elevation) were estimated from 1:100,000 topographic maps using a digital planimeter. On each sampling occasion mean wetted stream width, mean water depth and mean water velocity were estimated from a series of 40-60 survey points located randomly throughout the site. Using these data, together with total site length, the surface area and volume of each site on each sampling occasion were also estimated.

Table 4.1. Median and range of values for landscape, hydrologic and hydraulic variables used to define the environmental variability template for sites in the Mary River (n = 16 locations) and Albert River (n = 11 locations). Hydrologic variability characteristics were calculated for the four-year period (June 1993 to July 1997) leading up to and including the sampling period (June 1994 – July 1997). Hydraulic variability characteristics were calculated from instantaneous measures collected on each seasonal sampling occasion (maximum of 10 samples). CV refers to coefficient of variation and ARI refers to the annual return interval flood. The variable loadings on each of the first four components of a principal components analysis are also shown (see also Fig. 4.4). The percentage variation explained by each principal component is given in parentheses and the highest variable loadings on each principal component are shown in bold type.

	Mary River		Albert River		Principal component			
					1	2	3	4
Variable	Median	Range	Median	Range	(50%)	(14%)	(11%)	(8%)
Landscape								
Catchment area (km^2)	177	26–4851	99	18–713	0.10	**0.71**	-0.18	0.10
Distance from stream source (km)	35	10–211	34	10–95	0.02	**0.92**	-0.21	0.05
Elevation (m)	70	0–160	60	0–220	-0.14	**-0.86**	-0.39	0.07
Daily flow variability								
CV of daily flow (%)	580.5	427.9–742.1	650.1	563.7–872.5	-0.04	0.02	**0.92**	0.14
Baseflow contribution								
Baseflow index	0.11	0.05–0.13	0.17	0.09–0.18	-0.48	-0.35	**-0.51**	**0.57**
High flow intensity(>1.67 ARI)								
Number of high flow events	3	1–5	2	2–3	-0.20	0.01	0.15	**0.63**
Mean duration high flow events	1.3	1.0–3.2	3.5	3.0–3.5	-0.20	0.04	0.19	**0.91**
Skewness								
Maximum/median daily flow	1643	462–7970	687	406–1310	**0.75**	-0.05	0.32	-0.34
Mean/median daily flow	12.0	6.7–100.0	4.9	3.4–6.9	**0.83**	0.00	0.22	-0.25
Low flow intensity								
Number of zero flow events	9	0–36	0	0–0	**0.57**	-0.16	0.07	-0.13
Mean duration zero flow events	13.4	0.0–97.3	0.0	0.0–0.0	**0.79**	-0.05	0.15	-0.29
Hydraulic variability								
CV of site area (%)	33.2	6.9–77.9	15.2	3.7–47.3	**0.93**	0.05	-0.13	-0.01
CV of site volume (%)	59.0	10.5–95.4	28.0	12.4–74.3	**0.91**	0.17	-0.14	-0.03
CV of site wetted width (%)	22.8	5.7–68.5	12.1	3.9–31.3	**0.92**	0.17	-0.16	-0.03
CV of site mean depth (%)	30.5	11.3–71.8	15.6	8.4–42.0	**0.89**	0.17	0.03	-0.17
CV of site mean velocity (%)	78.1	0.0–173.4	37.0	17.5–141.9	**0.60**	-0.05	0.25	-0.21

Daily discharge data for each site was simulated using Integrated Quantity and Quality Models (IQQM – Podger *et al.* 1999). IQQM models for the Mary and Albert rivers were developed using 25 years of daily flow data (1st January 1974 – 31st December 1998) from multiple gauging stations in each river (Brizga *et al.* 2004; Brizga 2005) and supplied by the Queensland Department of Natural Resources and Mines. I validated IQQM discharge estimates by estimating discharge for the day of sampling at each study site on each seasonal occasion (collected at or near baseflow conditions) using the hydraulic survey data and the methodology detailed in Newbury & Gaboury (1993) and comparing these estimates with the discharge estimates based on the IQQM models. Discharge estimates using both methods were strongly correlated at all sites (Pearson's correlation coefficients > 0.8)

4.3.4. Data analysis

4.3.4.1. Characterisation of environmental variability

I summarised the degree of temporal variability in wetted width, water depth, water velocity, surface area and volume by calculating the coefficient of variation (standard deviation/mean X 100, hereafter termed CV) of the instantaneous measurements collected on each seasonal sampling occasion. These variables are hereafter collectively termed hydraulic variability characteristics. Hydrologic variability characteristics were calculated for the four-year period (June 1993 to August 1997) leading up to and including the sampling period (June 1994 – August 1997) to capture antecedent and prevailing hydrological conditions during the sampling period. I described low flow disturbance by calculating the total number and mean duration of zero flow events during the study period. I used a zero flow event independence criterion (i.e. the number of days between the last day of a zero flow event and the start of the next event) of seven days; consecutive events not deemed to be independent based on this criterion were defined as a single event. The relative size of the maximum flow and the skewness of flow events were described by calculating the maximum/median flow and the mean/median flow, respectively. Daily variability in flow was calculated using the CV of daily flows. The relative contribution of baseflow discharge to the total discharge during a study period gives an indication of the relative importance of groundwater inflows in maintaining flows during the dry season and hence providing longitudinal connectivity for fish. I expected that the relative importance of groundwater contributions to vary spatially, depending on regional and local geomorphology and stream channel characteristics. I estimated the baseflow component of the hydrograph, hereafter termed the baseflow index, using a three-way digital filter according to the method described in Grayson *et al.* (1996). High flow disturbance was described by calculating the number and mean duration of discharge events greater then the 1.67 year annual return interval threshold (estimated from the 25 year hydrologic record at each site using the annual duration series). This high flow threshold has been used by other workers to approximate bankfull flow conditions (e.g. Poff & Allan 1995) and hence the flow magnitude yielding close to maximum water velocities, turbulence, shear stress and stream power. Although the return interval of the bankfull flood undoubtedly varies with spatial variation in stream geomorphology and channel form (e.g. the degree of channel incision), I did not have sufficient

hydraulic survey data to construct detailed hydraulic models for each site and so used this standardised surrogate for bankfull discharge based on the long-term flow regime. The flood event independence criterion was defined as seven days for these calculations. Calculation of all flow variables described above was undertaken using the River Analysis Package (Marsh *et al*. 2003).

Preliminary analyses revealed a relatively high degree of intercorrelation among some of the 13 hydrologic and hydraulic variability descriptors so I used a principal components analysis (PCA) to described the major gradients of environmental variability in a smaller number of orthogonal components. I also included the three landscape variables in this analysis to examine whether the degree of environmental variability at a site was confounded by position in the landscape and catchments size, factors also known to influence fish assemblages (see Section 4.1). The PCA was based on the correlation matrix, and loadings of the original variables on each of the first four principal components were used to identify the dominant gradients in the data set.

4.3.4.2. Characterisation of fish assemblage stability and persistence

I calculated a series of indices to describe the relative degree of variation in fish assemblages at each site during the study period (i.e. incorporating intra- and inter-annual temporal variation). Connell & Sousa (1983) recommended that the minimum temporal requirement for a study of assemblage stability is one complete turnover for the assemblage. However Grossman *et al.* (1990) suggested that this is unnecessary for species with a quantifiable age structure (as is the case for many fish species) and instead recommended (p. 662) that "sampling should encompass at least one mean generation time of the assemblage dominants" to ensure that potential low adult mortality in conjunction with high longevity and low recruitment (Frank 1968, Davis & van Balricom 1978) do not yield artifactual evidence of stability. I estimated the mean generation time (i.e. the age at which sexual maturity is reached by females) for 26 of the 31 species sampled in this study for which life history data is available (Pusey *et al.* 2004, McDowall 1996) as 2.8 years ± 5.2 SD. When calculated for the 20 species collectively forming 95% of the total abundance (and excluding two species of *Anguilla*, which may live for well over 30 years before they reproduce), mean generation time was estimated as 1.1 years ± 0.9 SD. Both estimates of mean generation time are well within my 4-year study period.

There are many potential ways in which to characterise the sample of fish collected at a site. These can include the abundance and biomass of individual species, assemblage level characteristics (e.g. species composition, species relative abundance and species relative biomass), and the collective properties of assemblages (e.g. species richness, total abundance and total biomass). There are also many potential numerical or statistical methods to characterise the variability of these assemblage attributes. Temporal variation in the collective properties of fish assemblages at each site (i.e. total species richness, total standardised abundance and total standardised biomass) was described by the CV of data collected over the study period. Temporal variation in fish assemblage composition, species relative abundance and species relative biomass data was described by calculating the average Bray-Curtis similarity between all possible seasonal sampling combinations (hereafter referred to as total variability) and between each successive seasonal sample (hereafter referred to as sequential variability). I used the Bray-Curtis measure to estimate between-sample similarity as it is widely used in ecological studies and is regarded as an effective measure of ecological association for a range of multivariate data types (Faith *et al*. 1987; Legendre and Legendre 1998). However, two of the study sites were completely dry on one and two sampling occasions, respectively, and so contained no fish. Bray-Curtis similarity between samples cannot be calculated if one of the samples contains all zeroes (i.e. a complete absence of species), so for these three samples I replaced the missing similarity values with zeroes for calculations of average temporal similarity in fish assemblages. This is a conservative approach, as to exclude these fishless samples would have resulted in an underestimate of the true temporal variability at these sites. I also calculated the mean CV of fish assemblage members (Grossman 1990, Oberdorff *et al.* 2001) described in terms of individual species abundances and biomass. Here, I calculated the CV of abundance and biomass of each species collected on each sampling occasion and took the average for the entire assemblage at each site.

Finally, I calculated the average persistence of the species assemblage at each site during the study period. Assemblage persistence (P), the inverse of the turnover rate (T), describes the repeated extinction and immigration of populations in ecological assemblages (McArthur & Wilson, 1967; Oberdorff *et al.* 2001). Following Schoener and Spiller (1987) and Oberdorff *et al* (2001), the relative turnover rate (T) of each fish

assemblage over a unit time interval (i.e. between two sampling occasions) $t_2 - t_1$, was defined as:

$$T = (E + I) / (LSR\ t_2 + LSR\ t_1)$$

where E = extinctions of species already present, I = immigrations of new species, LSR t_1 = local species richness at time t_1 and LSR t_2 = local species richness at time t_2. T ranges from 0 (no turnover) to 1 (complete turnover) so persistence (P = 1 – T) ranges from 0 (no persistence) to 1 (complete persistence). I calculated the average of P for all possible sequential time period comparisons (i.e. total variability), and for each successive seasonal sample (sequential variability). Total variability and sequential variability indices calculated for fish assemblage composition, species relative abundance, species relative biomass and assemblage persistence were highly correlated for each fish assemblage data set (Pearson's r values all greater then 0.94), so I hereafter report only total variability data for these indices. This approach is consistent with the scale at which measures of environmental variability were estimated (i.e. for the entire study period rather than between successive sampling occasions).

The seven fish assemblage variability indices described above were calculated using all species and individuals collected at each site and sampling occasion. I also re-calculated these indices after excluding rare and uncommon species. My criteria for defining rarity necessarily varied, depending on the fish assemblage index. For indices describing variation in total species richness, assemblage composition and assemblage persistence, species were excluded if they were present in less than 50% of the sampling occasions at a site. For indices based on total abundance and relative abundance data, species were excluded if they individually formed less than 5% of the mean total abundance or mean relative abundance over the study period, respectively. For indices based on total biomass and relative biomass data, species were excluded if they individually formed less than 1% of mean total biomass or relative biomass, respectively. To allow comparisons with data presented in Grossman *et al.* (1990) and Oberdorrf *et al*. (2001), I calculated the mean CV of fish assemblage members after excluding species that were present in less than 50% of the sampling occasions at a site.

4.3.4.3. Relationships between environmental variability, fish assemblage variability and potential confounding factors.

The fish assemblage variability indices calculated for all seasonal samples (i.e. total variability and sequential variability) describe the relative degree of stability and persistence of fish assemblages through time at each site. High stability and persistence of fish assemblages would be suggestive of low environmental variability or high resistance to disturbance regimes, whereas high variability in fish assemblages and a strong correlation between fish assemblage variability and environmental variability would imply a low degree of resistance to disturbances. Relationships between indices of environmental variability (as summarised by the principal components analysis) and fish assemblage variability (log (x+1) transformed) at 27 sites in the Mary and Albert Rivers, were examined using Pearson's correlation. This analysis also examined whether any relationships detected between environmental variability and fish assemblage variability were an artefact of relationships with other landscape gradients related to catchment size and position in the stream network. The total number of species, total number of individuals or total biomass of fish may mediate or influence the degree of variability in fish assemblages and so may confound spatial patterns in the relationships between environmental variability and fish assemblage variability. To investigate this, I calculated the mean species richness, mean total abundance and mean total biomass at each site and examined relationships of these summary attributes with indices of fish assemblage variability using Pearson's correlation.

4.3.4.4. Characterisation of fish assemblage resilience

I specifically examined the resilience of fish assemblages (i.e. the ability to recover from disturbance events) using the temporal variability indices described above, but calculated on an annual time step (i.e. annual variability). A high degree of similarity between annual samples would suggest a strong ability to recover from disturbance, despite large intra-annual variation in environmental characteristics and fish assemblages at some sites resulting from possible short-term disturbance events. For these analyses I used Mary River data only (due to a higher frequency of sampling in comparison to the Albert River sites) and performed inter-annual comparisons calculated for winter samples (n = 4 years), spring samples (n = 3 years) and summer samples (n = 3 years). In this analysis I examine the notion that fish assemblages

should be consistent across years if habitat is also consistent (i.e. that fish are resilient to environmental variability and disturbance and will recover if habitat conditions return to the pre-disturbance state). I hypothesise that winter samples should be more concordant though time because stream hydrology and hence hydraulic habitat characteristics are less variable inter-annually than during spring and summer (during which time extreme high or lows occur more often). As described above for calculations of total variability in fish assemblages, I calculated annual variability indices (for assemblage composition, relative abundance, relative biomass and assemblage turnover) for all possible annual combinations (total annual variability) and for sequential annual comparisons (sequential annual variability) but all indices were highly correlated (Pearson's r values all greater then 0.90), so I report only total annual variability data. Annual variability indices were calculated using all species collected at each site and annual sampling occasion and re-calculated after excluding rare and uncommon species using the same criteria as described earlier. Indices of total annual variability of fish assemblages were compared for season using graphical methods (cumulative frequency distributions). I also used Spearman's rank correlation to examine whether the rank order of sites was consistent among years in terms of hydraulic characteristics and fish assemblage attributes (species richness, total numerical density, and total biomass density) and compared the concordances of these data between the winter, spring and summer annual comparisons. Between-year changes in the ranked abundance and biomass of each species pooled over all study sites for each annual sample were examined by Spearman's correlation. These analyses were conducted for each possible between-year comparison for each season to further test the degree of concordance among years, depending on the time of year (season) in which sampling was undertaken.

Paller (2002) suggested that computations that involve repeated use of the same data (such as all possible pairs of species counts) have the potential to violate the assumption of independence required for accurate statistical testing. I addressed this issue using Paller's (2002) approach of applying runs up and down tests and runs above and below the mean tests (Sokal & Rolf, 1981) calculated for sequential seasonal and annual sampling data, however these tests indicated no significant departures from randomness. To minimise the chances of inflated Type I error rates (false positives) due to the large number of comparisons in each set of correlation analyses, I used a Bonferroni correction method (the Dunn-Sidak procedure – Quinn and Keough, 2002) and used a conservative significance level of $p<0.01$.

4.4. Results

4.4.1. Environmental variability template

Study sites in the Mary River were generally located on larger streams than in the Albert River and so had larger upstream catchment areas, but sites in both rivers had similar median values for distance from stream source and elevation (Table 4.1). Streams in the Albert River never ceased to flow during the study period, however periods of zero flow occurred in 11 stream sites in the Mary River, with one site experiencing 36 individual zero flow events during the 4 year study period. The maximum mean duration of zero flow events was almost 100 days (Table 4.1), and one site experienced two very long individual zero flow events lasting 227 days and 475 days, respectively (this latter event commenced on 11/10/1996 and continued after the cessation of the study to 28/01/1998). Flow events in the Mary River tended to show greater skewness than flows in the Albert River (i.e. high ratios of maximum to median flow and mean to median flow), probably due to the frequency of extreme low flows and comparatively lower contribution of baseflow discharge than in the Albert River (Table 1). Between one and five high flow events (i.e. flows greater than the 1.67 year annual return interval) occurred at the Mary River sites during the study period, in comparison to between two and three events at Albert River sites, however high flows in the Albert River tended to persist for slightly longer periods on average. Although many sites in both rivers also experienced an 8-year annual return interval flood in January 1996, this had relatively little effect on habitat structure at most sites. Measures of hydraulic variability covered a greater range of conditions at sites in the Mary River than in the Albert River, with some sites being of similarly low variability among catchments, but others were much more variable during the study period (Table 4.1). Median CV values for each hydraulic variable were greater in the Mary River than in the Albert River. Principal components analysis reduced the initial 16 landscape, hydrologic variability and hydraulic variability descriptors to four components that accounted for 83% of the total variation in the data (Table 4.1). Component 1, explaining 50% of the variation, described a gradient of zero flow intensity and hydraulic variability (Table 4.1), with highly variable sites being arrayed positively on this axis (mostly sites located on western tributaries of the Mary River – Figures 4.2 and 4.4) and stable sites arrayed negatively on this axis (mostly upland and main channel sites in the Mary River and almost all Albert River sites – Figures 4.2 and 4.4).

Variables describing the skewness of flow also loaded positively on principal component 1, probably because the denominator in the calculation of these indices (median daily flow) tended towards very low flow values at sites with extended periods of zero flow, hence the respective ratios of maximum and mean flows to median daily flows was comparably larger than in sites that never ceased to flow. A gradient describing spatial variation in catchment size, site position in the stream network and elevation (Component 2), was orthogonal to all the hydrologic and hydraulic variability gradients, indicating that these landscape factors should not confound my interpretations of responses of fish to environmental variability *per se*. Component 3 described a gradient of daily flow variability and baseflow contribution (Table 4.1, Fig. 4.3) and Component 4 described the high flow characteristics of the study sites (Table 4.1).

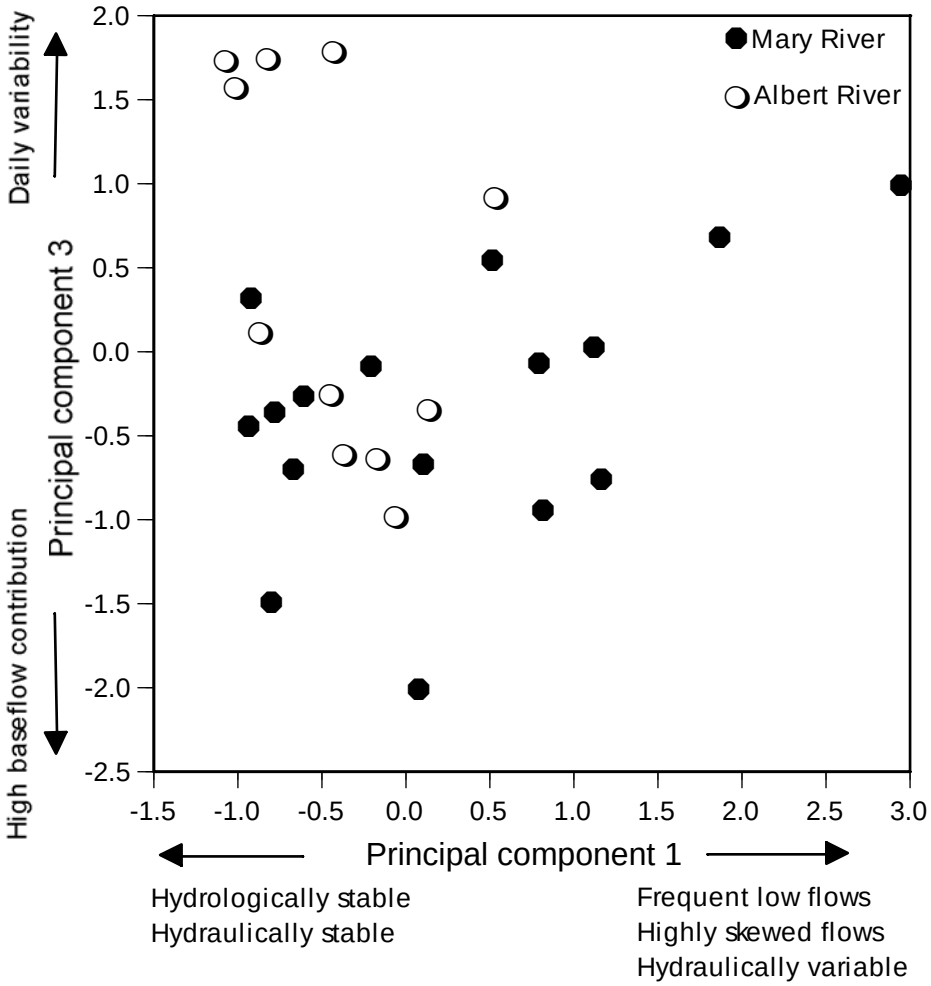

Figure 4.4. Spatial variation in Mary River and Albert River sites across an environmental variability template described by a principal components analysis of landscape, hydrologic and hydraulic variables (PC1 *vs* PC3). Principal component 1 (50% of the variance) describes a gradient of low flow and hydraulic variability and principal component 3 (11% of the variance) describes a gradient of daily flow variability and baseflow contribution. Variable loadings on each component are given in Table 4.1.

4.4.2. Fish assemblage variability and relationships with environmental variability and potential confounding factors

A total of 31 fish species from 14 families, 93,642 individuals and 933.2 (kg) of fish were collected from the 27 sites and 240 seasonal samples in the Mary and Albert Rivers during the study period. Fish assemblage variability indices calculated using all species and the same indices re-calculated after excluding rare and uncommon species were strongly correlated (Pearson's r values > 0.94 for most comparisons), except for mean CV of individual species abundance and biomass, which were less strongly correlated (r = 0.67 and 0.49, respectively) (Table 4.2). I hereafter mostly discuss the results based on variability indices calculated using all species and individuals. Many of the individual fish assemblage variability indices were strongly correlated with one another, especially indices describing variation in species richness, total abundance, species composition, species relative abundances and assemblage persistence, suggesting that environmental variation affected these attributes of fish assemblages in similar ways during the study period. Fish assemblages characterised in terms of biomass data generally appeared to fluctuate through time independently of the other fish assemblage attributes (Table 4.2).

Between-river comparisons of fish assemblage indices describing total variability during the study period revealed that the Mary River contained sites with a greater range of variability values than those of the Albert River, and this was consistent for all indices of fish assemblage variability (Fig. 4.5). Fish assemblages (described in terms of species richness, species composition and assemblage persistence) were generally highly concordant among all sampling occasions throughout the study period at most sites in the Mary River and all sites in the Albert River (Fig. 4.5). The majority of sites had very low CV values for species richness (usually < 30%), high average similarity in species composition (usually > 80%) and high persistence values (> 0.8). Exceptions to this pattern included three sites in the Mary River that were more variable than all other sites in both rivers. The CVs of total abundance (25 – 120%) and total biomass (40 – 210%) were comparatively larger than corresponding species richness CV values, indicating that total abundance and total biomass were more variable through time than the total number of species present at a site (Fig. 4.5). Similarly, variation in fish assemblages described in terms of species relative abundances and species relative biomass were comparatively more variable through time than species composition

(Bray-Curtis similarity values usually less than 80%) (Fig. 4.5). The mean CV of assemblage members described in terms of individual species abundance and biomass was generally high in both rivers (CV values usually ranging between 100 and 200%).

Table 4.2. Pearson's correlation coefficients for relationships between indices of biological variability (based on all species and individuals), environmental variability and biological co-variates at 27 sites in the Mary and Albert Rivers, south-eastern Queensland sampled on 7 – 10 occasions between 1994 and 1997. Indices of environmental variability are the principal component scores from the analysis presented in Table 4.1 and Figure 4.4. Significant correlations are shown in bold type ($p<0.01$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn and Keough, 2002)). Correlations between fish assemblage calculated before and after excluding rare and uncommon species are also shown (underlined), all except mean CV of individual species biomass were significant at $p<0.01$.

Variable	Acronym	CVRICH	CVTA	CVTB	SIMCO	SIMRA	SIMRB	MCVIA	MCVIB	MP
Biological variability index										
CV species richness	CVRICH	0.956								
CV total abundance	CVTA	**0.826**	0.997							
CV total biomass	CVTB	0.314	0.434	0.999						
Mean similarity species composition	SIMCO	**-0.931**	**-0.752**	-0.272	0.942					
Mean similarity relative abundance	SIMRA	**-0.562**	-0.449	-0.348	**0.701**	0.981				
Mean similarity relative biomass	SIMRB	-0.337	-0.341	**-0.622**	0.414	**0.575**	0.997			
Mean CV individual species abundance	MCVIA	0.503	0.498	-0.048	**-0.665**	-0.477	-0.013	0.664		
Mean CV individual species biomass	MCVIB	0.413	0.442	0.058	**-0.581**	-0.386	-0.024	**0.953**	0.491	
Mean persistence	MP	**-0.930**	**-0.746**	-0.285	**0.996**	**0.723**	0.435	**-0.661**	**-0.570**	0.985
Environmental variability index										
Low flow variability and hydraulic variability	PC 1	**0.748**	**0.566**	0.341	**-0.730**	**-0.720**	**-0.561**	0.250	0.129	**-0.742**
Catchment size	PC 2	-0.017	0.015	-0.005	-0.202	-0.474	-0.012	0.478	0.491	-0.208
Daily flow variability	PC 3	0.211	0.111	0.361	-0.269	-0.062	-0.488	-0.010	-0.045	-0.284
High flow intensity	PC 4	0.104	0.226	-0.038	-0.160	0.050	-0.082	0.426	0.468	-0.134
Biological covariates										
Mean species richness		-0.225	0.330	0.145	0.118	-0.395	-0.440	-0.309	-0.355	0.096
Mean total abundance		-0.052	-0.145	0.071	-0.005	-0.168	-0.047	0.099	0.082	0.031
Mean total biomass		-0.088	0.023	-0.275	-0.069	0.085	0.468	0.474	0.457	-0.070

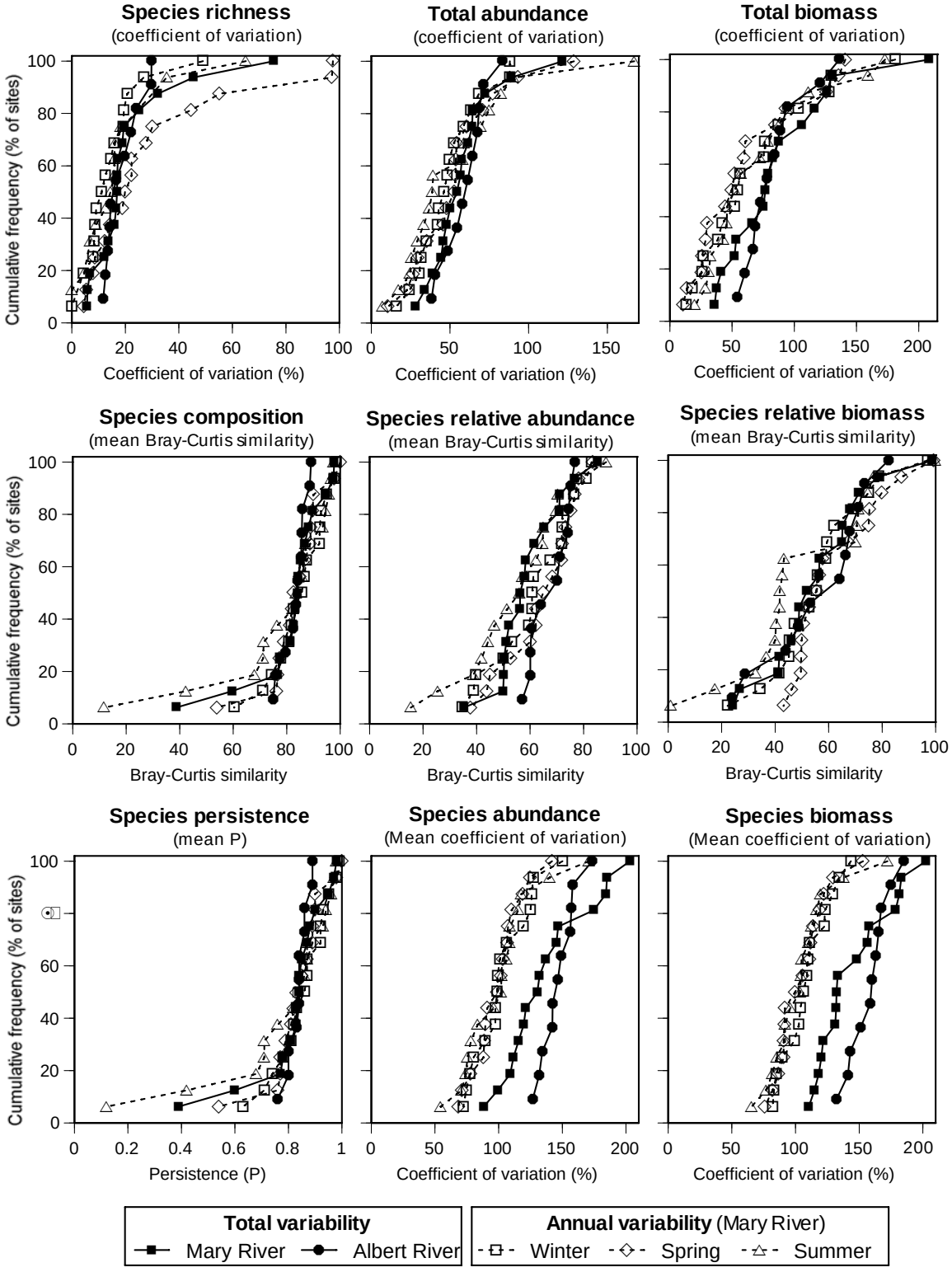

Figure 4.5. Cumulative frequency distributions of total variability in fish assemblage attributes during the study period for sites sampled in the Mary River (closed squares) and Albert River (closed circles). Also shown are cumulative frequency distributions of annual variability in fish assemblage attributes for comparisons of winter samples (open squares), spring samples (open diamonds) and summer samples (open triangles) in the Mary River. See text for explanation of each fish assemblage variability index.

All fish assemblage indices (except CV total biomass and mean CV of individual species abundance and biomass) describing total variability during the study period were strongly positively correlated (Pearson's $r > 0.61$) with the gradient of increasing environmental variability describing low flow and hydraulic variability (i.e. PC 1) (Table 4.2). Highest fish assemblage variability was observed at the subset of Mary River sites that were subject to high environmental variability due to repeated and/or extended periods of low flow. Streams on which these sites were situated ceased to flow repeatedly during the study period, often forming a series of isolated pools that sometimes dried out completely, resulting in highly variable hydraulic conditions (e.g. in terms of width, depth, surface area and volume). Fish assemblages in these drying pools became less diverse, fish densities sometimes increased as water levels contracted (the maximum numerical density recorded in a small isolated pool was 26.5 $fish.m^{-2}$ *versus* a mean across all sites and samples of 5.8 ± 4.1 SD), but fish populations ultimately declined until localised extinctions occurred (i.e. no fish remained) provided that the duration of zero flow was sufficient to cause complete desiccation and that the residual pools were not connected to the water table. Fish assemblage variability indices were not significantly correlated with the landscape environmental gradient (PC 2) or the other hydrologic variability gradients (PC 3 and PC4). None of the fish assemblage variability indices were correlated ($p>0.01$) with the potential biological covariates of mean species richness, mean total abundance or mean total biomass at each site (Table 4.2), suggesting that fish assemblages varied independently of the total species pool, or the total number and biomass of fish at the study sites.

4.4.3. Resilience

Fish assemblages in the Mary River were very consistent across years despite potentially substantial within-year disturbances (floods and extreme low flows) at some sites, suggesting a high capacity for fish assemblages to recover from disturbance provided that habitat conditions return to the pre-disturbance state. Hydraulic habitat characteristics were generally highly concordant among years at most sites, but more so for winter samples than for spring or summer samples. The rank order of sites in terms of each hydraulic habitat attribute was generally most strongly correlated and always significant ($p<0.01$) for annual comparisons of winter samples (mean Spearman's r values usually greater than 0.8) (Table 4.3). Incidences of zero flows, habitat

desiccation and consequently, major changes in hydraulic habitat characteristics, were more common during spring and summer than in winter. Mary River sites ranked in terms of species richness were highly correlated among years during the winter sampling occasion (mean Spearman's r = 0.727), but not as strongly correlated during spring (r = 0.595) or summer (r = 0.426) (Table 4.3). Total fish abundance and fish biomass were generally not strongly correlated among years (r values usually less than 0.5), however the ranking of sites based on species abundances and species biomass were highly concordant between years for all seasonal sampling periods (mean Spearman's r values usually greater than 0.88, all comparisons significant at $p<0.01$).

Table 4.3. Mean spearman's rank correlation coefficients (± SD) and number of significant correlations for relationships between years in the rank order of magnitude of hydraulic characteristics and fish assemblage attributes (species richness, total abundance and total biomass) among sites. Mean correlation coefficients for between-year relationships in the ranked abundance and biomass of each species pooled over all study sites each for annual sample are also shown. Analyses were conducted for every possible between-year comparison for each season (winter, spring and summer). Correlations were corrected for multiple comparisons using the Dunn-Sidak procedure (Quinn and Keough, 2002) with a significance level of $p<0.01$.

	Winter			Spring			Summer		
Variable	**Mean *r***	**SD**	**# sig.**	**Mean *r***	**SD**	**# sig.**	**Mean *r***	**SD**	**# sig.**
Site area	0.890	0.031	6/6	0.738	0.119	2/3	0.785	0.067	3/3
Site volume	0.869	0.040	6/6	0.759	0.013	3/3	0.644	0.027	2/3
Wetted width	0.833	0.096	6/6	0.644	0.160	2/3	0.720	0.104	2/3
Average depth	0.785	0.066	6/6	0.769	0.029	3/3	0.546	0.085	1/3
Average velocity	0.700	0.039	6/6	0.803	0.086	3/3	0.487	0.135	1/3
Species richness	0.727	0.116	6/6	0.595	0.103	1/3	0.232	0.426	1/3
Total abundance	0.495	0.072	3/6	0.537	0.051	1/3	0.317	0.247	1/3
Total biomass	0.214	0.173	0/6	0.441	0.092	0/3	0.227	0.158	0/3
Species abundance	0.889	0.059	6/6	0.886	0.016	3/3	0.920	0.039	3/3
Species biomass	0.717	0.156	6/6	0.881	0.038	3/3	0.922	0.039	3/3

Cumulative frequency distributions of sites based on indices of fish assemblage variability calculated on an annual basis (Fig. 4.5) for each season also indicate that winter samples were less variable among years than other sampling seasons, and that fish assemblages were resilient to within-year disturbance regimes. Fish assemblages (described in terms of species richness, species composition and species persistence) were generally highly concordant among the four annual samples collected in winter (Fig. 4.5). The exception to this was the comparatively high annual variability in these fish assemblage attributes at one site that was completely dry on the final winter sampling occasion (in 1997). This lead to greater variability in fish assemblage

attributes at this site as hydraulic habitat conditions had not yet returned to pre-disturbance conditions. For most fish assemblage indices, annual variability estimated for winter samples was lower than annual variability during spring and summer or for estimates of total variability during the entire study period (Fig. 4.5). Some sites sampled during spring and summer had higher CVs of species richness, lower average similarity in species composition and lower persistence values than comparisons made during winter. These sites had recently experienced or were experiencing periods of zero flow and desiccation at the time of sampling during spring and summer. The patterns described here were generally consistent for fish assemblage variability indices describing CV of total abundance and biomass, and similarity in species relative abundance and biomass (Fig. 4.5).

The differences between estimates of annual variability and total variability for the mean CV of assemblage members described in terms of species abundance and biomass were much more pronounced than differences observed for the other fish assemblage indices (Fig. 4.5). Much of the variability in individual species abundances and biomass was due to intra-annual (seasonal) variation and these attributes of fish assemblages were substantially more concordant on an inter-annual basis. Annual mean CVs of individual species abundance calculated using all species ranged between 56% and 162% (median 100%) (Fig. 4.5). Coefficients of variation of species abundances calculated only for prevalent species (i.e. occurring in 50% or more of annual samples) did not differ greatly, ranging between 55% and 171% (median 100%).

4.5. Discussion

4.5.1. Stability and persistence

The stability of an assemblage of organisms subject to disturbance may arise from resistance (the ability to withstand a disturbance) or resilience (sometimes referred to as elasticity but meaning the ability to recover to a pre-disturbance state) (Connell & Sousa 1983). The results of this study indicate that some attributes of fish assemblages (e.g. species richness, assemblage composition and assemblage persistence) were highly stable through time, both on an intra-annual and inter-annual basis, at the majority of sites examined. For some fish assemblage attributes, my indices of annual variability were equivalent to values reported elsewhere, but others appeared were more variable.

Paller (2002) reported that the mean CV of total species richness in undisturbed streams of the South Carolina coastal plains was 16%, roughly equivalent to the median values (20% or less) observed in this study. My measures of assemblage persistence were similar to those reported by Obdedorff *et al.* (2001), with the majority of sites in both studies usually having P values greater than 0.8. My estimates of temporal variability of total abundances (median CV around 50%) were slightly higher than reported by Paller (2002) (mean CV 44%). Furthermore, temporal similarity in assemblage structure based on species relative abundance data observed in this study (median Bray-Curtis similarity 60%) was slightly lower than reported by Paller (2002) (mean similarity 67%). Freeman *et al.* (1988) proposed an arbitrary classification scheme in which values of the mean CV of assemblage members greater than 76% were described as highly fluctuating. The majority of the Mary River sites examined in this study can therefore be classified as highly fluctuating based on this criteria, with my estimates of average assemblage variability based on the annual CVs of species abundances calculated for common species (occurring in 50% or more of annual samples) usually higher than 75% (range 55% – 171%, median 100%, Fig. 4.5). The number of years over which my CV estimates were derived was within the range (but at the lower end of the scale) of other similar studies, however my estimates of assemblage variability are comparable with studies of undisturbed streams in France (range 56 – 121%, Oberdorrf *et al.* 2001), France and west Africa (84 – 155%, Hugueny *et al.* 1995, cited in Oberdorrf *et al.* 2001) and several studies in the mid-western USA (70 – 135%, summarised by Grossman *et al.* 1990). The use of variability indices based on temporal fluctuations in populations of individual species does not however, describe assemblage-level behaviour or provide an index of variability of entire assemblages (Grossman *et al.* 1990, Matthews 1998). As concluded by Grossman *et al.* (1990), the relative degree of temporal variability in fish assemblages appears to depend on the assemblage attribute(s) of interest, the statistical or numerical manner in which the variability is quantified, the relative magnitude of environmental variability in the study region from which the data is collected, and probably, a range of other factors.

4.5.2. Covariates and confounding factors

This chapter revealed that indices of fish assemblage variability or environmental variability were not significantly correlated with the landscape environmental gradients such as catchment size or position in the stream network (i.e. PC 2, Table 4.2). This is

contrary to a dominant paradigm in stream ecology that fish assemblages are less temporally variable in environmentally stable lowland or main channel streams in comparison to hydrologically variable headwater streams (e.g. Horwitz 1978, Schlosser 1982, 1985, 1995). I suggest that for many rivers and streams in the south-eastern Queensland region, hydrologic and hydraulic habitat variability is a function of geomorphologic and climatic factors (relating to groundwater contribution and habitat permanence) and that variation in these factors do not necessarily correspond to catchment size or position in the stream network.

Sampling error associated with the spatial scale of sampling (i.e. undersampling of rare, uncommon or patchily distributed species) has the potential to influence impressions of temporal variability of biota (McArdle *et al.* 1990, Lohr & Fausch 1997, Paller 2002). The data used in this chapter was based on standardized and intensive sampling of three mesohabitat units equivalent to a riffle-run-pool sequence. In Chapter 3 I showed that sampling at this spatial scale yielded reach-scale estimates of fish assemblage attributes highly similar to those sampled at twice reach length (i.e. 6 mesohabitats, Chapter 3). Therefore I argue that observed temporal variability of fish assemblages was not a consequence of undersampling. In addition, rare or uncommon species (i.e. those most likely to be underestimated by undersampling) appeared to have little influence on estimates of fish assemblage variability, probably because environmental disturbances associated with extended periods of low flow and hydraulic variability were such a strong structuring force on rare and common species alike. The absence of relationships between fish assemblage variability indices and the mean total species richness, abundance or biomass of the study sites, suggests that these factors did not confound my descriptions of temporal variability and relationships with environmental variability. This is consistent with theoretical predictions (Tilman *et al.* 1998) and the findings of Oberdorrf *et al*. (2001).

4.5.3. Relationships of fish assemblage variability with environmental variability

Most descriptors of fish assemblage variability used in this study were strongly associated with increasing environmental variability. Interestingly however, indices describing the mean CV of assemblage members based on individual species abundances or biomass were not found to be positively associated with any of the environmental variability gradients. This is contrary to the results of the only other

study available that have directly examined the relationship between this index of assemblage variability (mean CV of assemblage members) and environmental variability (Oberdorff *et al.* 2001). My results suggest that the abundance and biomass of individual species may fluctuate through time in response to other environmental or biological mechanisms not accounted for in this study (e.g. recruitment effects, resource availability, and/or biotic interactions), but that the temporal variability of entire assemblages (e.g. species composition and assemblage structure) and their collective properties (e.g. species richness, total abundance and total biomass) are more strongly related to environmental disturbances. The subset of sites examined in this study that were characterised by high environmental variability also contained comparatively variable fish assemblages (as has been observed by Ross *et al.* (1985), Mathews *et al.* (1988) and Oberdorff *et al.* (2001)). This suggests that fish assemblages were not resistant to strong disturbances caused by extended periods of low flow, hydraulic habitat variation and occasional habitat desiccation. However, fish assemblages were highly resilient to these natural hydrologic disturbances, provided that habitat conditions returned to the pre-disturbance state.

4.5.4. Mechanisms enabling resilience to disturbance

Resilience to disturbance could have arisen by a number of mechanisms including: 1) colonisation by adult fish moving from adjacent and/or distant stream reaches, 2) *in situ* reproduction from newly colonised adult fish and subsequent recruitment of juveniles, 3) colonisation by new recruits dispersing from natal habitats elsewhere in the catchment, or 4) a combination of these processes. It is impossible, on the basis of the data collected in the present study, to determine which of these mechanisms was responsible for the observed resilience as the study period was longer than the generation time of many of the small-bodied species and *in situ* reproduction may well have occurred. Comparisons of length frequency histograms for individual species to detect the size or source of colonists were generally uninformative (data not shown).

Many of the fish species present in the study rivers are known to undertake movements and migrations at a range of spatial scales for the purposes of feeding, reproduction and dispersal into new habitats (Pusey *et al.* 2004). In fact, a mass dispersal phase appears characteristic of juveniles and sub-adults of many species occurring in south-eastern Queensland. Periodic localised extinction and recolonisation episodes are a feature of

many tributary streams in rivers of this region due to frequent drying episodes that result from extended periods of zero flow (Fig. 4.3). Pusey *et al.* (1993) reported re-establishment of fish assemblages following severe flooding in the Mary River. The pronounced temporal variation and unpredictability of the hydrologic regime, and hence habitat availability, may have acted as selective environmental filters (*sensu* Poff 1997) over very long time scales thereby influencing the subset of species able to colonise and persist in the region. Resident species may have evolved specific traits over long periods of time allowing high tolerance to inimical water quality conditions in low flow refuge habitats, as well as the production of recruits to coincide with favourable habitat conditions and a capacity for rapid and extensive dispersal or colonisation (Poff & Ward 1989, Detenbeck *et al*. 2002, Poff & Allan 1995, Taylor 1997, Pusey *et al.* 1998b, Labbe & Fausch 2000). It would be instructive to monitor recolonisation at short time intervals to examine the sequence of species appearance, the size/age composition of colonists (as an indication of the source of colonists) and the rate of re-establishment of the original fish assemblages.

Models of species dispersal and ultimately settlement in a particular habitat are varied. In streams of south-eastern Queensland, recolonisation of hydrologically disturbed sites is unlikely to be a random process or the result of passive diffusion from refuge areas elsewhere in the stream network (*sensu* Sheldon 1984b). Rather, it may be a deterministic process governed by habitat selection and species assortment along preferred environmental gradients. Fretwell (1972) suggested that optimal behaviour by colonisers results in an 'ideal free distribution' in which no individual would increase its fitness by being elsewhere. Such hypotheses make the assumption that individuals can perceive or make qualitative judgements as to the suitability of a particular habitat (Bernstein *et al.* 1988). Experimental defaunation and habitat manipulations (e.g. Meffe & Sheldon 1990, Harvey & Stewart 1991, Peterson & Bayley 1993, Bayley & Osborne 1993) provide evidence for active habitat selection by stream fishes. Meffe and Sheldon (1990) argued that the observed resilience of fish assemblages in blackwater streams following perturbation (defaunation in this case) was due to an overriding influence of habitat structure which they had previously identified as being strongly correlated with assemblage structure (Meffe & Sheldon 1988).

In the context of the present study, it is difficult to accept that passive diffusion or random colonisation should lead to the recovery of fish assemblages in the absence of a

strong mediating influence of habitat structure. This view is also supported by the concordance between the extent of habitat change and fish assemblage change observed in the Mary and Albert rivers. Moreover, examination of the relationship between landscape and local scale habitat gradients and fish assemblage attributes such as species composition (Chapter 5) and species richness (Chapter 6) clearly shows that habitat is strongly associated with fish assemblages in south-eastern Queensland rivers and streams (see also Pusey *et al.* 1993, 2000).

4.5.5. Implications of temporal variability for river health assessment

Temporal variation in fish assemblages can be observed at intra-annual and inter-annual time scales and impressions of temporal variability of biota may differ according to whether or not sampling regimes are synchronised with temporal cycles of species composition and abundance (Taylor *et al*. 1996, Paller 2002). This has important implications for stream management and bioassessment programs that aim to evaluate the health or integrity of aquatic ecosystems based on departures of biotic assemblages from the expected natural condition, and that aim to assess the magnitude and likely sources of impact of human disturbances. Wilcox *et al.* (2002) cautioned that successional changes in biotic assemblages following major hydrologic disturbance may occur over periods of years and that repeat sampling of sites in years with different histories of past hydrologic disturbance would not yield similar results, even if the intensity of human disturbance remained constant. Hence, criteria used to define the reference condition would need to take long-term changes into account (Wilcox *et al*. 2002). In hydrologically variable environments, it is possible that valid definitions of reference conditions need to be developed separately for each of several hydrological histories (reflecting long-term recovery from major hydrologic disturbances) and/or seasons (reflecting intra-annual variation in antecedent and prevailing hydrologic conditions and natural seasonal changes in fish assemblages). In sites with variable hydrological regimes and disturbance histories, substantially different conclusions from bioassessment of a site could be drawn from different years or times of year, even if data were collected identically on each sampling occasion and there was no change in human disturbance. High natural variability in fish assemblages, driven by variable environmental conditions, may lead to highly complex procedures to accurately and precisely define the reference condition. This could also restrict development of reference conditions and biotic assessment applications to stringent qualifying

antecedent and prevailing hydrological conditions, potentially making them costly and ultimately impractical for wide adoption by management agencies (Wilcox *et al*. 2002).

Inter-annual comparison of fish assemblage attributes revealed that fish assemblages sampled during winter were less variable among years than other sampling seasons. This is in agreement with the initial hypothesis that winter samples should be more concordant though time because stream hydrology and hence hydraulic habitat is usually (but not always) less variable inter-annually than during spring and summer (during which time extreme high or lows occur more often). In the context of designing temporal sampling strategies for stream bioassessment programs, sampling during spring and summer, when extreme natural environmental disturbances due to low flows or floods are more likely (Fig. 4.3), may make the detection of changes in fish assemblages due to anthropogenic impacts more difficult. In contrast, sampling during winter should minimise the chances of natural disturbances causing changes in fish assemblages that cannot be predicted from simple environmental descriptors (as are used in the predictive models described in Chapters 5 and 6) and hence reduces the chances of incorrectly diagnosing a site as impacted by human activity (i.e. committing a Type 1 error). Sampling at a time of year when longitudinal movement by fish is not restricted by low flows and fish are able to assort along preferred environmental gradients also maximises the opportunity to detect relationships between fish assemblages and natural habitat gradients and to construct predictive models of these relationships that factor out this source of natural spatial variation in fish assemblages (see Chapters 5 and 6).

Fish assemblage attributes that respond to anthropogenic disturbances but that exhibit low natural temporal variability are potentially the most sensitive yet robust indicators of human impacts for use in bioassessment programs (Paller 2002). Total numbers and biomass of individuals and the abundance and biomass of individual species were comparatively more variable in the study area than measures of total species richness, assemblage composition and assemblage structure (based on species relative abundances). This suggests that measures of individual species abundance and biomass may not be appropriate candidate indictors of human disturbance in south-eastern Queensland rivers and streams, unless the extent of human impact is extreme.

In the next chapter (Chapter 5) I evaluate the ability to develop and apply a multivariate

predictive model of fish assemblage composition using relationships with natural environmental gradients. Regions subject to strongly seasonal and/or unpredictable environmental fluctuations may be less amenable to the development and application of such predictive models.

Chapter 5: Development and application of a predictive model of freshwater fish assemblage composition to evaluate river health

5.1. Synopsis

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. I 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 relatively high environmental variability due to the unpredictable nature of rainfall and river discharge. The model was considered 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 the model was comparable to outcomes from such studies. In addition, the 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 that resulted in habitat desiccation and local fish extinctions).

This Chapter forms the basis of the following journal manuscript:

Kennard, M.J., Pusey, B.J., Arthington, A.H., Harch, B. D. & Mackay, S.J. (In Press). Utility of a multivariate modelling method for prediction of freshwater fish assemblages and evaluation of river health. *Hydrobiologia*.

5.2. 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*. 2001) 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 or health 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 evaluating their potential use as indicators of river health in Australia. However, bioassesment 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 multimetric 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*. 2001) 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 (Horwitz 1978, Poff & Ward 1989, Poff & Allen 1995, Pusey *et al*. 2000, Williams *et al*. 2003), and hence accurately define the reference condition (*sensu* Reynoldson *et al*. 1987), may be difficult in systems of high environmental variability. 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 test 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 modeling (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 (Turak *et al*. 1999, Smith *et al*. 1999).

In this chapter, I construct a predictive model of fish assemblage composition based on relationships with a small number of catchment scale and local scale environmental features. I construct the model using a set of least-disturbed reference sites sampled on one occasion during one season. I 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. I 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.

5.3. Methods

5.3.1. Reference, validation and test site data sets

A data set 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 (Figure 5.1). Reference were selected 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).

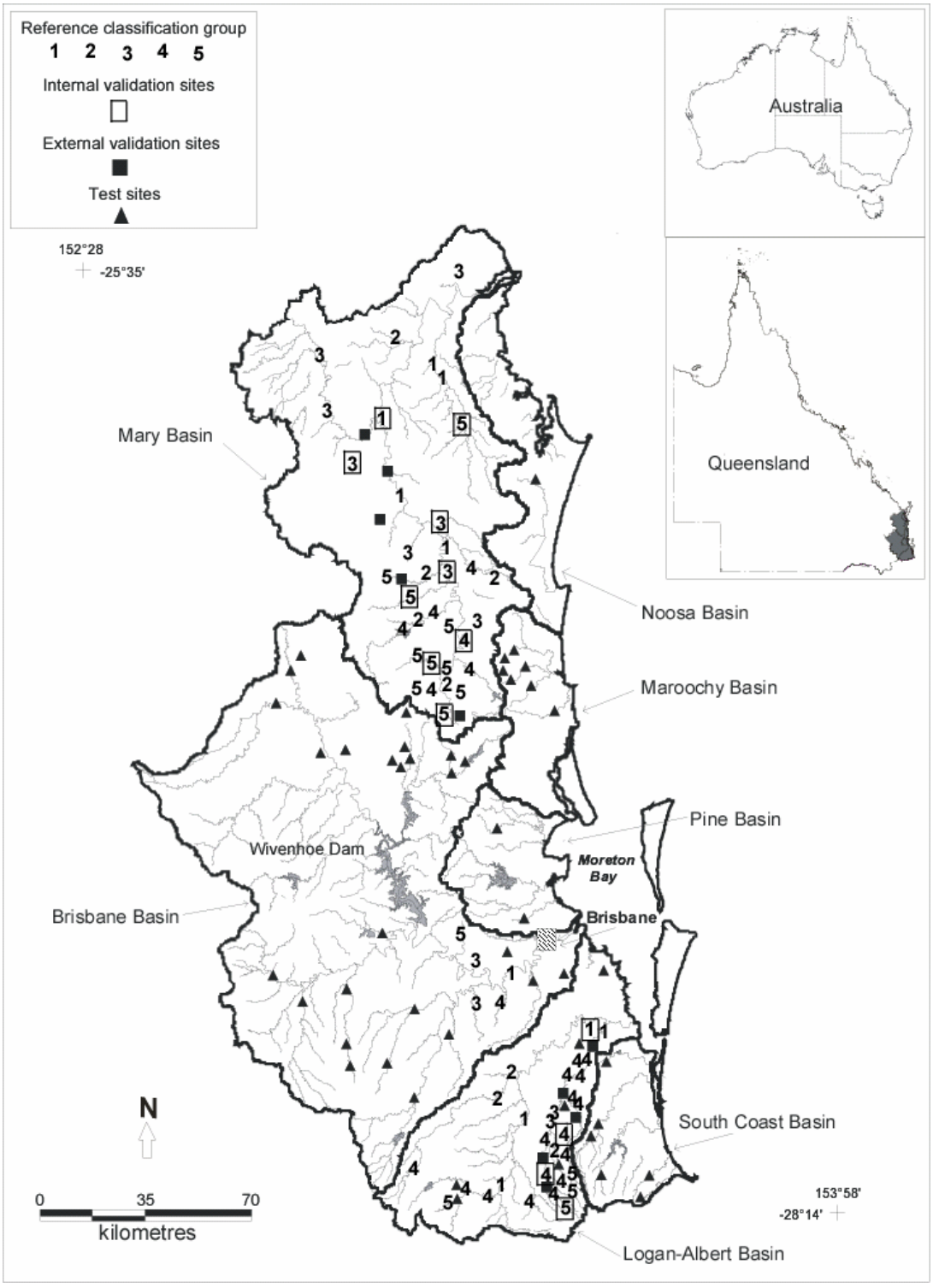

Figure 5.1. Location of reference sites (numbered by classification group membership), validation sites and test sites in south-eastern Queensland (Note: some sites located close together overlay each other and hence may not visible on map). Major impoundments are also depicted. The inset shows the location of the study area in Queensland, Australia.

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. I constructed the predictive model using data collected on the first winter sampling occasion for each site and river. As described in Chapter 4, the four-year sampling period was characterised by a highly variable hydrologic regime during which some rivers of the study region 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. I 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, Chapter 4), 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.

I 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 data sets. 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 data set 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 data set comprised the remaining ten least-disturbed reference sites withheld from the original reference data set 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. 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 5.1). The exception to this was a small number of test sites located on streams with slightly smaller catchment areas (three sites), or were closer to the river mouth (four 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; I therefore considered that the three data sets (reference, validation and test sites) were acceptable for initial model development, validation and testing.

Table 5.1. Range and median values of environmental predictor variables at reference, validation and test sites. 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 *).

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 ($m.sec^{-1}$)	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

5.3.2. Fish sampling procedures

Fish assemblages were sampled in accordance with the protocol recommended in Chapter 3 and that was consistent among all reference, validation and test sites. Each of three contiguous individual mesohabitat units (i.e. riffles, runs or pools) within each reach was intensively sampled and data subsequently combined to represent each site. 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.$10m^{-2}$).

5.3.3. Estimation of environmental variables and characterisation of human disturbance gradient

Catchment and local scale environmental characteristics of the study sites were estimated according to a standard protocol described in Chapters 3 and 4 (Table 4.1). 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.

I 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 (Table 5.2). 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. I hypothesise 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 (Table 5.2). I recognise that many of the variables used to characterise the disturbance gradient may vary along natural environmental gradients, however I did not have the capacity to account for this natural variation in the present study. I 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) provide further justification and rationale for the use of these variables to describe the disturbance gradient. Methods used to measure each disturbance variable are given in Table 5.2.

Table 5.2. Variables used to quantify the source and intensity of anthropogenic disturbance at each site. Variables describe human land use, water chemistry, riparian vegetation and in-stream habitat characteristics. A description of each variable, the expected generalised response to disturbance (in parentheses) and the range of values observed at the test sites are given. Numbers in superscript refer to the methods used to measure each variable.

Variable	Description	Minimum	Maximum
Land use [1]			
% catchment cleared	Percentage of total catchment area cleared of native vegetation	0	90.0
% catchment grazed	Percentage of total catchment area subject to cattle grazing	0	87.0
% catchment cropped	Percentage of total catchment area subject to agricultural cropping	0	24.6
% catchment urban	Percentage of total catchment area subject to urban development	0	66.2
Water chemistry			
Conductivity ($\mu S.cm^{-1}$) [2]	Measure of total concentration of dissolved inorganic ions (increase)	91	5300
Turbidity (NTU) [2]	Measure of decreased ability of water to transmit light due to total suspended particulate matter (increase)	1	200
pH [2]	Measure of water acidity or alkalinity based on the concentration of hydrogen ions (increase or decrease)	5.2	9.1
Total nitrogen ($mg.l^{-1}$) [3]	Measure of nutrient pollution (increase)	0.1	7.9
Total phosphorus ($mg.l^{-1}$) [3]	Measure of nutrient pollution (increase)	0.01	7.1
Dissolved oxygen diel range ($mg.l^{-1}$) [4]	Range of dissolved oxygen recorded over 24 hour period (increase)	0.5	12.4
Temperature diel range (^{o}C) [4]	Range of water temperature recorded over 24 hours period (increase)	0.7	9.1
Riparian vegetation [5]			
Riparian cover (%)	Reach-scale estimate of percent canopy cover of the stream (decrease)	0	95.8
In-stream habitat [6]			
Mud (%)	Visual estimate of the percentage of stream bed covered by mud (<0.06 mm maximum particle diameter) (increase)	0	100.0
Aquatic macrophtyes (%)	Visual estimate of the percentage of stream bed covered by aquatic macrophytes (increase)	0	61.6
Filamentous algae (%)	Visual estimate of the percentage of stream bed covered by filamentous algae (increase)	0	42.4
Submerged terrestrial vegetation (%)	Visual estimate of the percentage of stream bed covered by invasive terrestrial weeds (increase)	0	33.9

[1] Estimated from GIS databases

[2] Mean of three measurements using Greenspan sensors and DT50 data logger

[3] Single sample taken in unfiltered, detergent-washed bottle; laboratory analysis

[4] Range calculated from half-hourly measurements recorded by data logger over 24 hour period

[5] Mean of three measurements using spherical densiometer

[6] Mean of 40-60 individual estimates surveyed at $1m^2$ points located randomly throughout site

5.3.4. Statistical methods

5.3.4.1. Development of predictive model

I 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). I 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). I chose this somewhat arbitrary threshold as it is frequently used in RIVPACS-style applications in Australia and North America, and it allowed a comparison of the accuracy and precision of the 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).

I 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, I compared frequency distributions, means and standard deviations of O/E scores generated for the reference sites used to construct the model. I 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, I also evaluated the match between O and E using simple linear regression models. I 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 I also compared the width of the 10^{th} and 90^{th} 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). I 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.

5.3.4.2. Model validation and the effect of temporal variation on model performance

For each validation data set I 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. I 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, I used an approach similar to Barmuta *et al*. (2003). For each data set I 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. I 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, I examined whether O/E score for temporal samples of validation sites remained within the reference band (based on the $90^{th} – 10^{th}$ percentile of reference site O/E scores).

5.3.4.3. Model testing and sensitivity to disturbance

The sensitivity to human disturbance of the 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. I used *t*-tests to determine if mean O/E scores for the test sites differed significantly from those of reference sites. I related test site O/E scores to the suite of variables describing the source and intensity of disturbance at the test sites (Table 5.2). 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. A similar approach has been used elsewhere (e.g. Meador *et al.* 2003, Sloane and Norris 2003). 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 data set. 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).

5.4. Results

5.4.1. 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.

5.4.2. Model development: classification and discriminant analysis

I 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 (Figure 5.1) 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 variables could significantly discriminate between site groups (Table 5.3, $p<0.001$). 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.

5.4.3. 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 5.4). 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 5.4). 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 5.4).

Table 5.3. Mean density (number of fish.100m^{-2}) (± SE) and frequency of occurrence (percentage of sites) of the 24 fish species within each reference site group defined by UPGMA classification. 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 ($p<0.001$).

UPGMA 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.sec^{-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

Table 5.4. 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%. The width of the reference band (90^{th} – 10^{th} 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.

	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

Frequency distributions of reference site O/E scores at PO_{50} were more tightly distributed around unity than those generated at PO_0 (Figure 5.2), resulting in a narrower width of the reference band (90^{th} – 10^{th} percentile) (Table 5.4), also suggesting greater precision in the match between observed and expected assemblages.

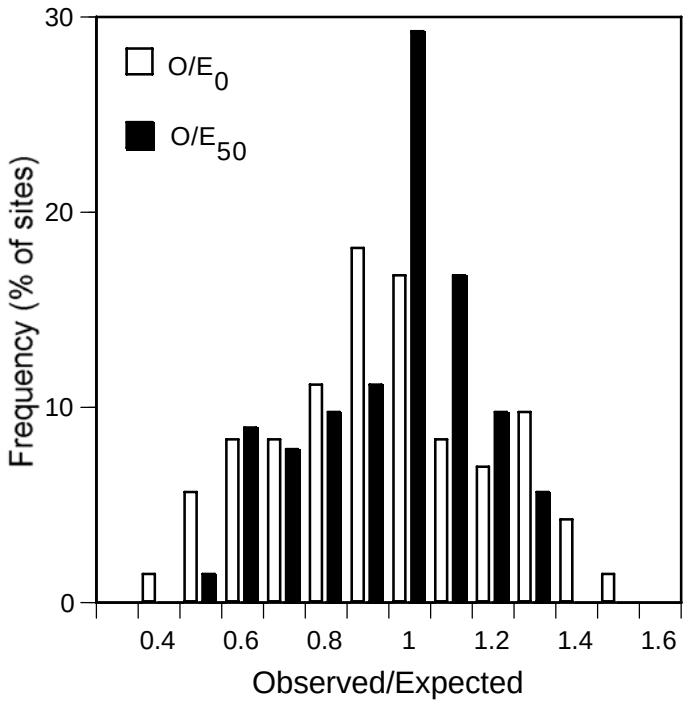

Figure 5.2. Frequency distributions of observed over expected ratios for the 72 reference sites at probability of occurrence thresholds of PO>0% (open bars) and PO>50% (closed bars).

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 ($R^2 = 0.43$) (Figure 5.3a & b). Although not 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 (Figure 5.3a & 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 ($P<0.001$) (Figure 5.3c & 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. I 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.

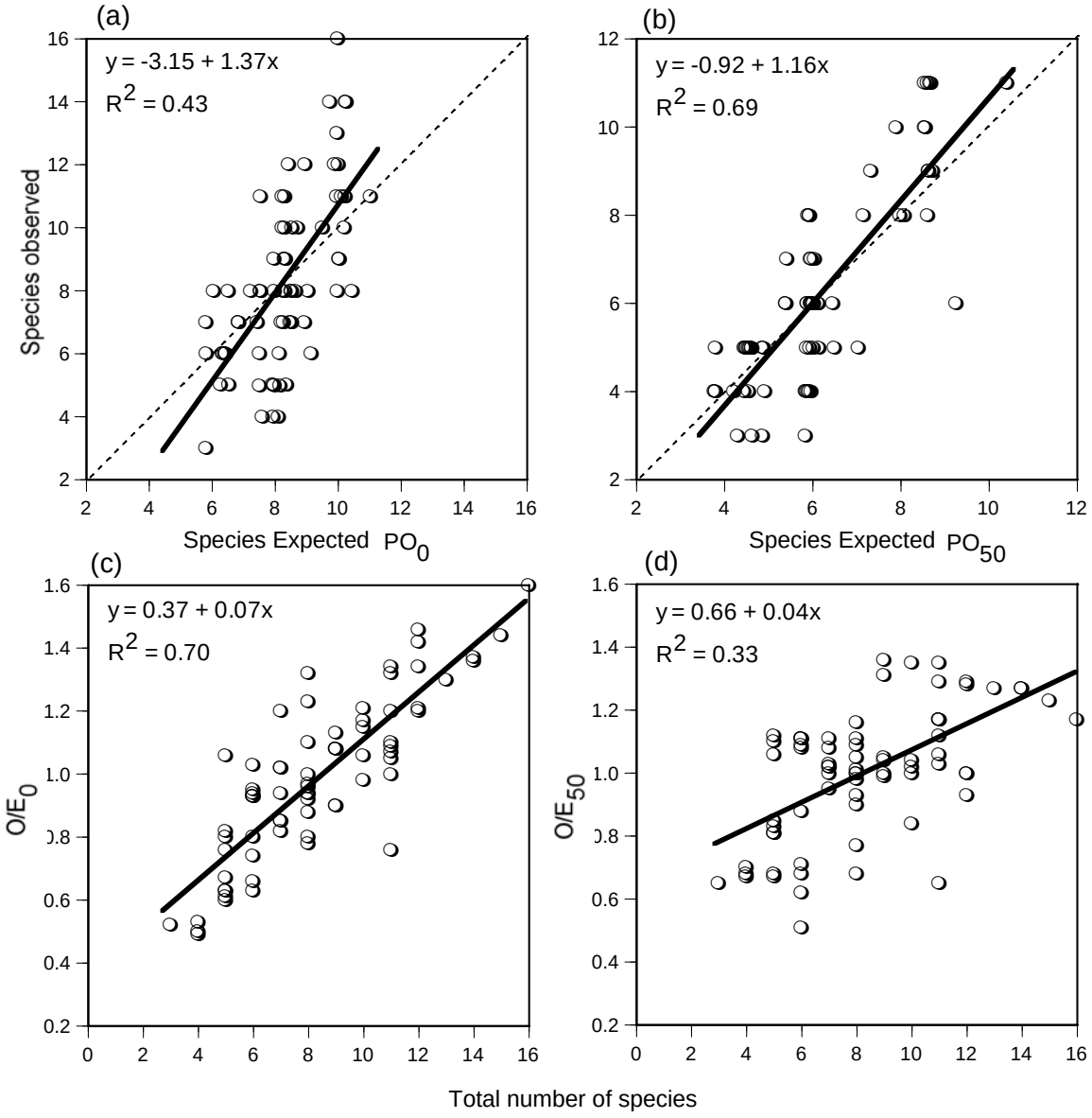

Figure 5.3. Relationship between expected and observed values for (a) PO_0 and (b) PO_{50} probability of occurrence thresholds at reference sites. The diagonal dashed lines represent the line of perfect agreement between the two measures. Regression lines and equations for each plot are also shown. 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.

5.4.4. 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 ($R^2 = 0.59$, Figure 5.4a) and for sites and samples foreign to the reference model ($R^2 = 0.62$, Fig. 5.4b). 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 I 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).

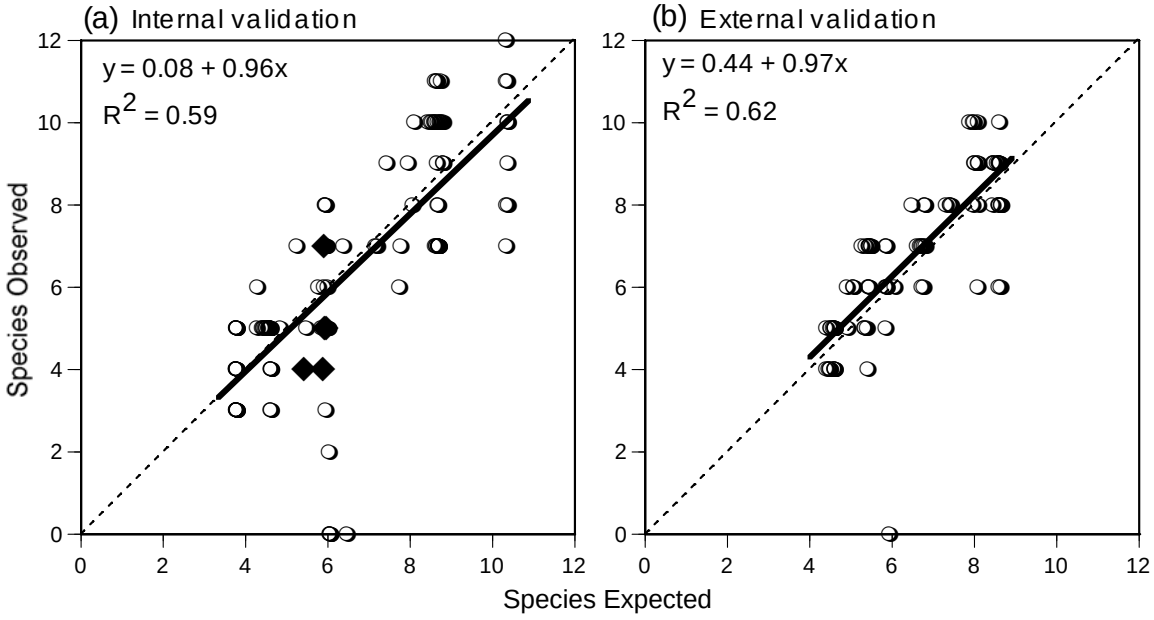

Figure 5.4. Relationship between expected and observed values for (a) internal validation samples and (b) external validation samples at the PO_{50} probability of occurrence threshold. The five internal validation sites sampled during spring 2000 are shown as black diamonds (note that two sites directly 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 data set, $p>0.05$ for H_o: slope = 1 and H_o: Intercept = 0.

The degree of temporal concordance and synchrony of ranked O/E scores was generally weak among rivers and validation data sets (Figure 5.5, Table 5.5). 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 5.5).

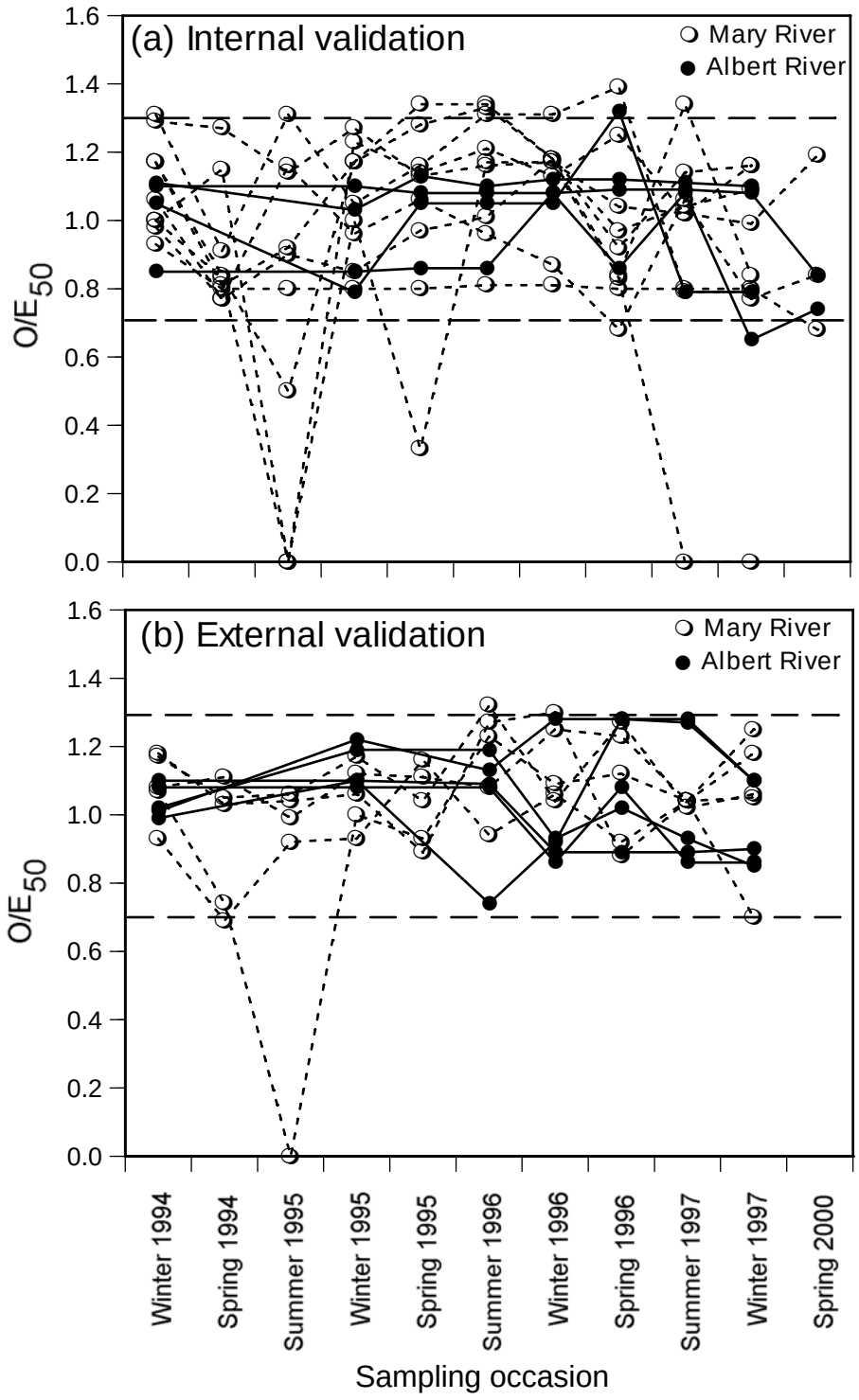

Figure 5.5. Temporal variation in O/E_{50} scores for (a) internal validation samples and (b) external validation samples in the Mary River (open circles) and Albert River (closed circles). The 90^{th} – 10^{th} percentile reference band is depicted with horizontal dashed lines. Internal validation sites sampled in Winter 1994 (Figure 5.5a) 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.

Table 5.5. 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. 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 OE_{50} scores through time.

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

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 5.5). 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 sites O/E scores for each sampling occasion remained within the reference band (Figure 5.5a & b and Figure 5.6a), 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 (Figure 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 (Figure 5.5a & b). These sites were located on tributary streams that ceased to flow for prolonged periods, becoming either small isolated pools or desiccating completely.

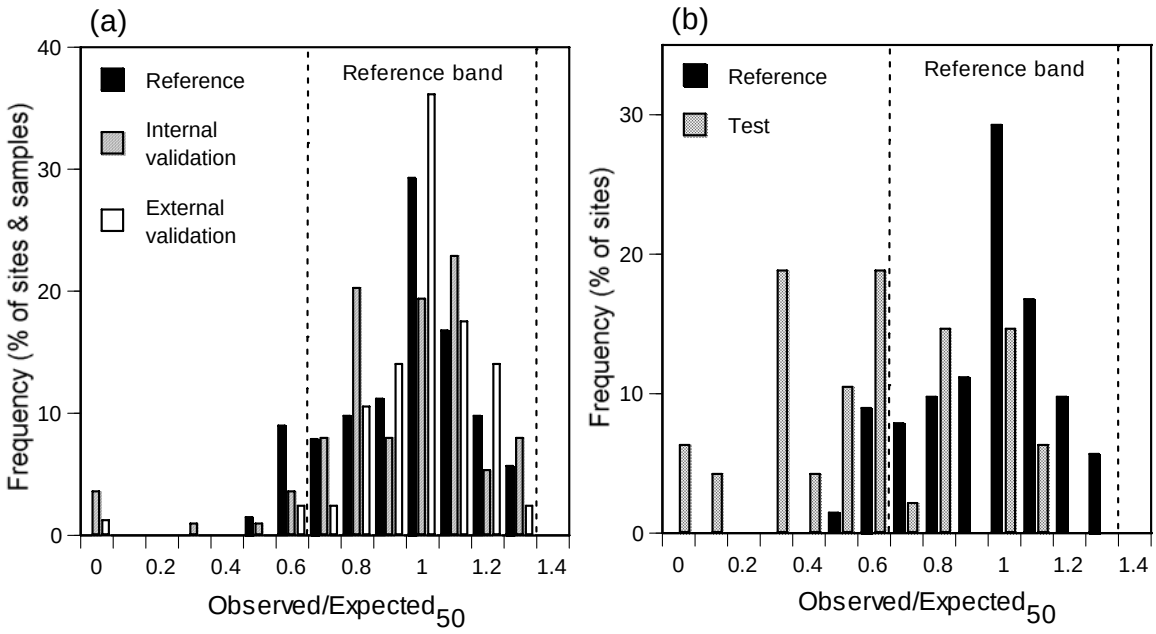

Figure 5.6. Frequency distributions of O/E_{50} ratios for (a) reference, internal validation and external validation sites and (b) reference and test sites). Vertical dashed lines indicated the width of the reference band.

5.4.5. Testing the ability of the predictive model to detect human disturbance

Principal components analysis reduced the initial 16 disturbance variables to five components that accounted for 79% of the total variation in the data (Table 5.6). Component 1 described a gradient of land use (clearing and grazing) and water chemistry (diel temperature range, pH and conductivity). Component 2 was associated with riparian vegetation degradation, aquatic vegetation infestations and high diel dissolved oxygen range. Component 3 reflected a nutrient gradient, Component 4 was associated with muddy substrates, high turbidity and cropping in the catchment and Component 5 described catchment urbanisation and infestations of submerged terrestrial vegetation. 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, $p>0.05$). I 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.

Table 5.6. Principal components analysis of 16 disturbance variables from the 47 test sites in south-eastern Queensland. 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.

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 macrophtyes	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**

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 (Figure 6b): this latter result is suggestive of biological impairment at these test sites. A multiple regression model using disturbance gradient principal components 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 5.7). 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 5.7. 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. 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.

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	-
PC3	High nutrients	-
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%

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) (Figure 5.7). 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 (Figure 5.7). 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 (Figure 5.7). These sites were characterised by a relatively high percentage of urban development in the catchment, high total nitrogen levels and high amounts of filamentous algae. These results may indicate that *C. stercusmuscarum* 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.

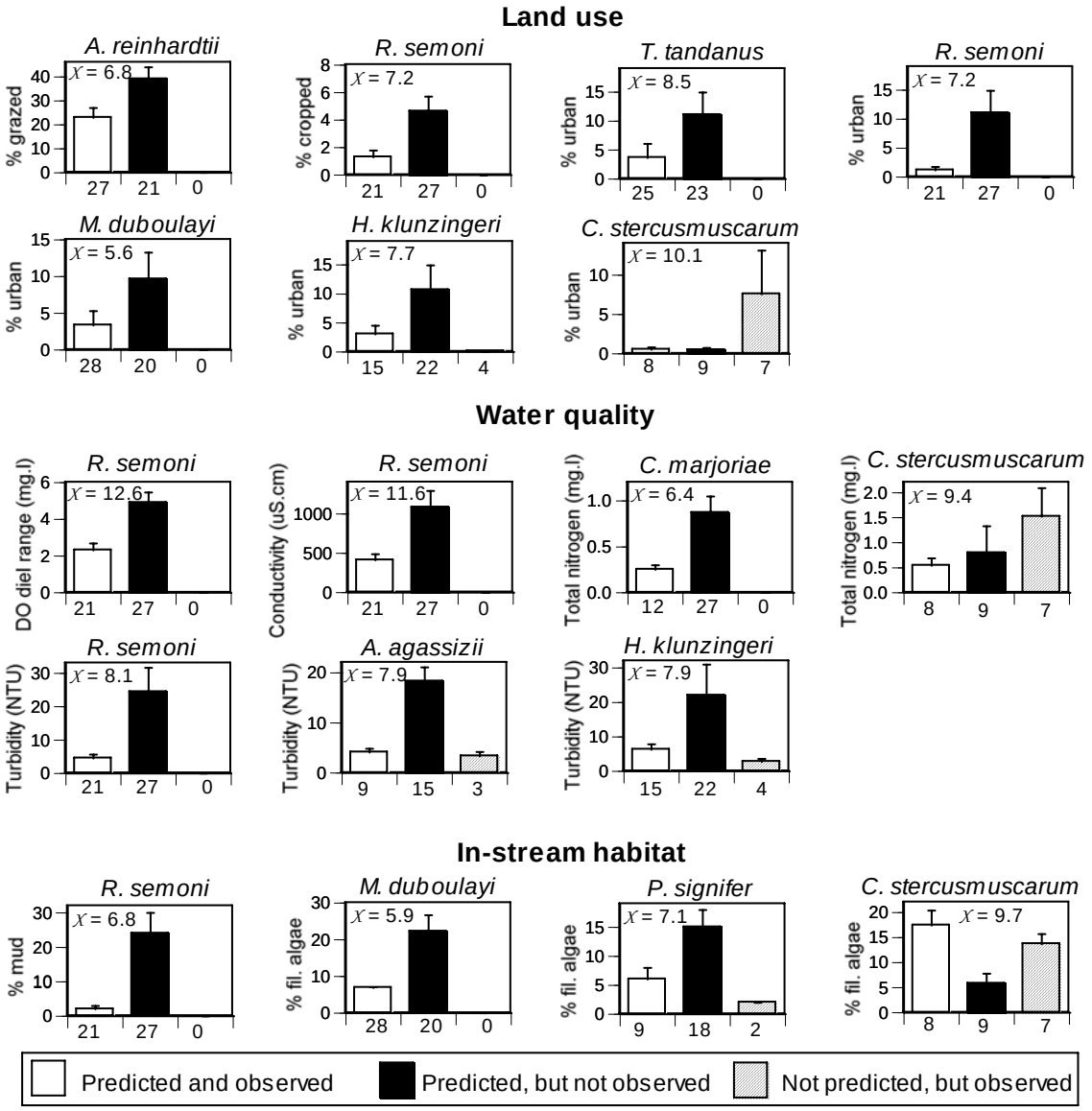

Figure 5.7. Difference in mean values (± SE) of disturbance variables significantly different at sites where each species was predicted (at the PO_{50} level) and observed to occur (open bars), sites where each species was predicted to occur but was not observed (closed bars), and sites where each species 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 and Keough, 2002). Sample sizes for each site category are shown below the x-axis of each plot.

5.5. 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 stream

health assessment. The data from which the 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 stream biota and environmental predictor variables least affected by human activity. The 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 the 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 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. I 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 *et al*. 1999, 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 (Turak *et al*. 1999, Smith *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 the 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 and 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%. My 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. I 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 (Chapter 3). The potential benefits of developing a model based on combined seasons data may be worthy of evaluation.

Temporal variation in fish assemblage composition did not influence the ability of the model 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*. 1990 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*. 2001, Metzeling *et al*. 2002, Paller 2002, Scarsbrook 2002) can affect impressions of the degree of temporal variability or persistence of biotic communities (see also Chapter 4) 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). The 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).

Several sites in the Mary River were highly variable through time, with O/E_{50} scores falling below the reference band on several occasions (Figure 5.5). These sites were located on tributary streams that ceased to flow for prolonged periods and either became small isolated pools, or completely dried out. I 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. I interpret the rapid return of O/E scores to near unity following disturbance events as evidence of this (Figure 5.5, see also Chapter 4).

The 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 this study introduced a source of error that has potential to compromise the validity of the test site predictions. However, based on an evaluation of a limited number of sites tracked through time, my 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 the test site data was collected on a single sampling occasion, I 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).

I concur with Joy & Death (2000, 2002, 2002) that a multivariate predictive modeling 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. This 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. I 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. Chapter 7), and many other attributes of fish assemblage structure and function (eg. 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). I 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 (see Chapter 6 for further discussion of this issue). Furthermore, I 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.

Chapter 6: Accurately defining the reference condition for summary biotic metrics: a comparison of four approaches

6.1. Synopsis

Protocols for bioassessment often relate changes in summary metrics that describe aspects of biotic assemblage structure and function to environmental stress (e.g. the Index of Biotic Integrity - IBI, Karr 1981, Karr *et al*. 1986). Biotic assessment using multimetric indices now forms the basis for setting regulatory standards for stream quality and a range of other goals related to water resource management in the USA and elsewhere. Biotic metrics are typically interpreted with reference to the expected natural state to evaluate whether a site is degraded. It is critical that natural variation in biotic metrics along environmental gradients is adequately accounted for, in order to quantify human disturbance-induced change. A common approach used in the IBI is to examine scatter plots of variation in a given metric along a single stream size surrogate and a fit a line (drawn by eye) to form the upper bound, and hence define the maximum likely value of a given metric in a site of a given environmental characteristic (termed the 'maximum species richness line' - MSRL). In this chapter I examine whether the use of a single environmental descriptor and the MSRL is appropriate for defining the reference condition for a biotic metric (native fish species richness) and for detecting human disturbance gradients in rivers of south-eastern Queensland, Australia. I compare the accuracy and precision of the MSRL approach based on a single environmental predictor, with three regression-based prediction methods (Simple Linear Regression (SLR), Generalised Linear Modelling (GLM) and Regression Tree modelling (TREE)) that use (either singly or in combination) a set of landscape and local scale environmental variables as predictors of species richness. I compared the frequency of classification errors from each method against set biocriteria and contrast the ability of each method to accurately reflect human disturbance gradients at a large set of test sites. The results of this chapter suggest that the MSRL based upon variation in a single environmental descriptor could not accurately predict species richness at minimally disturbed sites when compared with SLRs based on equivalent environmental variables. Regression-based modelling incorporating multiple environmental variables as predictors (GLM and TREE) more accurately explained natural variation in species richness than did simple models using a single environmental predictor. Prediction error arising from the MSRL was substantially higher than for the regression methods

and led to an increased frequency of Type I errors (incorrectly classing a site as disturbed). I suggest that problems with the MSRL arise from the inherent scoring procedure used and that the method is limited to predicting variation in the dependent variable along a single environmental gradient.

This Chapter forms the basis of the following journal manuscript:

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6.2. Introduction

A common approach to bioassessment has been to relate changes in summary metrics that describe aspects of biotic assemblage structure and function to environmental stress. Summary metrics have been advocated as an effective means of encapsulating the complexity of natural communities sufficiently to assess the types and strengths of human impacts and to communicate results of studies to others (e.g. environmental managers) (Karr *et al*. 1986, Fausch *et al*. 1990, Barbour *et al*. 1995, Karr & Chu 1999, Simon 1999, and references therein).

A comprehensive multimetric index (Barbour *et al*. 1995) for the assessment of aquatic systems integrating summary metrics based on species richness and composition, trophic composition and individual abundance and condition was first developed for fish (the Index of Biotic Integrity - IBI, Karr 1981). The approach was subsequently adapted for macroinvertebrates (DeShon 1995, Barbour *et al*. 1996, Fore *et al*. 1996) and periphyton (Barbour *et al*. 1999) and has been applied in a range of aquatic ecosystems throughout the world (e.g. Steedman 1988, Oberdorff and Hughes 1992 Davis & Simon 1995, Hay *et al*. 1996, Huguenay *et al*. 1996 Lyons *et al*. 1995, Ganasan and Hughes 1998, Harris & Silveira 1999, Hughes & Oberdorff 1999, Toham & Teugels 1999, Barbour & Yoder 2000, Belpaire *et al*. 2000, Kesminas & Virbickas 2000, Angermeier & Davideanu 2004).

The central goal of bioassessment is to decide whether a site exposed to stress is impaired while minimizing Type I (incorrectly classifying a site as impaired) and Type II (incorrectly classifying a site as unimpaired) errors (Bailey *et al*. 1998, Linke *et al*. 1999). Biotic metrics are typically interpreted by reference to an expected natural state (the reference condition approach, Reynoldson *et al*. 1997) in order to evaluate whether a site is degraded. However, classification errors can arise from a failure to accurately define the expected state, particularly for metrics that are expected to vary naturally across biogeographic regions or along environmental gradients (Oberdorff *et al*. 2001). Variation in fish assemblage attributes along natural environmental gradients must therefore be adequately accounted for, in order to quantify human disturbance-induced change (Bunn 1995, Smogor & Angermeier 1999a, 2001, Oberdorff *et al*. 2001).

Local and regional scale factors are important determinants of local variation in fish species composition, abundance and biomass (Jackson & Harvey 1989, Schlosser 1991, 1995, Schlosser & Angermeier 1995, Smogor *et al*. 1995, Poff 1997). The hierarchical arrangement of habitats within rivers (Frissell *et al*. 1986) ensures that processes important in determining the distribution of fishes at large spatial scales may also determine distributions at other sub-ordinate scales within that hierarchy (i.e. the concept of landscape filters, Poff 1997). Total fish species richness, and the number of species or individuals belonging to various taxonomic or functional groups (e.g. defined on the basis of habitat use, reproductive style, etc), are important component metrics in bioassessment protocols such as the IBI. Where such metrics are thought to vary among regions, or along natural environmental gradients, scoring criteria and stratification procedures are typically developed such that the expected reference condition can be more accurately defined. In regional applications of the IBI to riverine ecosystems, a single environmental variable (often related to stream size) is most commonly used as a basis for metric stratification. Such stratifying variables have included catchment area, stream order, distance from source, altitude, stream gradient, and stream width (Fausch *et al*. 1984, Leonard & Orth 1986, Steedman 1988, Bramblett & Fausch 1991, Simon & Emery 1995, Hughes *et al*. 1998, Harris & Silveira 1999, Toham & Teugels 1999, Belpaire *et al*. 2000). The assumption that stratification by a single environmental descriptor is sufficient to account for natural spatial variation in IBI metrics and the consequences of this for bioassessment has been queried by some researchers. Osborne *et al*. (1992) showed that stratification by stream order alone led to bias in defining the expected condition for individual metrics and hence total IBI scores as the effect of stream location in the drainage network, an important determinant of local fish assemblages (Gorman 1986, Osborne & Wiley 1992) was not accounted for. Oberdorff *et al*. (2001, 2002) further highlighted the potential inadequacies of stratification along a single environmental gradient and so included multiple predictors of regional and local variation in species composition as a precursor to developing IBI type metrics.

After stratifying by stream size surrogates, the upper bounds of the reference condition expected are defined using the 'maximum species richness line' (MSRL) (Fausch *et al*. 1984, Karr *et al*. 1986), which defines the maximum likely value of species richness (and other metrics) in a site of a given environmental characteristic (e.g. stream size) and therefore represents the expected condition for a stream site in excellent condition. The degree to which a given site deviates from the MSRL is regarded as a measure of

the magnitude of degradation at the site (Karr *et al*. 1986). It has been argued that this conservative scoring procedure (i.e. comparing with the highest expected value for a given metric) provides a sensitive measure of environmental degradation and minimises type II error rates (incorrectly classifying a site as unimpaired). However, the implications of the MSRL scoring procedure for misclassification errors resulting from Type I error (incorrectly classifying a site as impaired) has not been fully evaluated (but see Oberdorff *et al*. 2002), yet is critical in regional bioassessments.

In this chapter I examine whether stratification by a single environmental descriptor and the use of scoring system based on deviations from the MSRL is appropriate for defining the reference condition for a fish assemblage metric (native species richness) derived for rivers of south-eastern Queensland, Australia. Native species richness is a commonly used measure of the general ecological condition of aquatic ecosystems and species richness metrics are important components of the IBI, generally (but not always) being expected to decline with increasing environmental stress (Harris 1995, Oberdorff *et al*. 2001, 2002). I develop and validate predictive models based on a set of least-disturbed reference sites and use the models to predict species richness at a set of test sites impacted to varying degrees by human disturbance. I compare the predictive accuracy of the MSRL approach with three regression-based methods that use a range of local and landscape variables as predictors of species richness. I also compare the frequency of classification errors from each method against set biocriteria and the ability of each method to accurately reflect a human disturbance gradient.

6.3. Methods

6.3.1. Reference, validation and test site data sets

A data set comprising sixty-two reference sites (least-affected by human activity) were used to develop predictive models of the number of native fish species expected to occur on the basis of environmental variables. Reference sites were located in the Mary, Brisbane, Logan and Albert Rivers (Fig. 5.1) and were selected on the basis that they were minimally disturbed using criteria described in Chapter 5 (Section 5.3.1). Each reference site was sampled once between July and October over the period 1994 and 1997. Hydrological conditions during the sampling period (late winter and Spring) are typically characterised by low and stable flows (Pusey *et al*. 2000, 2004, Chapter 4).

Validation of the predictive models was performed using a data set comprising ten additional sites in the Mary and Albert Rivers sampled in spring 1997 and five of the original reference sites that were re-sampled in spring 2000 (hereafter termed validation sites). Forty-eight test sites were selected to test the predictive models and examine whether differences in observed *versus* predicted fish assemblage structure was related to known gradients in anthropogenic disturbance (particularly impacts associated with catchment land use and associated local riparian, in-stream habitat and water quality degradation). These test sites ranged from being minimally disturbed to highly impacted (for further description of test sites see Chapter 5, Section 5.3.3). Test sites were sampled in September and October 2000. I consider that reference, validation and test and sites are valid for comparison as they encompassed the same range of relative catchment positions and stream sizes, were sampled at a similar time of year and under similar hydrological conditions of low and stable discharge (Chapter 5).

6.3.2. Fish sampling procedures

Fish assemblages were sampled in accordance with the protocol recommended in Chapter 3 and was consistent among all reference, validation and test sites. Each of three contiguous individual mesohabitat units (i.e. riffles, runs or pools) within each reach was intensively sampled and data subsequently combined to represent each site. Those fish species known to either breed or spend a major proportion of their life cycle in freshwaters (see Pusey *et al*. 2004) were included in counts of species richness at each site. Non-native species and estuarine vagrants were not included in estimates of local species richness (Harris & Silveira 1999).

6.3.3. Estimation of environmental variables and characterisation of disturbance

Catchment and local scale environmental characteristics of the study sites were estimated according to the protocol described in Chapter 5 (Section 5.3.3). The potential sources and intensity of anthropogenic disturbance at each test site were as described in Chapter 5.

6.3.4. Statistical methodology

6.3.4.1. Modelling approaches used to define the reference condition

Four alternative approaches: the 'Maximum Species Richness Line' (MSRL), Simple Linear Regression (SLR), Generalised Linear Modelling (GLM) and Regression Tree modelling (TREE), were used to develop models describing the relationship between a set of environmental variables (either singly or in combination) and species richness at the reference sites. The intention of the regression modelling was to select a subset of environmental variables able to provide the most parsimonious explanation for variation in species richness and suitable for predicting species richness at novel sites (Norris & Georges 1993). I judged the degree to which species richness observed at the reference sites deviated from that predicted by each method as a measure of the accuracy of the prediction (for reference sites). I also externally validated the models with an independent data set (the validation sites) to give a more realistic estimate of prediction error (Olden & Jackson 2000).

Predictor variables included six landscape or local scale environmental descriptors (upstream catchment area, proximity to river source and mouth, elevation, stream width and maximum depth) known to be important influences on, or correlates of, fluvial species richness (Gorman & Karr 1978, Lake 1982, Schlosser 1982, 1985, Gorman 1986, Meffe & Sheldon 1988, Davies 1989, Osborne & Wiley 1992, Oberdorff *et al*. 1993, Pusey *et al*. 1993, 1995, Smogor *et al*. 1995, Pusey & Kennard 1996, Belliard *et al*. 1997, Gehrke & Harris 2000). Local fish assemblages are influenced by both large and local scale environmental factors and their interaction with the biology (e.g. resource requirements, life cycle and movement) of the available species pool (Jackson & Harvey 1989, Poff & Ward 1990, Poff & Allan 1995, Schlosser 1995, Schlosser & Angermeier 1995, Angermeier & Winston 1998). The choice of predictor variables reflects this mixture of influences. Importantly, the environmental variables are usually minimally affected by human activity (although stream width and depth may be affected by riparian slumping and/or sedimentation in some erosive stream types). Relationships among environmental variables were evaluated using Pearson’s correlations. I used the Dunn-Sidak procedure (Quinn & Keough 2002) to correct for multiple comparisons.

6.3.4.2. Maximum Species Richness Line (MSRL)

The graphical procedure established by Fausch *et al*. (1984) and Karr *et al*. (1986) was used to standardize for variation in species richness by each environmental variable. Species richness at each reference site was plotted against each environmental variable (on a $\log_{10}$ scale for four of six variables – see results) and a line was drawn by eye to form the upper bound, enclosing approximately 95% of the sites. This 'maximum species richness line' (MSRL) defines the maximum likely value of species richness in a site of a given environmental characteristic. The degree to which a site deviates from the MSRL is regarded as a measure of the magnitude of degradation at the site (Karr *et al*. 1986). Typically, the area below the MSRL is trisected, and sites falling in the upper, middle and lower thirds are allocated arbitrary scores of 5, 3 or 1, respectively, to reflect this deviation from reference conditions defined by the MSRL. I also evaluated an alternative scoring procedure developed by Minns *et al.* (1994) and applied by Ganasan & Hughes (1998) and Hughes *et al*. (1998), where site scores are obtained by linear interpolation between the expected upper threshold (defined by the MSRL) and lower threshold values (no species). The score is calculated by dividing the species richness observed (O) by the value predicted (P) from the MSRL and then multiplying by 10. Thus species richness is scored on a continuous scale ranging from 0 to 10, denoting poor to good site condition. It is argued that such a continuous scoring procedure reduces variances when metric values differ by less than 1 but are scored as different categories, and offers a more accurate and interpretable depiction of the data (Hughes *et al*. 1998). I multiplied by 100 (thus giving a percentage of the predicted value defined by the MSRL) instead of 10 to make results comparable with the scoring procedures used in the other prediction methods below.

6.3.4.3. Simple Linear Regression (SLR)

Simple Linear Regression (SLR) models were developed to predict species richness based on variation in each environmental predictor variable separately and were fitted using ordinary least squares regression. This method fits a regression line between the scatter of data points that minimises the sum of the squared deviations between each observed and predicted value of species richness (Quinn & Keough 2002). Prior to analysis, the distribution of environmental variables was inspected for normality and the

presence of outliers, and variables were $\log_{10}(x+1)$ transformed where necessary (see Results).

6.3.4.4. Generalised Linear Modelling (GLM)

Generalised Linear Modelling (GLM) enables the nature of the response variable to be modelled appropriately by allowing different distributional forms to be used (here a Poisson distribution was used for the count variable - species richness). Environmental predictor variables were selected by GLM in a stepwise manner whereby a model including all variables was fitted initially and then variables were successively added or dropped according to the additional significant variation they explain. Variables were selected using simultaneous stepwise forward and backward entry and removal and Akaike's Information Criterion (Akamoto *et al*. 1986) was used to determine the significance of dropping or adding variables from the models. The total amount of variation in species richness at the reference sites explained by the selected environmental predictors was given as an approximate R^2 value. I also report here the amount of variance explained by each predictor but do not interpret their meaning further. This is particularly important as correlation between predictor variables (Green 1979, Norris & Georges 1993) and potential bias in model selection using stepwise procedures (Olden & Jackson 2000) means that the ecological significance of each of each variable cannot be determined. I did not include interaction terms in the final model as preliminary analyses revealed that their inclusion only marginally improved the approximate R^2 values (by less than 2%) but added to model complexity. GLM's were fitted using S-PLUS 2000 (Statistical Sciences 1999).

6.3.4.5. Regression Tree Modelling (TREE)

Regression Tree modelling (TREE) was used to understand the structural relationships within the reference site database and formulate homogeneous groups of reference sites, according to their environmental and biological characteristics (i.e. species richness). This approach can identify those environmental variables that play an important discriminatory role in defining homogeneous groups of reference sites, if they exist. These variables can then be used for prediction of biological characteristics at new sites. When presented with data from a new site, prediction from the tree-based models can be

used to identify which reference sites used in the model formulation are similar to the new site on the basis of environmental variables, and hence are suitable for comparison. I considered the mean species richness of each reference site group as the predicted value for validation and test sites.

Tree-based modelling has gained popularity as a screening method for variables, for summarising relationships in large multivariate data sets, and for providing a flexible non-parametric alternative to Generalised Linear Modelling for regression problems (e.g. Michaelsen *et al*. 1994, Rathert *et al*. 1999, De'ath and Fabricus 2000). The TREE model implemented here was fitted by binary recursive partitioning, whereby the reference site data set was successively divided into increasingly homogenous subsets. The partitioning process can also reveal interactions amongst environmental variables and examines increasingly smaller and ecologically structured spatial scales of the data because each successive split is performed in the context of all previous splits (Rathert *et al*. 1999, Venables & Ripley 1999). For each division, the TREE model selects the environmental predictor variable that minimized the residual sum of squares of the two sub-groups relative to the parent group. The values of the selected explanatory variable for each division defined the splitting threshold. The tree can be pruned to remove noise and simplify the relationships in the data without sacrificing the goodness-of-fit of the model. A ten-fold cross-validation procedure was used to determine optimum tree size by dividing the data into 10 equal subsets, with nine used to develop the model and the tenth used for testing. This cross-validation procedure was conducted for a sequentially increasing number of splits. By identifying the complexity parameter (C_p) that had the largest average cross-validated relative error value within one standard deviation of the minimum average cross-validated relative error (known as the one standard error rule, Breiman *et al*. 1984), optimum tree size was determined. Tree-based modelling was implemented using the rpart library of functions (Therneau & Atkinson 1997) within S-PLUS 2000 (Statistical Sciences 1999).

6.3.4.6. Validation and testing of models: direct comparison of model accuracy, error rates and ability to characterise the disturbance gradient

I performed an external test of the predictive ability of each modelling method and combination of environmental variables by predicting species richness at the 15 least-disturbed validation sites. Validation sites were considered to be predicted accurately if

the distribution of validation site residuals (the difference between the observed and predicted value defined by the MSRL) resembled those of the reference sites. The accuracy and precision of each prediction method was further evaluated by calculating the Root Mean Squared Error (RMSE) of the prediction for reference and validation sites. The RMSE is calculated as the square root of the mean of the squared differences between the observed values and those predicted by each method (equivalent to the residual from the predicted value). The lower the RMSE value for each site type and method, the lower the bias and error associated with the prediction.

Biocriteria (*sensu* Bailey *et al*. 1998) were established to assess the error rates associated with predictions from each method. The proportion of minimally disturbed reference and validation sites failing the biocriteria defined using each prediction method then represented the probability of committing a Type I error (incorrectly failing a site). I also compared the proportion of test sites failing the biocriteria and hence the probability of classing them as disturbed. Using the MSRL prediction method, sites scoring less than 5 using the trisection method (described above), and sites scoring less than 75% of the value of species richness defined by the MSRL, were considered to have failed these biocriteria. These biocriteria thresholds were considered justified as they form the basis for interpreting site scores defined by the MSRL in the IBI methodology (see Karr *et al*. 1986 and Hughes *et al*. 1998). Biocriteria were defined for the SLR, GLM and TREE prediction methods in a similar manner whereby those sites scoring less than 75% of the predicted value of species richness derived from each model were considered to have failed the biocriteria.

The relative ability of the three prediction methods to accurately reflect the human disturbance gradient was evaluated using a *post-hoc* approach. I related test site O/P scores generated using each method to the suite of variables describing the source and intensity of disturbance at the test sites (Chapter 5, Table 5.2). As described in Chapter 5 (Section 5.3.4.3), the 16 disturbance variables ($\log_{10}$ (x+1) transformed) were reduced to a smaller number of orthogonal gradients, using principal components analysis to avoid the potential problem of correlation between predictor variables. Importantly, the disturbance gradients identified by the PCA analysis were not confounded by variation along natural environmental gradients (no relationships between principal component scores and catchment and local site physical characteristics) (Chapter 5). Stepwise

Generalised Linear Modelling (GLM) was used to predict species richness O/P scores on the basis of the disturbance gradient principal components. The relative ability of each prediction method to reflect the disturbance gradient was determined by the strength of the relationship between O/P scores and the disturbance gradient components. This was assessed by comparing the amount of variance (R^2) in index scores explained by each GLM model. All analyses were conducted using S-PLUS 2000 (Statistical Sciences 1999).

6.4. Results

6.4.1. Defining the reference condition

6.4.1.1. Maximum species richness line (MSRL)

An example of the MSRL for the relationship between catchment area and species richness is presented in Figure 6.1. On average, reference and validation sites contained approximately four species less than predicted by the MSRL, and were sometimes overestimated by more than 8 species. The MSRL developed for elevation performed slightly better than those developed for other environmental variables (as judged by the lower mean magnitude of residuals for reference and validation sites) (Figure 6.2). These data suggest that the MSRL approach was consistently biased towards over-prediction of species richness at reference and validation sites.

6.4.1.2. Simple Linear Regression (SLR)

Pair-wise relationships between environmental variables (Table 6.1) reveal that correlations among variables were often significant ($p<0.05$) but there was often much unexplained variation between variables (as indicated by Pearson's *r* values usually less than 0.5). Significant regression relationships ($p<0.05$) between species richness and single environmental variables including catchment area, distance from source, distance to mouth and elevation were observed (Table 6.1), however there was also substantial unexplained variation in species richness predicted by the models (as indicated by the R^2 values all below 19%). The difference between predicted and observed values at reference sites usually varied between ± 2 species but were centred around zero for each

model, and tended to over-predict species richness at validation sites by between 1 and 2 species (Figure 6.2).

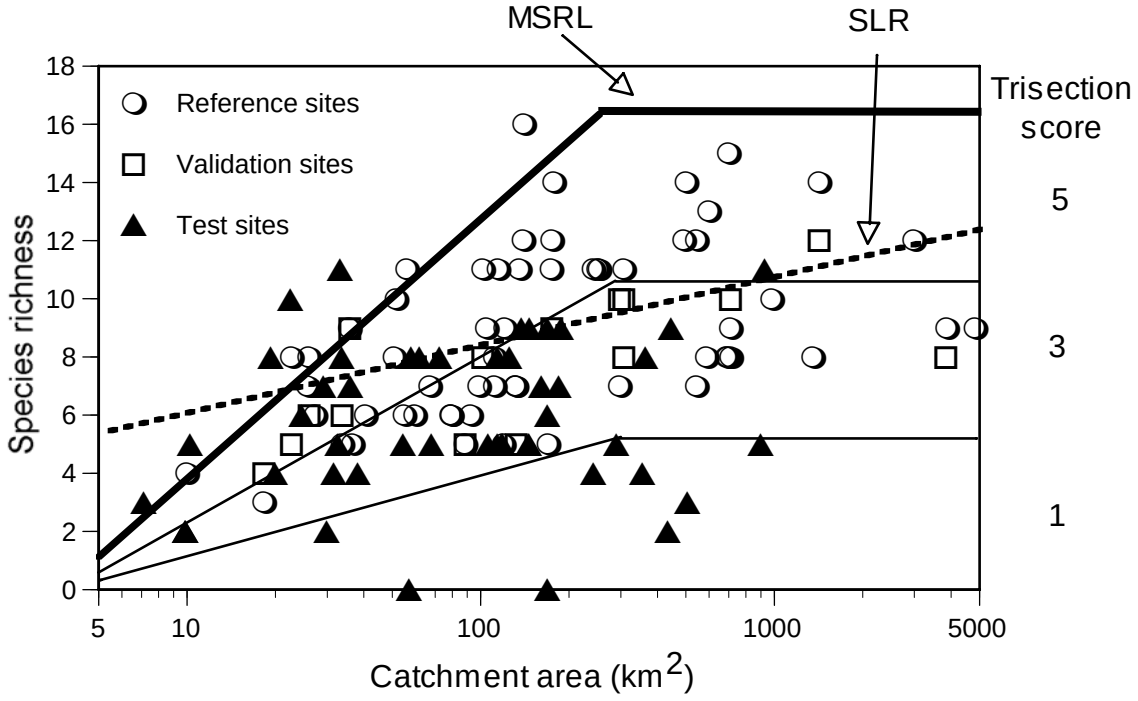

Figure 6.1. Species richness versus $\log_{10}$ catchment area for reference sites. The maximum species richness line (MSRL), trisections used for metric scoring and the simple linear regression line (SLR) are also shown. Validation and test sites are also shown on plot. Note that sites overlaying each other may be obscured on the plot.

Table 6.1. Pearson's *r* correlation coefficients for relationships between environmental variables at reference sites. Variables transformed ($\log_{10}$ (x+1)) prior to analysis are denoted by ^{L}. Correlations significant at $p<0.05$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn & Keough 2002) are denoted by *. Also shown are R^2 values for Simple Linear Regression relationships between species richness and individual environmental variables (significance levels for each relationship are given in parentheses).

		CAREA	DISTS	DISTM	ELEV	WIDTH	MAXDEP
Upstream catchment area (CAREA) ^{L}							
Distance from stream source (DISTS) ^{L}		0.832*					
Distance to river mouth (DISTM)		-0.156	-0.323				
Elevation (ELEV)		-0.556*	-0.613*	0.426*			
Mean wetted width (WIDTH) ^{L}		0.488*	0.429*	0.052	-0.240		
Maximum depth (MAXDEP) ^{L}		-0.029	-0.056	0.075	0.083	0.218	
Species richness	R^2	18.8	11.0	13.1	16.3	0.08	0.04
	p	(0.001)	(0.011)	(0.005)	(0.002)	(0.673)	(0.503)

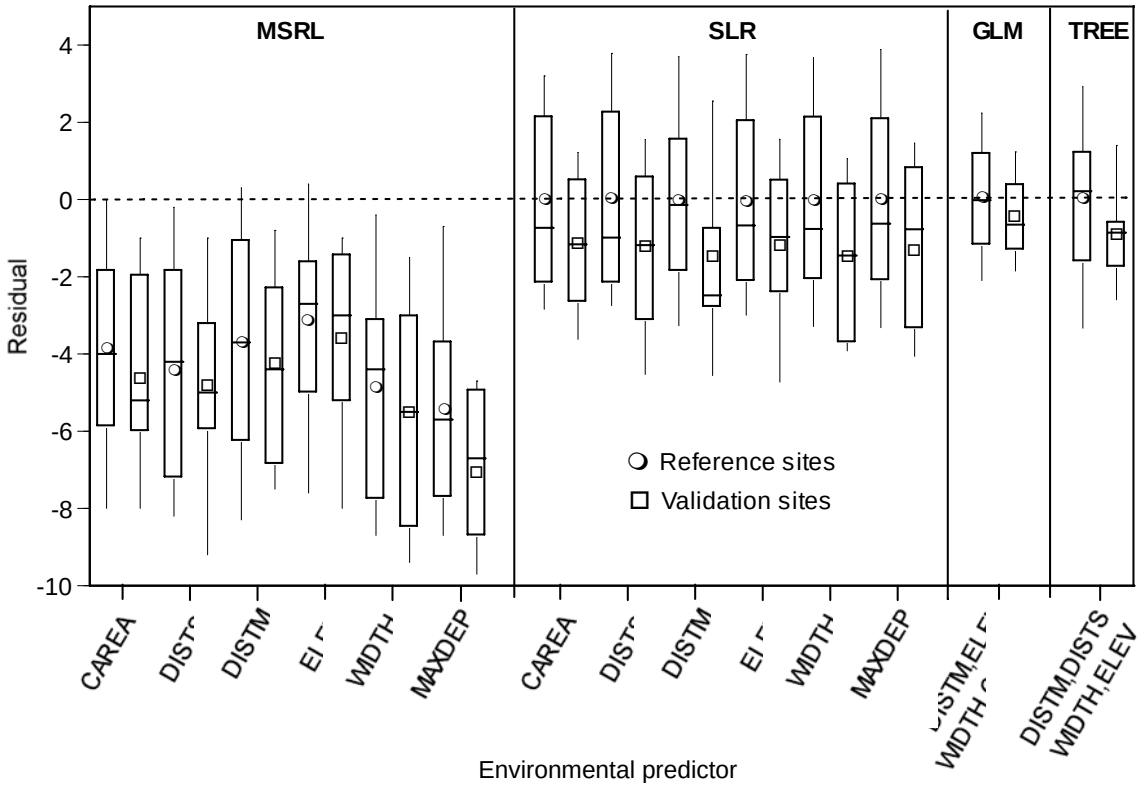

Figure 6.2. Box plots of variation in the magnitude of the residuals (difference between values predicted and those observed) from each prediction method using each environmental predictor variable for reference and validation sites. The lines at the top, middle and bottom of each box represent the 75th percentile, median and 25th percentile, respectively. Upper and lower bars represent 90th and 10th percentiles and means are represented by symbols.

6.4.1.3. Generalised Linear Modelling (GLM)

The stepwise GLM model, based on four environmental predictor variables, was highly significant ($p < 0.0001$) and explained a substantial amount of the variation in species richness at the reference sites (approximate $R^2 = 69\%$) (Table 6.2). Distance to river mouth and elevation explained the largest amount of variation in species richness at the reference sites (almost 43% and 12% of the total variance, respectively; Table 6.2). Wetted stream width and catchment area accounted for a further 14% of the variation. External model validation revealed that the developed model predicted species richness at the validation sites reasonably well, as most sites fell within the range of the reference data set predictions (Figure 6.3a) and the predicted and observed values were significantly and positively related ($R^2 = 52\%$, $p<0.001$). The distribution of validation residuals generally matched that of the reference data, being centred around zero

(Figure 6.2), although species richness was over- or under-predicted at some validation sites (but usually by less than one species).

Table 6.2. Summary of Generalised Linear Model for predicting species richness values at the 62 reference sites according to catchment and local site descriptors. The relative importance of each predictor variable fitted in the model is indicated by the sums of squares and the percent of total variance explained (approximate model R^2 = 69%, $p<0.0001$). The C_p statistic indicates the terms included in the model (those greater than the Null C_p value).

Predictor variable	df	Sum of squares	% of variance explained	C_p Statistic
Null model				22.46
Distance to river mouth (km)	1	17.93	43.2	39.61
Elevation (m)	1	4.96	11.9	26.63
Mean wetted width (m)	1	3.00	7.2	24.67
Catchment area (km^2)	1	2.78	6.7	24.46

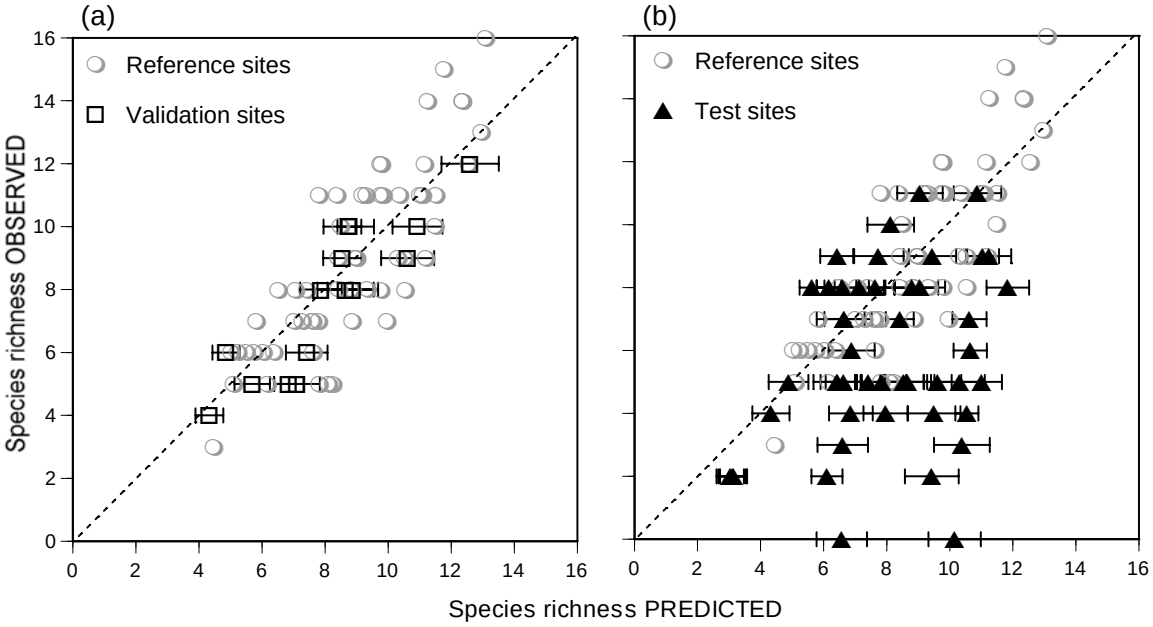

Figure 6.3. Species richness predicted by the GLM model versus observed values for (a) the reference sites and validations sites and (b) the reference sites and test sites. Standard errors around predicted values for validation and test sites are also shown.

6.4.1.4. Regression tree modelling (TREE)

After cross-validation, TREE was able to explain 62% of variation in species richness at the reference sites, formulating five relatively homogenous groups of sites (Figure 6.4). Four environmental variables were selected as predictors by the TREE (Figure 6.4), with distance to river mouth and distance from stream source being selected as the first

two splitting variables and explaining the largest amount of variation in species richness (explaining 26% and 22% of the total variance, respectively). The remaining two splits used wetted width and elevation as discriminating variables and collectively explained a further 14% of the total variance. External validation revealed that species richness predicted for the validation sites was within the range of reference site values of the respective group to which they were allocated by the regression tree model (Figure 6.4). The distribution of validation residuals suggested that the model tended to slightly under-predict species richness at validation sites (on average by about 1 species) (Figure 6.2).

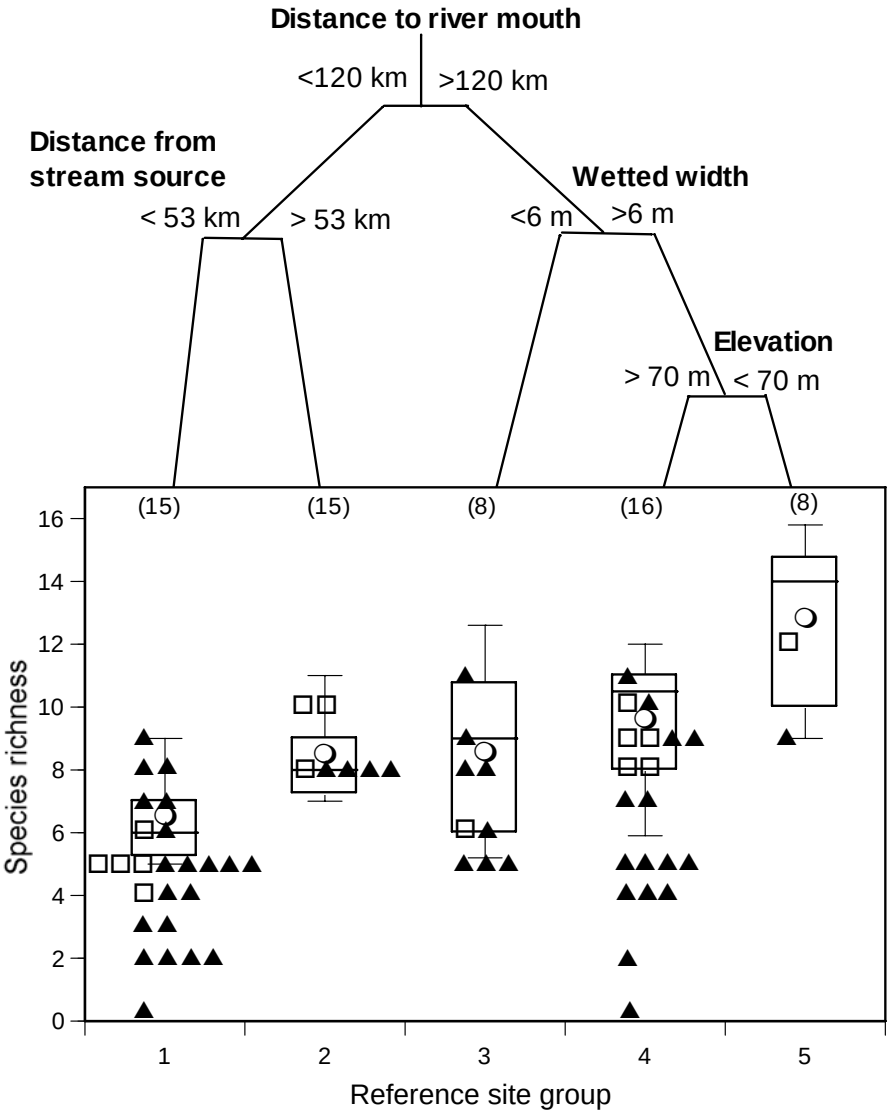

Figure 6.4. Regression tree for predicting species richness at reference sites, environmental variables used in forming the tree and their critical values for determining the splits. The distribution of values for species richness in each reference site group is given in the box plot. The number of sites within each reference site group is given in parentheses. The predicted group membership (using the regression tree) and observed values for species richness at validation (open squares) and test sites (closed triangles) are also shown.

6.4.2. Direct comparison of model error rates and ability to characterise the disturbance gradient at test sites

The data presented above suggest that MSRL's based on single environmental predictor variables were biased towards over-prediction of species richness at reference and validation sites. Linear regressions based on single environmental variables (SLR) were more accurate but still tended to over-predict at validation sites. The GLM model based on a linear combination of four environmental variables showed the least bias, and the TREE model that split sites into homogenous groups based on similarities in environmental variables also accurately modelled variation in species richness, although with a slight tendency for over-prediction. Root Mean Squared Error (RMSE) plots confirm these results, revealing that the error associated with prediction using the MSRL was substantially higher than for prediction using SLR, GLM and TREE methods (Figure 6.5). This was consistent for prediction of reference and validation site data. The MSRL based on elevation had the lowest prediction error, but was twice as high as RMSE value derived from the SLR for the same environmental predictor. Consistent with the results presented earlier, prediction error using the TREE method was intermediate between the GLM and all other methods.

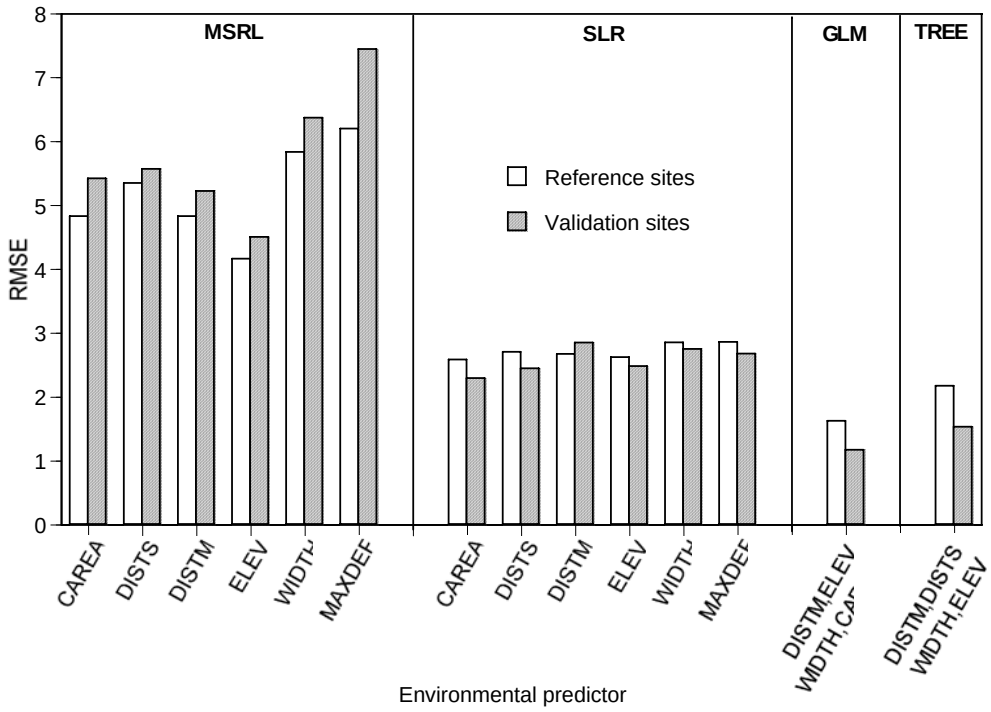

Figure 6.5. Comparison of residual mean squared error (RMSE) scores for each prediction method and each environmental predictor variable for reference and validation sites.

The proportion of reference, validation and test sites failing the biocriteria defined using each prediction method was much greater for the MSRL than for the SLR, GLM and TREE methods. The chances of committing a Type I error (incorrectly failing a site) using biocriteria based on MSRL trisection scores <5 were 51% and 62% for reference and validation sites, respectively (Figure 6.6). Type I error rates based on biocriteria defined by MSRL O/P scores <75% were also high (43% and 62% for reference and validation sites, respectively). In contrast, biocriteria (O/P scores <75%) defined by the SLR based on elevation yielded lower error rates (22% and 33% of reference and validation sites failed the biocriteria) and Type I error rates for reference and validation sites using biocriteria defined by the GLM and Tree methods were always less than 15%. These data collectively suggest that high failure rates for test sites (77-84%) as assessed by both MSRL scoring methods, are inaccurate and overestimated, compared with the SLR, GLM and TREE methods, which indicated that between 52% and 62% of test sites failed the biocriteria and hence may be impacted by human disturbance (Figure 6.6).

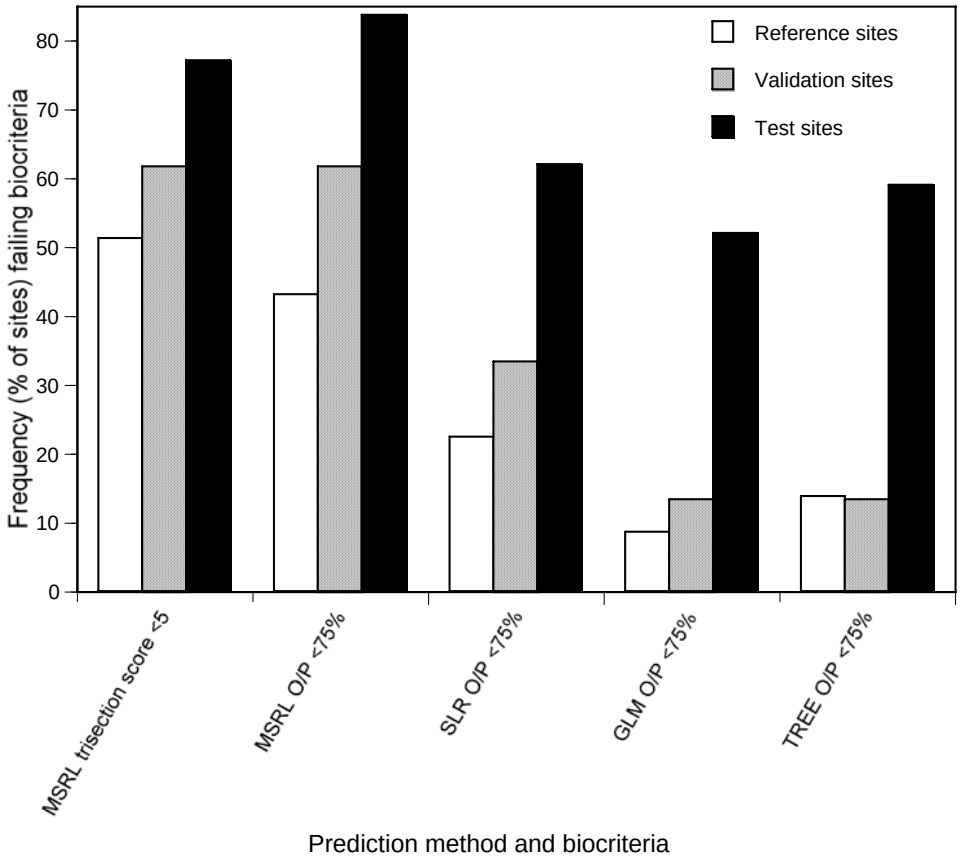

Figure 6.6. Frequency (%) of reference, validation and test sites failing pre-defined biocriteria for each prediction method. Biocriteria were defined on the basis of the MSRL trisection method (those sites scoring less than 5 fail) or species richness Observed/Predicted scores (O/P scores <75% fail) (note that elevation was used as the environmental predictor variable for the MSRL and SLR methods).

O/P scores at test sites derived using the GLM predictive method more accurately reflected the human disturbance gradient than did the other prediction methods (Table 6.3). A multiple regression model using disturbance gradient principal components as predictors of variation in O/P scores at test sites was highly significant ($p<0.001$) and could explain 62% of the variance in the data (Table 6.3). The relationship between disturbance gradient variables and MSRL-derived O/P scores was weakest of the four methods tested (R^2 = 47%), but statistically significant ($p<0.001$). All regression models selected the same four disturbance principal components as predictors, with the components describing catchment land use, water quality and in-stream habitat degradation (PC1 and PC4), explaining the highest amount of variation in O/P scores for each model (Table 6.3). These results clearly suggest that species richness at the test sites deviated substantially from expected with increasing levels of disturbance and that O/P scores derived using the GLM method (and to a lesser extent SLR and TREE) was better able to characterise this gradient of disturbance intensity than were scores derived using the MSRL.

Table 6.3. Comparison of the ability of the four prediction methods to accurately characterise the disturbance gradient using multiple regression models to predict variation in species richness O/P scores at the 48 test sites according to variation in the disturbance gradient variables (principal components). For each GLM model 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. All models were significant at $p<0.001$.

Disturbance gradient predictor		**Species richness prediction method**			
Principal component	Description	GLM (ELEV)	SLR (ELEV)	GLM	TREE
PC1	Intensive catchment land use (clearing and grazing) and degraded water quality (high diel temperature range, pH and conductivity)	23.1	26.2	26.0	29.9
PC2	Degraded riparian vegetation, aquatic plant infestation and high diel DO range	8.5	6.9	9.5	7.4
PC3	High nutrients				
PC4	Intensive catchment land use (cropping), degraded habitat (muddy substrate) and high turbidity	10.0	17.5	21.2	14.8
PC5	Intensive catchment land use (urbanization) and degraded habitat (semi-aquatic weed infestation)	5.2	6.9	5.6	6.6
	GLM R^2	46.8%	55.4%	62.3%	58.6%

6.5. Discussion

This chapter has demonstrated the importance of adequately accounting for natural variation in biotic metrics for them to be useful as accurate indicators of river health. Failure to do so can lead to an incorrect assessment of the degree of impact at a site based on that metric. I suggest that the ability of the MSRL approach to accurately define the reference condition is compromised by the inherent scoring procedure used and that it is limited to predicting variation in the dependent variable along a single environmental gradient.

6.5.1. Metric scoring and Type I errors - Comparisons between MSRL and SLR

The results of this chapter suggest that the MSRL based upon variation in a single environmental descriptor poorly predicted species richness at minimally disturbed reference and validation sites, when compared with an SLR based on equivalent environmental variables. I attribute the high Type I error rates of the MSRL scoring procedure to the manner in which the predictive line is fitted to the data and hence used to define the expected condition (i.e. fitting a predictive line through the 95th percentile of sites representing those with the highest values of the metric along the environmental gradient). Fausch *et al*. (1984) argued that points lying below the MSRL derived for a set of least-disturbed sites from streams in Illinois in the mid-western United States, may be due inadequate sampling because the slope of a regression line fit through a more intensively sampled data set from an earlier study in the same region, was similar to their MSRL. It was therefore concluded that the MSRL was a better representation of true species richness than one provided by fitting a linear regression line through their data (Fausch *et al*. 1984). However, assuming equivalent sampling effort and efficiency among sites (as in this thesis), points lying below the MSRL derived from a set of least-disturbed sites represent natural variation in the metric along a given environmental gradient and possibly interactions with other environmental gradients (see also Wiley *et al*. 2003). The results of this chapter suggest that a more realistic representation of this variation in local species richness at reference sites is derived from the SLR whereby a line is fit through the scatter of points such that the sums of squares of the difference between observed and expected values is minimised.

Approaches to discerning relationships of biotic metrics along natural environmental gradients and defining the reference condition such as SLR should be based upon sites representing minimally or least disturbed sites for the region (but see Wiley *et al*. (2003) and Breine *et al*. (2004) for alternative modelling approaches that include disturbed sites). Some researchers (e.g. Simon & Lyons 1995, Harris & Silveira 1999) have advocated the use of the MSRL to define the expectations for biotic metrics because it does not require a set of exclusively minimally disturbed sites (which may not exist for some regions) to develop the predictive relationship. Instead, a common practice has been to select a large number of sites that may include some that are highly impacted but also presumably includes some that are minimally disturbed and these latter sites are then used to define the expected condition. However, the originators of the MSRL approach (Karr *et al*. 1986) and subsequent researchers (e.g. Yoder & Rankin 1995, Smogor & Angermeier 1998b, Rankin & Yoder 1998) caution against this. The inclusion of a large number of degraded sites can confound attempts to discern relationships between stream size surrogates and the selected metric and result in a lower 95th percentile and hence decrease the MSRL. Attempts to more accurately estimate the slope of the MSRL by applying simple linear regression models (e.g. Yoder & Rankin 1995), trendline regression (Belpaire *et al*. 2000) or quantile regression (Cade & Noon 2003), and to estimate scoring thresholds (e.g. Liang & Menzel 1997) also suffer from the potential inadequacy of overestimating the expected condition for metrics that vary along multiple natural environmental gradients.

The critical issue here is to decide on what basis the expected reference condition for each metric is defined as this sets the biocriteria upon which metric deviations are scored. The use of other scoring thresholds based upon the 50th or 25th percentile of reference site values (e.g. Hannaford & Resh 1995, Barbour *et al*. 1996, Reynoldson *et al*. 1997) have been criticised on the basis that their choice is arbitrary and because the proportion of sites below these thresholds automatically fail (Hannaford & Resh 1995, Gerritsen 1995, Karr & Chu 1999). However, this chapter showed that the use of the MSRL based on relations between species richness and elevation led to at least 40% of reference sites and >60% of validation sites failing the generally accepted (and also arbitrary) biocriteria commonly used in the IBI based upon deviations from the 95th percentile (i.e. trisection score <5, or O/P score of <75%). In contrast, SLR based on the same environmental predictor yielded error rates less than half of those observed for the MSRL.

6.5.2. Single versus multiple environmental gradients – comparisons between SLR, GLM and TREE

Regression-based modelling incorporating a combination of environmental variables as predictors (GLM and TREE) more accurately explained natural variation in species richness than did simple models using single environmental predictors (MSRL and SLR). The GLM and TREE regression models selected a similar set of environmental variables as predictors. Both models revealed that variation in species richness at the reference sites was most strongly related to relative position within the stream network (proximity to stream source or river mouth), stream size (catchment area and stream wetted width) and geographic location (elevation). These 'landscape filters' (*sensu* Poff 1997) appear to be sufficiently associated with variation in fish species distributions in south-eastern Queensland that a substantial proportion of the variation in local species richness could be modelled accurately. These results support the conclusions of Oberdorff *et al*. (2001, 2002) and Wiley *et al*. (2003) that multiple environmental predictors of natural regional and/or local variation in biotic metrics may be required to derive accurate indicators of river health and to avoid over-prediction bias associated with the MSRL approach.

De'ath & Fabricus (2000) suggested that regression tree modelling can often identify simple descriptive models for complex ecological data more effectively than linear regression models, without sacrificing predictive accuracy. In this chapter, I observed that the GLM model was able to explain a greater proportion of the variance at reference sites (69% versus 62% for the TREE model), although there was little difference in RMSE values between models for predicting at reference, validation or test sites. In comparison to GLM, the TREE model tended to slightly over-predict species richness at the validation sites (where the predicted value for a new site was the mean of the reference sites in the group to which it had been assigned). This may be related to the forced imposition of a grouped structure to the reference site data by the TREE model, where in reality no such discrete groupings may have existed. Fish assemblages in the rivers of south-eastern Queensland appear to vary along multivariate environmental gradients rather than form discrete groups of sites with similar biota (Pusey *et al*. 1993, 2000, Chapter 5). However, the potential loss of sensitivity in prediction using the TREE model was minimal, test site O/P scores derived using the GLM and TREE methods were in close accordance and both models were able to

accurately characterise the disturbance gradient. Given that TREE models sacrifice little in terms of predictive accuracy and that the tree structure is conceptually simple (Figure 4) and straightforward for prediction at new sites, such an approach have greater appeal to managers and the wider community over complex GLM models.

6.5.3. Implications for assessment of river health

The MSRL scoring method and the apparent inability to adequately account for natural variation in species richness by stratifying along a single environmental gradient, obscured the ability of the metric to accurately detect a disturbance "signal" at the test sites, relative to the three regression methods. Species richness at the test sites deviated substantially from expected with increasing levels of disturbance and O/P scores derived using the SLR, TREE and GLM methods were better able to characterise this gradient of disturbance intensity than could the MSRL (as judged by the magnitude of the R^2 values presented in Table 6.3). Variation in species richness O/P scores at test sites was strongly associated with catchment land use, water quality and local in-stream habitat degradation. These results support the view that human impacts on local fish assemblages are scale dependent, and potentially affected by processes operating at both local and landscape scales (e.g. Roth *et al*. 1996, Allan *et al* 1997, Stauffer *et al*. 2000, Chapter 5).

The compounding of classification errors is potentially high if scores for individual summary metrics are summed to produce a final index (as is usually the case with integrative multimetric indices such as the IBI) (Suter 1993, Norris 1995, Reynoldson *et al*. 1997), however this has yet to be fully evaluated. Nevertheless, the increased frequency of Type I errors (incorrectly classifying a site as impaired) has important implications for remediation efforts. A commonly held view is that Type II errors (failure to diagnose an impairment) will have more serious environmental consequences due to greater recovery times of ecosystems or their structural and functional components, than Type I errors, which usually result in only short-term economic costs (Toft & Shea 1983, Andrew & Mapstone 1987, Peterman 1990, Fairweather 1991, Dayton 1998). Thus, the increased chance of rehabilitation dollars being misdirected to those areas incorrectly identified as being impaired may be seen as less consequential than a failure to correctly identify those areas in more urgent need of rehabilitation. In this regard, it could be argued that the high type I error rate of the MSRL provides a

greater sensitivity to deviation from reference condition. Following the precautionary principle this may be acceptable from an environmental conservation perspective but given that resources for rehabilitation are generally scarce, bioassessment methods in which the expected condition for biotic indices is accurately defined and hence Type I errors are minimised, is highly desirable. Moreover, those river reaches incorrectly identified as impaired and hence wrongly targeted for remediation may be important, though unusual, examples of the extent of natural biological variation.

Chapter 7: Are alien fish a reliable indicator of river health?

7.1. Summary

The ability of many introduced fish species to thrive in degraded aquatic habitats and their potential to impact on aquatic ecosystem structure and function suggest that introduced fish may represent both a symptom and a cause of declines in river health and the integrity of native aquatic communities. The varying sensitivities of many commonly introduced fish species to degraded stream conditions, the mechanism and reason for their introduction and the differential susceptibility of local stream habitats to invasion due to the environmental and biological characteristics of the receiving water body, are all confounding factors that may obscure the interpretation of patterns of introduced fish species distribution and abundance and therefore their reliability as indicators of river health. In this chapter I address the question of whether alien fish (i.e. those species introduced from other countries) are a reliable indicator of the health of streams and rivers in south-eastern Queensland, Australia. I examine the relationships of alien fish species distributions and indices of abundance and biomass with the natural environmental features, the biotic characteristics of the local native fish assemblages and indicators of anthropogenic disturbance at a large number of sites subject to varying sources and intensities of human impact. Alien fish species were found to be widespread and often abundant in south-eastern Queensland rivers and streams, and the five species collected were considered to be relatively tolerant to river degradation, making them good candidate indicators of river health. Variation in alien species indices was unrelated to the size of the study sites, the sampling effort expended or natural environmental gradients. The biological resistance of the native fish fauna was not concluded to be an important factor mediating invasion success by alien species. Variation in alien fish indices was, however, strongly related to indicators of disturbance intensity describing local in-stream habitat and riparian degradation, water quality and surrounding land use, particularly the amount of urban development in the catchment. Potential confounding factors that may influence the likelihood of introduction and successful establishment of alien species and the implications of these factors for river health assessment using alien species are discussed. I conclude that the potentially strong impact that many alien fish species can have on the biological integrity of natural aquatic ecosystems, together with their potential to be used as an initial basis to diagnose other forms of human disturbance impacts, suggest that some

alien species (particularly species from the family Poeciliidae) can represent a reliable 'first cut' indicator of river health.

This Chapter forms the basis of the following journal article:

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7.2. Introduction

Successful invasion by introduced organisms is widely regarded as being more likely in anthropogenically disturbed environments (e.g. Elton 1958, Orians 1986, Hobbs 1989 2000, Case 1996, Moyle & Light 1996a & b, Lozon & MacIsaac 1997). Introduced freshwater fish, in particular, have commonly been documented to thrive in degraded aquatic habitats in many areas of the world (e.g. Moyle & Nichols 1973, Cadwallader 1979, Arthington *et al.* 1983, Leidy & Fiedler 1985, Arthington *et al.* 1990, Gehrke *et al*. 1995, Gido & Brown 1999, Brown 2000, Meador *et al.* 2003b). Introduced fish may directly impact on native fish by predation, resource competition, interference with reproduction and/or the introduction of parasites and diseases (Meffe 1984, Courtenay & Meffe 1989, Arthington 1991, Ross 1991, Crowl *et al.* 1992). They may also indirectly affect native fish by altering habitat conditions and/or ecosystem processes (e.g. productivity, food web attributes) due to foraging and other activities (Taylor Courtney & McCann 1984, Flecker & Townsend 1994, Roberts *et al*. 1995, Arthington & McKenzie 1997). Introduced fish may therefore represent both a symptom and a cause of declines in river health (*sensu* Rapport *et al.* 1998) and the integrity of native fish communities.

The apparently strong relationship between introduced fish species and degraded stream conditions, and their potential impact on native species, has led to the frequent use of introduced fish as indicators of biological integrity and river health. The presence, richness, relative abundance and/or relative biomass of introduced species (or their complement – the relative abundance/biomass of native species) are often incorporated as component metrics in applications of the Index of Biotic Integrity (IBI) (Karr 1981, Karr *et al*. 1986) and other river bioassessment studies (e.g. Hughes & Gammon 1987, Crumby *et al*. 1990, Bramblett & Fausch 1991, Minns *et al.* 1994, Lyons *et al*. 1995, Ganasan & Hughes 1998, Hughes *et al*. 1998, Maret 1998, May & Brown 2002, Moyle & Marchetti 1998, Moyle & Randall 1998, Wichert & Rapport 1998, Harris & Silveira 1999, Belpaire *et al*. 2000, Brown 2000).

The reliability of indicators of river health based on the presence, abundance and/or biomass of introduced fish species may be confounded by a number of factors, making assessment of the causes of declining river health potentially difficult, and even erroneous. The use of introduced species as an indicator of the degraded end of a

disturbance gradient will only be applicable if those species comprising the index are highly tolerant of human induced disturbances (Hughes & Oberdorf 1998). Key attributes of species successfully invading degraded habitats are hypothesised to include broad physiological tolerances to environmental conditions, generalist resource requirements and a variety of life history attributes enabling them to persist where many native species could not (Arthington & Mitchell 1986, Bruton 1986, Lodge 1993, Williamson & Fitter 1996, Ricciardi & Rasmussen 1998, Rosecchi *et al.* 2001, Koehn 2004 Marchetti *et al.* 2004). However, there are many commonly introduced fish species (e.g. salmonids) that do not possess these attributes and are not highly tolerant of the common forms of perturbation in streams and rivers such as those associated with agricultural land use and urbanisation. Indeed, all introduced species are likely to have differential tolerances to the range of stressors in streams and no species is tolerant of all stressors (Cairns 1986, Suter 2001). Human disturbance is therefore not a requisite for successful invasion by introduced species (Niemela & Spence 1991, Lodge 1993, Townsend 1996), and particular habitats may contain introduced organisms simply because they were introduced there (e.g. intentionally for recreational fishing, as a biological control agent, or via aquarium release), or have recently gained access via historically unconnected pathways (e.g. by inter-basin transfers) (Vermeij 1991, Bunn & Arthington 2002, Gido *et al.* 2004). For example, Marchetti *et al.* (2004) evaluated multiple steps in the invasion process and showed that social factors related to human interest in a species (e.g. propagule pressure and prior invasion success) were strong predictors of successful establishment, spread and integration by alien species.

Areas may be differentially susceptible to invasion, irrespective of (anthropogenic) disturbance intensity, due to the environmental characteristics (e.g. natural or artificial barriers that prevent colonisation, or habitat conditions that may or may not suit the life history requirements of the invading biota), the biological characteristics of the receiving water body or interactions between these factors (Fausch *et al*. 2001, Byers 2002). For example, the richness, abundance and/or composition (i.e. presence of predators and/or superior competitors) of the native biota are biological attributes widely believed to promote a degree of invasion resistance (see Baltz & Moyle 1993, Lodge 1993, Moyle & Light 1996b, Levine & D'Antonio 1999 for reviews and examples), but the universality of this concept is increasingly being questioned (e.g. Lodge 1993, Levine & D'Antonio 1999, Meador *et al*. 2003b, Gido *et al*. 2004). In addition, coexistence between native and introduced species may be facilitated by

natural abiotic disturbances (e.g. floods) that periodically depress populations of introduced species, but not native species that have evolved mechanisms to withstand these disturbances (e.g. Meffe 1984, Minckley & Meffe 1987, Pusey *et al*. 1989, Brown & Moyle 1997). Finally, assessments of the impacts of introduced species on local native fish fauna are potentially confounded by the impacts that human disturbances may also have on the native fish fauna (Moyle *et al.* 2003).

Introduced fish may include 'exotic' or 'alien' species (terms often used to refer to species introduced from other countries) and native species or genetic stocks introduced or translocated within or beyond their natural ranges (Harris 1995). I hereafter use the term 'alien' as I am here concerned only with this component of the introduced fish fauna as an indicator of river health (given that many Australian translocated native species are comparatively intolerant of river degradation and so would likely respond in an opposite manner to degradation). The study area in south-eastern Queensland contains at least ten alien species from four families (Poeciliidae, Cyprinidae, Cichlidae and Cobitidae) that are thought to have established self-maintaining populations (Arthington *et al*. 1983, Kailola *et al*. 1999, Pusey *et al.* 2004). In this chapter I address the question of whether alien fish are a reliable indicator of the health of streams and rivers in this region by testing three null hypotheses.

(1) The distribution of alien fish species is not related to natural environmental gradients in streams.

For alien fish to be a reliable indicator of river health, it is necessary that variation along natural environmental gradients be distinguished from variation due to human disturbance-induced change. I therefore evaluated the relationships of alien fish with catchment and local scale environmental features in a large number of stream sites.

(2) The presence, abundance and biomass of alien fish is independent of the biotic characteristics of the local native fish community.

I evaluated relationships of alien fish with the biotic characteristics of the local native fish fauna at the study sites. A strong inverse relationship between population characteristics of alien and native species could suggest either that alien species are impacting upon native species (a form of biological disturbance) or that sites with high

native richness are less invasible. Human disturbance factors may also reduce the biological resistance of the native fish fauna, enabling invasion by alien species. I attempted to elucidate the relative importance of these factors as they can potentially confound interpretations of alien fish as an indicator of river health.

(3) *The presence, abundance and biomass of alien fish is not related to indicators of anthropogenic disturbance.*

I evaluated relationships of the alien fish fauna with indicators of human disturbance, a necessary requisite for alien fish to be reliable indicators of river health.

7.3. Methods

7.3.1. Data sets

I examined whether the presence, abundance and biomass of alien fish species were related to known gradients in anthropogenic disturbance (due to catchment land use and associated local riparian and in-stream habitat degradation) at the 48 test sites. These sites ranged from being minimally disturbed to highly impacted (see Chapter 5 for further description of these sites). Test sites were sampled in September and October 2000. One test site I sampled contained no fish and so was excluded from the analyses. Seventy-two additional reference sites that were least-affected by human activity (described in Chapters 5 and 6) were used as a basis for predicting the number of native fish species expected to occur at the test sites in the absence of anthropogenic disturbance. Each reference site was sampled once between July and October over the period 1994 and 1997. Hydrological conditions during the sampling period (late winter and Spring) are typically characterised by low and stable flows (Pusey *et al.* 2000, 2004). As discussed in Chapters 5 and 6, I consider that test and reference sites are valid for comparison as they encompassed the same range of relative catchment positions and stream sizes, were sampled at a similar time of year and under similar hydrological conditions of low and stable discharge.

7.3.2. Fish sampling procedures

Fish assemblages were sampled in accordance with the protocol recommended in Chapter 3 and was consistent among all reference and test sites. Each of three contiguous individual mesohabitat units (i.e. riffles, runs or pools) within each reach was intensively sampled and data subsequently combined to represent each site. All fish collected were identified to species, counted, measured (standard length to the nearest mm) and native fish were returned alive to the point of capture. Alien fish were euthanased (using benzocaine - MS222), and not returned to the water (in accordance with the Queensland Fisheries Act 1994). The weight of each fish (both native and alien species) was estimated by reference to existing relationships between body length and mass for each species (Pusey *et al*. 2004). Fish abundance and biomass data were transformed to numerical densities (number of individuals.$10m^{-2}$) and biomass densities ($g.10m^{-2}$) at each site.

7.3.3. Estimation of environmental variables and characterisation of disturbance

Catchment and local scale environmental characteristics of the study sites were estimated according to the protocol described in Chapter 5 (Section 5.3.3). The potential sources and intensity of anthropogenic disturbance at each test site were as described in Chapter 5 (Section 5.3.3). I hypothesised that 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 native and alien fish.

7.3.4. Statistical methods

Various indices were calculated to describe variation in alien fish species parameters at the test sites. These comprised the relative abundance and relative biomass of alien fishes collected at each site (expressed as a percentage of the total catch), and the total numerical density and biomass density of alien fish collected at each site. The use of a river health index based on all alien species present may be overly simplistic for river systems in which alien species with varying life history characteristics and differential tolerances to environmental stressors are included in the final index. To address this, I calculated alien fish species indices separately for the two fish families collected in the

present study (Poeciliidae and Cyprinidae, see results) and examined relationships with the original indices that included all alien fish species.

I examined whether relationships existed between alien fish indices and the amount of sampling effort expended at each site (as estimated by total stream length sampled, total sampling area, total sampling volume, total fish abundance and total fish biomass) using Spearman's rank correlation. Similarly, relationships of alien fish indices with the full suite of catchment variables and local site physical characteristics were also assessed using Spearman's rank correlation. If such relationships exist, it would be difficult to separate the variation associated with human disturbance impacts from that due to sampling effort and variation along natural environmental gradients.

Relationships of alien fish indices with the native fish species richness, abundance and biomass observed at the study sites were examined graphically using biplots and statistically using Spearman's rank correlation. I also tested the premise that local native fish assemblages with high species richness are more resistant to alien species invasion (as defined by the relative magnitude of alien species indices) by correlating the alien species indices with the number of native species expected to occur at each site in the absence of any anthropogenic stress. In this analysis it was necessary to remove the potentially confounding effect that anthropogenic stress (due to human disturbance factors) and the likely negative biological impact of alien species may have had upon some sites by depressing the native fish fauna, hence enabling alien species to invade and persist. I did this by distinguishing those sites relatively free from anthropogenic stress, and with high biological integrity, from those in which the native fish fauna may have been affected by anthropogenic disturbance. I then examined relationships between alien fish species indices and native fish species richness at each set of sites separately. The ratio of species richness observed (O) to species richness predicted (P) in the absence of stress was used to define biological integrity. Those sites with O/P ratios >0.75 contained relatively intact fish assemblages and therefore were judged to be of high biological integrity. I predicted the number of native species that should occur in the absence of stress (abiotic or biotic) using a predictive modelling approach (Generalised Linear Modelling – GLM) described in detail in Chapter 6. This multiple regression model was based on relationships between native species richness and four environmental variables (site distance from the river mouth, altitude, upstream catchment area, mean site wetted width) derived from 62 least-disturbed reference sites.

The model was internally robust (approximate model R^2 = 69%, $p<0.001$) and could accurately predict native species richness at 10 independent validation sites foreign to the reference model (R^2 for validation site predictions = 59%, $p<0.001$). Full details of model development and validation are provided in Chapter 6. I assumed that sites with O/P scores close to unity (i.e. >0.75) were also relatively unaffected by anthropogenic disturbance as O/P scores were strongly inversely related to increasing human disturbance intensity (Chapter 6, Table 6.3).

The relative ability of the alien species indices to accurately reflect the human disturbance gradient was also evaluated using a *post-hoc* approach. Non-parametric Mann-Whitney rank tests (Mann & Whitney 1947) were used to elucidate relationships between the disturbance variables and the presence or absence of alien species. The magnitude of individual disturbance variables at those sites where alien species were present was compared with corresponding values at sites where alien species were absent. Variation in alien species index scores at test sites were related to a suite of variables describing the source and intensity of disturbance at those sites (detailed in Chapter 5, Table 5.2). Bivariate relationships between alien species index scores at the test sites and the disturbance variables were established using Spearman's rank correlations to ascertain whether any simple relationships existed. Multiple regression was also used, acknowledging that the presence, abundance and biomass of alien species can potentially reflect a range of disturbance mechanisms interacting at a range of spatial scales. As described in Chapter 5 (Section 5.3.4.3), the 16 disturbance variables ($\log_{10}$ (x+1) transformed) were reduced to a smaller number of orthogonal gradients, using principal components analysis to avoid the potential problem of correlation between predictor variables. Importantly, the disturbance gradients identified by the PCA analysis were not confounded by variation along natural environmental gradients (no relationships between principal component scores and catchment and local site physical characteristics) (Chapter 5). Stepwise Generalised Linear Modelling (GLM) was used to predict alien species index scores on the basis of the disturbance gradient principle components. The relative ability of each alien species index to reflect the disturbance gradient was determined by the strength of the relationship between index scores and the disturbance gradient components. This was assessed by comparing the amount of variance (R^2) in index scores explained by each GLM model. All analyses were conducted using S-PLUS 2000 (Statistical Sciences 1999).

7.4. Results

7.4.1. Characteristics of the fish fauna

Thirty-nine species of freshwater fish (defined here as those species that either breed or spend a major proportion of their life cycle in freshwater) are native to south-eastern Queensland, and at least fifteen additional species, of which five species are Australian natives, have been introduced to the region (Table 7.1). Quantitative sampling of the fish fauna resulted in the collection of 30 species (excluding sea mullet and bony bream), 4943 individuals and 69.1 kg of fish from the 47 sites (Fig. 7.1). Five alien fish species from two families were collected (Family Poeciliidae: eastern Gambusia - *Gambusia holbrooki*, swordtail - *Xiphophorus helleri*, and platy - *X. maculatus*; Family Cyprinidae: carp - *Cyprinus carpio* and goldfish - *Carassius auratus*) (Fig. 7.1a), all of which are thought to be relatively tolerant to river degradation (Arthington *et al*. 1990, Arthington & McKenzie 1997). Poeciliids comprised over 98% of the total number of alien fish collected (total of 1041 individuals) and this family was dominated by *Gambusia holbrooki* (87% of alien fish collected). This species was also the most abundant and second most widespread of all species collected (native and alien), forming 18.4% of the total number of fish collected and occurring at 60% of sites (Fig. 7.1a). The remaining alien species collectively comprised a further 3% of the total catch and each species occurred at less than 10% of sites. Duboulay's rainbowfish (*Melanotaenia duboulayi*), firetailed gudgeon (*Hypseleotris galii*) and flyspecked hardyhead (*Craterocephalus stercusmuscarum fulvus*) were the most common native species, forming a further 37% of the total number of fish collected. Two native species, longfinned eel (*Anguilla reinhardtii*) and eel-tailed catfish (*Tandanus tandanus*), dominated the total catch in terms of biomass, collectively comprising over 85% of the total biomass collected (Fig. 7.1b). The five alien species collectively comprised only 2.5% of the total biomass, with cyprinids (mostly *C. carpio*) dominating the catch (71% of the total alien fish biomass), although this family occurred at only two sites.

Table 7.1. Native and introduced freshwater fish species present in south-eastern Queensland (including all coastal catchments from the Burnett River south to the border with New South Wales). Species native to the region are denoted by N, translocated native species by T (? denotes species of uncertain origin) and alien species introduced from other countries and thought to have established by A (source: Pusey *et al.* 2004). Species collected during the present study are denoted by *.

Taxon	Common name		Taxon	Common name		
Neoceratodontidae			**Terapontidae**			
Neoceratodus forsteri (Krefft)	Lungfish	N	*Leiopotherapon unicolor* (Günther)	Spangled perch	N	*
Anguillidae			*Amniataba percoides* (Günther)	Barred grunter	T	
Anguilla reinhardtii Steindachner	Longfinned eel	N *	*Bidyanus bidyanus* (Mitchell)	Silver perch	T	
A. australis Richardson	Shortfinned eel	N *	**Nannopercidae**			
Clupeidae			*Nannoperca oxleyana* Whitley	Oxleyan pygmy perch	N	*
Nematalosa erebi (Günther)	Bony bream	N *	**Kuhliidae**			
Osteoglossidae			*Kuhlia rupestris* (Lacepede)	Jungle perch	N	
Scleropages leichardti Günther	Saratoga	T	**Apogonidae**			
Retropinnidae			*Glossamia aprion* (Richardson)	Mouth almighty	N	*
Retropinna semoni (Weber)	Australian smelt	N *	**Mugilidae**			
Ariidae			*Mugil cephalus* Linnaeus	Sea mullet	N	*
Arius graeffei Kner & Steindachner	Fork-tailed catfish	N	*Myxus petardi* (Castelnau)	Freshwater mullet	N	
Plotosidae			**Gobiidae: Eleotridinae**			
Tandanus tandanus Mitchell	Eel-tailed catfish	N *	*Gobiomorphus australis* (Krefft)	Striped gudgeon	N	*
Neosilurus hyrtlii Steindachner	Hyrtl's tandan	N	*G. coxii* (Krefft)	Cox's gudgeon	N	*
Porochilus rendahli (Whitley)	Rendahl's catfish	N	*Hypseleotris galii* (Ogilby)	Firetailed gudgeon	N	*
Hemiramphidae			*H. klunzingeri* (Ogilby)	Western carp gudgeon	N	*
Arrhamphus sclerolepis krefftii Günther	Snub-nosed garfish	N	*H. compressa* (Krefft)	Empire gudgeon	N	*
Atherinidae			*Hypseleotris* sp.4 (Undescribed)	Midgely's carp gudgeon	N	
Craterocephalus marjoriae Whitley	Marjorie's hardyhead	N *	*Hypseleotris* sp.5 (Undescribed)	Lake's carp gudgeon	T?	
C. stercusmuscarum fulvus Ivantsoff, Crowley & Allen	Flyspecked hardyhead	N *	*Mogurnda adspersa* (Castelnau)	Southern purple-spotted gudgeon	N	*
Melanotaeniidae			*Philypnodon* sp. (Undescribed)	Dwarf flathead gudgeon	N	*
Melanotaenia duboulayi (Castelnau)	Duboulay's rainbowfish	N *	*P. grandiceps* (Krefft)	Flathead gudgeon	N	*
Rhadinocentrus ornatus Regan	Softspined sunfish	N *	**Gobiidae: Gobiinae**			
Pseudomugilidae			*Redigobius bikolanus* (Herre)	Speckled goby	N	
Pseudomugil signifer Kner	Southern blue-eye	N *				
P. mellis Allen & Ivantsoff	Honey blue-eye	N *	**Alien species**			
Synbranchidae			**Cyprinidae**			
Ophisternon sp. (Undescribed)	Swamp eel	N *	*Cyprinus carpio* Linnaeus	European carp	A	*
Scorpaenidae			*Carassius auratus* Linnaeus	Goldfish	A	*
Notesthes robusta (Günther)	Bullrout	N	**Cobitidae**			
Centropomidae			*Misgurnus anguillicaudatus* Cantor	Oriental weatherloach	A	
Lates calcarifer (Bloch)	Barramundi	N	**Poeciliidae**			
Chandidae			*Gambusia holbrooki* (Girard)	Eastern Gambusia	A	*
Ambassis agassizii Steindachner	Olive perchlet	N *	*Xiphophorus helleri* Heckel	Swordtail	A	*
A. marianus Günther	Estuary perchlet	N	*X. maculatus* (Günther)	Platy	A	*
Percichthyidae			*Poecilia reticulata* (Peters)	Guppy	A	
Maccullochella peelii mariensis Rowland	Mary River cod	N	*P. latipinna* (Le Sueur)	Sailfin molly	A	
Macquaria novemaculeata (Steindachner)	Australian bass	N *	**Cichlidae**			
M. ambigua (Richardson)	Golden perch	T *	*Oreochromis mossambicus* (Peters)	Mozambique mouthbrooder	A	
			Amphilophus citrinellus (Günther)	Midas cichlid	A	

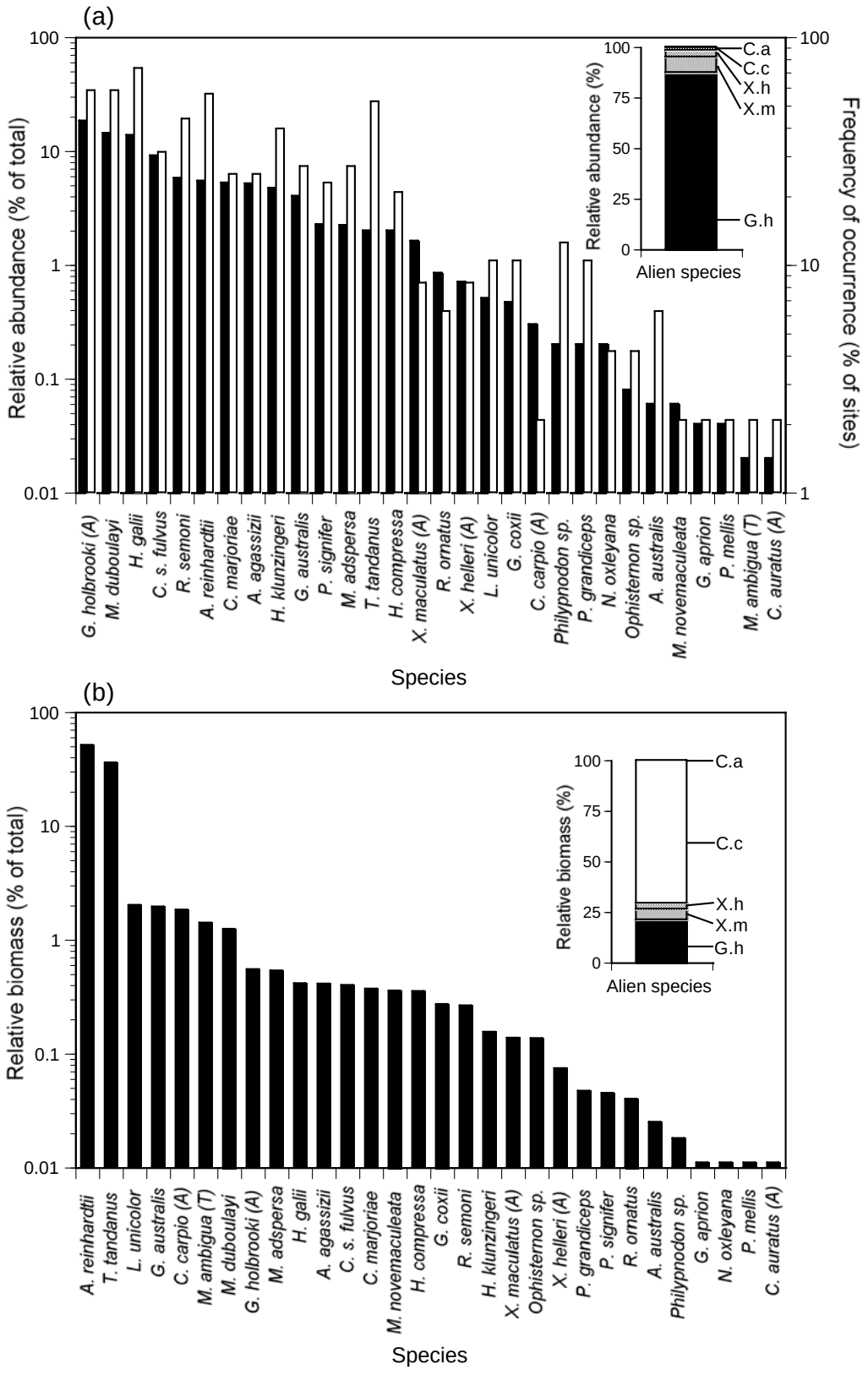

Figure 7.1. Biological characteristics of the fish fauna at the study sites showing (a) relative abundance (closed bars, scale on left axis) (n=4943 individuals) and frequency of occurrence (open bars, scale on right axis) (n=47 sites), and (b) relative biomass (total of 69.1 kg). Alien species are denoted by A and translocated native species by T, in parentheses. Inset histograms show the relative abundance (n=1041 individuals) and relative biomass (total of 1.8 kg) of alien species only (species names are abbreviated to the first letter of the genus and species, respectively).

7.4.2. Relationships of alien fish with sample effort, catchment variables and site physical characteristics

Indices of alien fish abundance (% abundance alien and total numerical density alien) and biomass (% biomass alien and total biomass density alien) were highly correlated with each other (Spearman's $r > 0.9$, Table 7.2). Variation in these indices was dominated by the contribution of poeciliid species (mainly *G. holbrooki*), with little influence from species of cyprinids. For example, alien fish indices were highly correlated with % abundance poeciliids and % biomass poeciliids (Spearman's $r > 0.95$), but not % abundance and biomass of cyprinids (Spearman's $r < 0.29$). Alien fish indices were not significantly correlated ($p>0.05$) with variables describing the size of the study site, the sampling effort expended or the total abundance or biomass of fish collected (Table 7.2). No significant ($p>0.05$) relationships existed between alien fish indices and catchment variables or site physical characteristics (Table 7.2).

7.4.3. Relationships of alien fish with the native fish fauna

There were no significant relationships between alien species relative abundance and biomass and the species richness, total numerical density and total biomass density of native fish observed at the study sites (Fig. 7.2). Similarly, no relationships were found using alien species density and biomass density data (results not shown). The wedge-shaped scatter of the data and the strongly negative slope of the upper bounds of each plot do indicate, however, that there was a decreasing relative abundance and biomass of alien fish associated with increasing species richness, numerical density and biomass density of native fish (Fig. 7.2). This suggests that there may be a threshold above which alien species are not able to invade or persist at certain sites, possibly due to the combined effect of high native species richness and high biological integrity, factors that may decrease the likelihood of invasion.

Table 7.2. Spearman's rank correlation coefficients for relationships between alien fish species indices (abundance and biomass) and variables describing sampling effort and landscape and local scale environmental data at the 47 sites sampled. Also shown are significant rank correlations between alien fish indices and disturbance gradient variables. Correlations significant at $p<0.05$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn and Keough 2002) are denoted by *.

	% abundance alien fish	% biomass alien fish
Alien species indices		
% biomass alien fish	0.961*	-
Total numerical density alien fish	0.966*	0.933*
Total biomass density alien fish	0.967*	0.935*
% abundance poeciliids	1.000*	0.960*
% abundance cyprinids	0.274	0.281
% biomass poeciliids	0.959*	0.996*
% biomass cyprinids	0.274	0.281
Site dimensions and sample effort		
Stream length sampled	-0.282	-0.203
Sampling area	-0.203	-0.194
Sampling volume	-0.048	-0.022
Total abundance	0.245	0.251
Total biomass	-0.167	-0.283
Catchment variables		
Upstream catchment area	0.072	0.107
Distance from stream source	0.091	0.115
Distance to river mouth	-0.276	-0.219
Altitude	-0.247	-0.221
Site physical characteristics		
Mean wetted width	0.032	0.094
Maximum depth	0.046	-0.058
Maximum velocity	-0.302	-0.361
Disturbance gradient variables		
% catchment cleared	0.447*	0.443*
% catchment cropped		0.373*
% catchment urban	0.460*	0.471*
Conductivity	0.380*	0.425*
Riparian cover	-0.435*	-0.467*
Aquatic macrophtyes	0.399*	0.458*
Submerged terrestrial vegetation	0.447*	0.404*
Mud		0.393*

I attempted to remove the potentially confounding effect that anthropogenic stress (abiotic and biotic) may have had on the native fish fauna at the study sites by distinguishing those sites with high biological integrity (as defined by O/P scores) from those in which the native fish fauna may have been affected by anthropogenic disturbance. I observed only weakly negative relationships of alien fish species indices with the ratio of observed to predicted native species richness (Fig. 7.3a & b). Furthermore, sites with high O/P scores (and therefore considered to be of high biological integrity) often also contained a high relative abundance and biomass of alien species (Fig. 7.3a & b). There were also no significant negative relationships ($p>0.05$)

of alien species indices with native species richness at the subset of sites considered to be of high biological integrity (native species richness O/P scores >0.75), at sites with reduced biological integrity (native species richness O/P scores <0.75) or across the entire site database (Fig. 7.3c & d). Sites predicted to contain a relatively high number of native species also often contained a high relative abundance and biomass of alien species (whether or not they were of high or low biological integrity). These results strongly suggest that sites with high native species richness were not less invasible, irrespective of their biotic integrity.

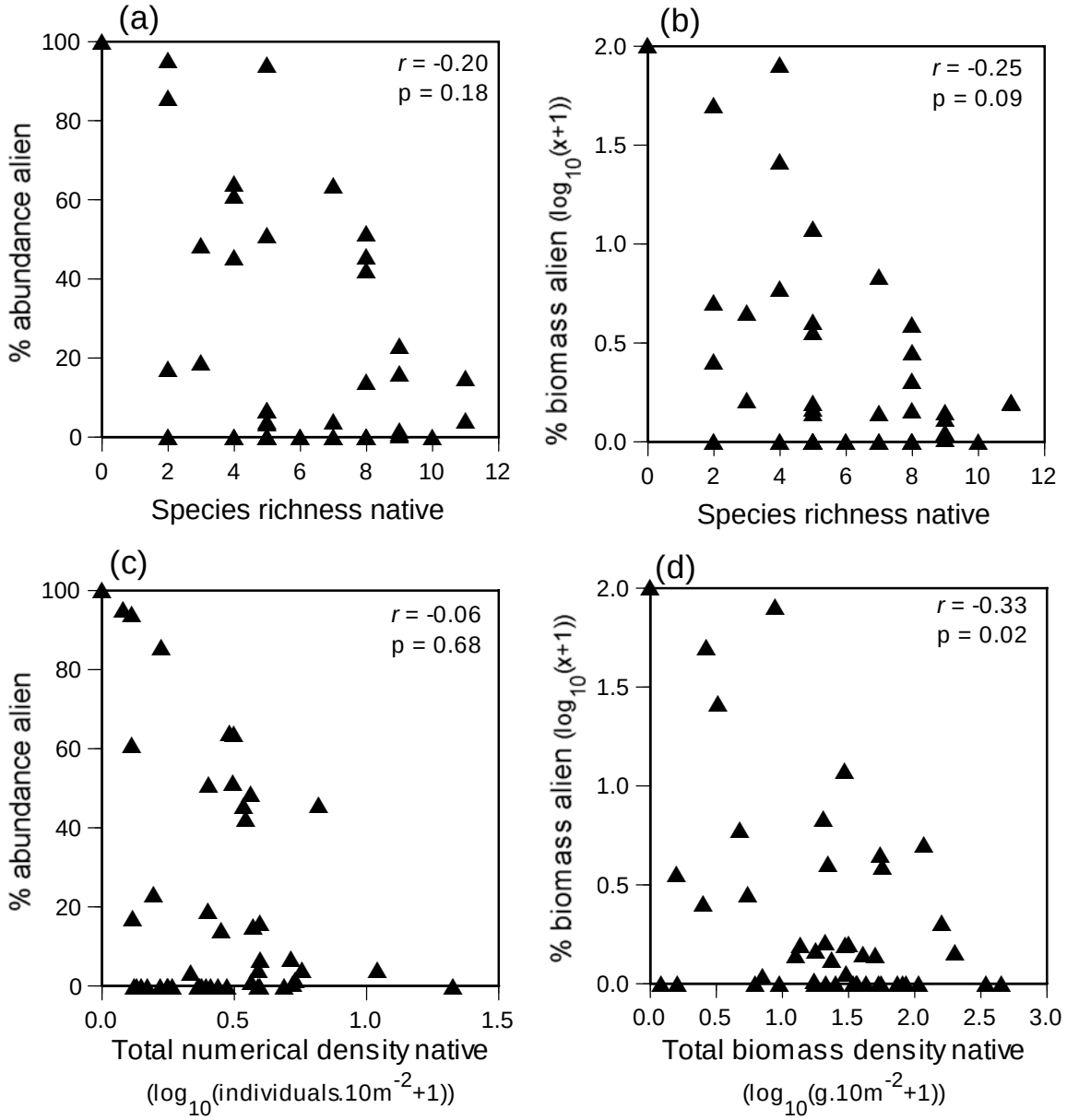

Figure 7.2. Relationships of (a) alien species relative abundance and (b) alien species relative biomass with native species richness observed at the study sites. Also shown are relationships of alien species relative abundance (c) and relative biomass (d) with total densities and biomass densities of native species. Spearman's rank correlation coefficients and their significance levels for each plot are also shown. Note that some axes are plotted on a $\log_{10}$ (x+1) scale for clarity.

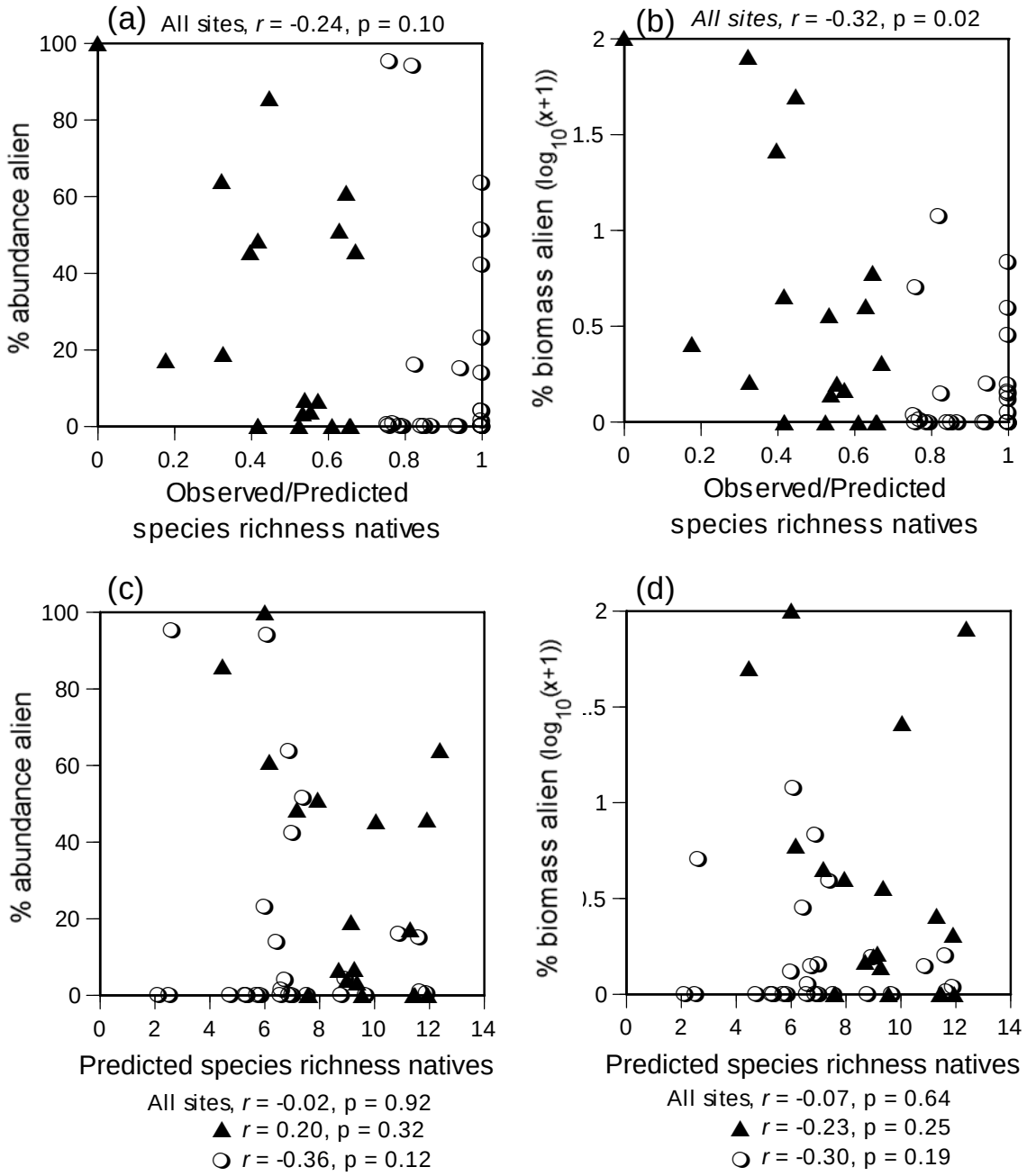

Figure 7.3. Relationships of (a) alien species relative abundance and (b) alien species relative biomass with the ratio of observed to predicted native species richness at the study sites. Sites considered to be of high biological integrity (O/P scores >0.75, n = 27 sites) are denoted by open circles, and those of low biological integrity (O/P scores <0.75, n = 20 sites) by closed triangles. Also shown are relationships of alien species relative abundance (c) and relative biomass (d) with predicted native species richness. The same symbols are used for each site type. Spearman's rank correlation coefficients and their significance levels for each plot are also shown. Note that the relative biomass data are plotted on a $\log_{10}$ (x+1) scale for clarity.

7.4.4. Relationships of alien fish with indicators of human disturbance

Sites where alien fish were present were characterised by significantly higher intensities of disturbance due to human land use practices (% of upstream catchment cleared, % cropped and % urban) than those sites without alien species (Fig. 7.4). These sites also had significantly wider ranges in diel dissolved oxygen concentrations, higher conductivity, lower riparian vegetation cover, muddy substrates and infestations of aquatic macrophytes (mostly alien weed species) and filamentous algae. Rank correlations between alien species indices and disturbance descriptors revealed similar patterns (Table 7.2). Disturbances related to land use (% cleared, % cropped, % urban), water chemistry (conductivity) and riparian and instream habitat degradation (riparian cover, mud, aquatic macrophytes, submerged terrestrial vegetation) were significantly correlated with the alien fish indices at the study sites (Table 7.2).

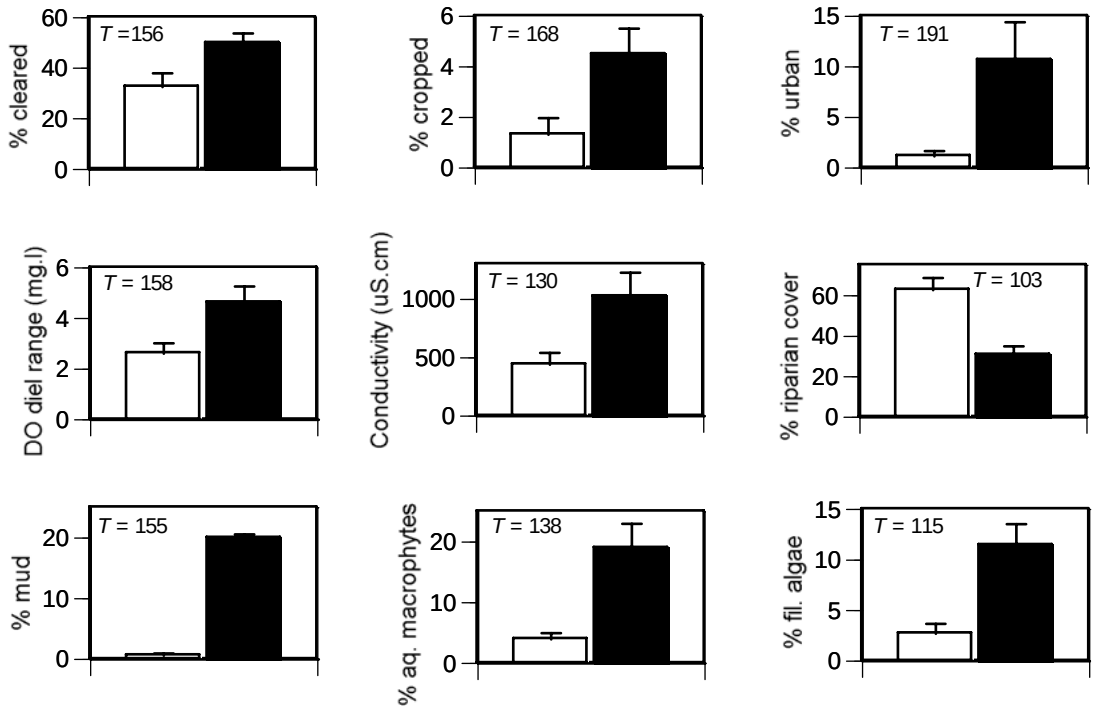

Figure 7.4. Mean (± SE) values of disturbance variables significantly different at sites where alien species were present (closed bars, n=28 sites) and absent (open bars, n=19 sites). Mann-Whitney test statistics (*T*) are given for each comparison; all were significant at $p<0.05$ after correction for multiple comparisons using the Dunn-Sidak procedure (Quinn & Keough 2002).

Multiple regression models using disturbance gradient principal components as predictors of variation in alien fish indices at test sites were highly significant ($p<0.0001$) and could explain 76% and 57% of the variance in the relative abundance and relative biomass of alien fish, respectively (Table 7.3, Fig. 7.5). Both regression models selected three disturbance principal components (PC2, PC4 and PC5) as predictors (Table 7.3). These results collectively suggest that the presence and relative abundance of alien fish was strongly related to the intensity of human disturbance as measured by surrounding land use, water quality, local riparian and in-stream habitat degradation.

Table 7.3. Summary of multiple regression models to predict variation in alien species relative abundance and biomass at the 47 test sites according to variation in the disturbance gradient principal components. For each GLM model 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.

Predictor (Principal component)	**Disturbance gradient description**	**% abundance alien fish**	**% biomass alien fish**
PC1	Catchment land use (clearing, grazing) and water quality (temperature diel range, pH, conductivity)	-	-
PC2	Riparian vegetation degradation, aquatic plant infestation, high diel DO range	19.8	19.4
PC3	High nutrients	-	-
PC4	Catchment land use (cropping), habitat degradation (muddy substrate) and high turbidity	19.6	18.5
PC5	Catchment land use (urbanisation) and habitat degradation (submerged terrestrial weeds)	36.2	19.2
	GLM R^2	75.7%	57.1%

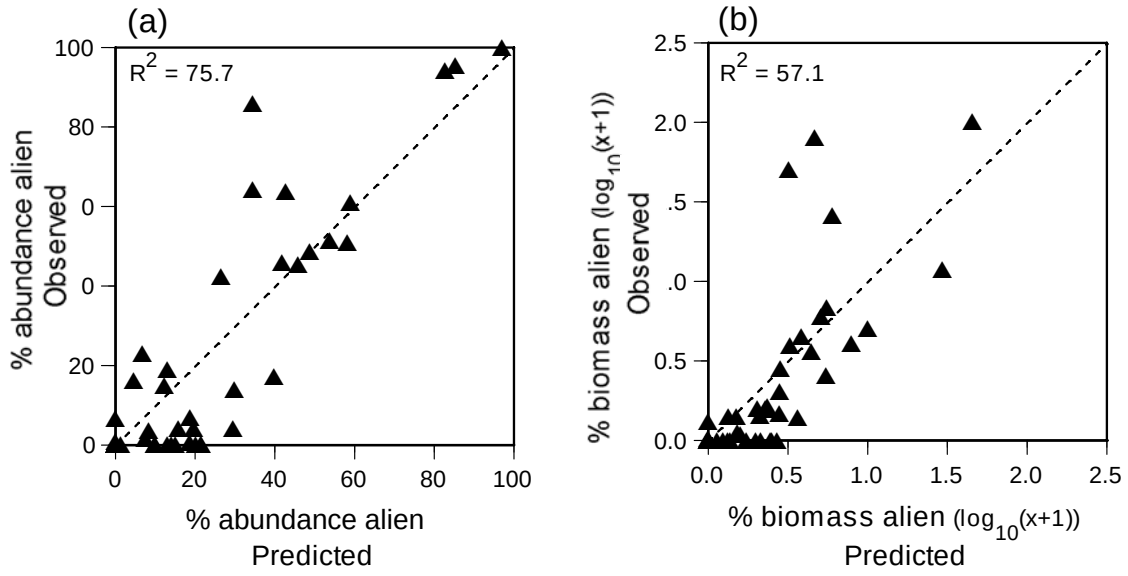

Figure 7.5. Relationships between alien species relative abundance (a) and relative biomass (b) predicted by multiple regression models and the values observed at each site. The disturbance variables used as predictors for each model are given in Table 3. Dashed lines indicate hypothetical 1:1 relationships between predicted and observed values. The approximate model R^2 is given for each plot.

7.5. Discussion

This chapter has shown that alien fish species are widespread and often abundant in south-eastern Queensland rivers and streams. The five alien fish species collected (eastern Gambusia, swordtail, platy, carp and goldfish) are all thought to be relatively tolerant to river degradation (Arthington *et al*. 1983, 1990, Arthington & McKenzie 1997), making them good candidate indicators of river health. The analyses revealed that variations in alien species distribution, local abundance and biomass were not related to the sizes of the study sites, the sampling effort expended or variation along natural environmental gradients. I could therefore rule out these as factors potentially confounding interpretations of alien fish as indicators of river health in the study area.

I observed no significant relationships of alien species indices with the species richness, total numerical density and biomass density of native fish present at the study sites. Although human disturbance factors may have reduced the biological resistance of the native fish fauna and enabled invasion by alien species, it is difficult to assess the relative importance of these potential confounding factors (i.e. the interaction between

habitat degradation and reduced biotic resistance) in mediating invasion success by alien species without direct experimentation. However, the results of this study suggest that at those sites where these confounding factors were removed (i.e. the subset of sites with high biological integrity), high species richness did not confer increased invasion resistance. A similar pattern was observed at sites with reduced biotic integrity. From these data, I conclude that the biological resistance of the native fish fauna was not an important factor mediating invasion success by alien fish species, supporting the findings of Meador *et al.* (2003b) and Gido *et al*. (2004) for North American streams.

Alien species were present at some undisturbed sites of high biological integrity, probably because they were introduced there or dispersed there from the original point of introduction, and were able to persist there because the environmental characteristics present suited their life history requirements. This has also been observed elsewhere; for example, populations of eastern Gambusia and swordtail occur in relatively undisturbed aquatic habitats within national parks and state forests in south-eastern Queensland (Arthington & Marshall 1999, Kennard, personal observation). The coexistence of a diverse assemblage of native species together with a high abundance and biomass of alien species at some sites may occur because insufficient time has elapsed for the negative impact of alien fish on native species to be realised. Alternatively, their coexistence may be facilitated by natural abiotic disturbances (e.g. floods and extended droughts) that periodically depress populations of alien species, but not native species that have evolved mechanisms to withstand these disturbances (e.g. Meffe 1984, Minckley & Meffe 1987, Pusey *et al*. 1989, Brown & Moyle 1997, May & Brown 2002). The flow regimes of many south-eastern Queensland rivers and streams are highly variable and unpredictable in comparison to other Australian rivers, extremely high discharge events and extended periods of zero flow occur naturally in this region, and so may constitute natural abiotic disturbances (Pusey *et al*. 1993, 2000) in these rivers.

The number of introduction occasions is thought to be an important factor influencing successful establishment of fish, birds and other organisms (Ross 1991, Case 1996, Cassey 2001, Marchetti *et al.* 2004). Alien fish species distributions, abundance and biomass data, as assessed in the present study, reveal nothing of the relative frequency of introductions but do indicate the outcome of successful species invasion. Invasion success was strongly related to the human disturbance gradient, particularly the amount

of urban development in the catchment. In Australia, habitat modifications associated with the successful establishment of alien species include impoundment, diversion, channelisation and regulation of rivers; desnagging, loss of riparian vegetation, bank erosion and sedimentation; thermal and chemical pollution and the presence of introduced plants (Arthington *et al*. 1983, 1990). Many of these disturbances were important correlates with the presence, abundance and biomass of alien fish collected during this study. I interpret these observations by suggesting that alien species are more likely to be introduced in urbanised areas, are more tolerant of associated degraded habitat conditions and possess life history attributes enabling them to persist at sites where native species could not. These conclusions remain tentative as this study was conducted over a short time span (a single sampling occasion), however I suggest that once an alien species has invaded an area and habitat conditions remain favourable, it is likely to persist there. Nevertheless, the ability of alien fish indices to reflect human disturbance to streams may be confounded by several factors. The relatively strong relationships of alien fish with proximity to urban areas, as demonstrated in the present study, may simply reflect the increased likelihood of introductions (e.g. intentional aquarium releases or accidental escapees from artificial ponds) in these areas, and may not necessarily be associated with degraded stream habitat or water quality. Conversely, river reaches may be anthropogenically disturbed but alien species are not present because they are unable to access these areas due to natural or artificial barriers, or simply because they have not been introduced there. (See also Moyle *et al.* 2003).

The use of a river health index based on all alien species present may be overly simplistic for river systems in which alien species with varying life history characteristics and differential tolerances to specific human impacts are included in the final index. For example, Maret (1998) suggested that the widespread introduction of intolerant salmonid species in central North America confounded the use of introduced species as an indicator of habitat degradation. This problem could arise in south-eastern Australian streams and rivers where salmonids have become established (Cadwallader 1979, Arthington & Mitchell 1986, Crowl *et al*. 1992). In northern Australia, the alien species of poeciliids, cyprinids and cichlids present have entirely different life history requirements, reproductive styles and different tolerances to environmental stressors (see Milton & Arthington 1983, Arthington & Mitchell 1986, Arthington *et al.* 1986, Bruton 1986). Although intuitively obvious, caution should be exercised when

interpreting indices of river health based on alien species and reference should be made to the composition of species from which each index is derived. Nevertheless, an alien species index (particularly one based largely on poeciliids, and mainly *G. holbrooki*, such as that examined in the present study) may be a simple and effective 'first cut' indicator of river health.

The results of this study suggest that streams and rivers affected by human activity and modification are more likely to be susceptible to invasion by alien fish species. The presence of alien species can therefore be used as an indicator of degraded stream conditions and these areas can be given appropriate attention for remediation. However, the impact of alien species at degraded sites may be as much, or more, disruptive of the native fish fauna than the adverse physical and chemical conditions present, and may therefore represent a severe form of biological disturbance (Ganasan & Hughes 1998). Although human-induced physical and chemical changes to streams can often be reversed or at least ameliorated, alien species are difficult to control and may be impossible to eradicate (Courtenay & Hensley 1980, Courtenay & Stauffer 1984, Ganasan & Hughes, 1998, Koehn *et al.* 2000). Nevertheless, habitat restoration activities (e.g. flow restoration, introduction of woody debris or riparian vegetation rehabilitation) may help prevent the establishment of alien fish populations, assist in the management of those already present (e.g. by reducing abundances) and benefit native fish populations (Arthington *et al*. 1990, Koehn *et al*. 2000, Marchetti & Moyle 2001, Brown & Ford 2002).

Alien species are indicators of biological integrity in two fundamental respects. Firstly, their presence represents a deviation from the historical natural condition of the fish community (i.e. the pre-introduction condition). Secondly, alien fish species have been associated with declines in, or extirpation of, native fish in a range of systems because of predation, competition and/or transmission of disease. In an analysis of 31 studies, Ross (1991) suggested that introduced fishes resulted in declines of native species in 77% of cases studied. The apparently strong impact that many alien fish species have on native fish species, together with the notion that they can also be useful as an initial basis to diagnose other forms of human disturbance impacts, suggest that some alien species can represent a reliable indicator of river health. Ultimately, indicators based on the presence, abundance and biomass of alien species have potentially broad appeal because of their practicality (i.e. relative ease of sampling, identification and analysis)

and conceptual simplicity (it is easy to communicate results to managers and the wider community).

I conclude that alien fish can be a reliable indicator of river health, but with the following provisos: 1) the local fish assemblage is accurately determined with standardised sampling methods that result in equivalent levels of efficiency in collecting both native and alien species; 2) those alien species generally regarded as intolerant of degraded physical and chemical conditions (e.g. salmonids) are excluded from summary indices and 3) consideration is given to confounding factors such as the possibility that alien species may have been deliberately introduced into relatively undisturbed areas (e.g. for recreational angling, biological control or through aquarium release).

Chapter 8: General discussion

8.1. The need for quantitative methods to assess river health

Natural functioning aquatic ecosystems deliver critical goods, services and long-term benefits to human welfare (Costanza *et al*. 1997, Baron *et al*. 2002). However, impacts of human modifications to riverine landscapes have meant that as aquatic ecosystems degrade, they become incapable of supplying goods and services to the same capacity as in the past (Rapport *et al.* 1998). Although aquatic ecosystems have numerous significant intrinsic values (Nash 1990), the diminished ability of degraded ecosystems to sustain economic activity (Costanza *et al.* 1997) and human health (McMichael 1993, 1997) has led to a greater recognition that their protection, remediation and restoration is critically important. Quantitative procedures are therefore required to assess aquatic ecosystem health and monitor biotic responses to remedial management.

Monitoring and assessment programs must be sufficiently well-designed and conducted to be able to deliver on their core intentions, that is, to be able to determine whether natural systems are changing or have already changed in response to a human induced perturbation. In reality, this translates to the simultaneous minimisation of the frequency of Type I (incorrectly classifying a site as impaired) and Type II (incorrectly classifying a site as unimpaired) errors in the most cost-effective manner possible. In the introduction to this thesis, I identified five key requirements of a quantitative and defensible river health assessment program that need to be evaluated before the chosen indicators can be validly applied for river health assessment in a given river or region. The five requirements were: 1) quantify error associated with sampling of biological data; 2) assess natural ranges of spatial and temporal variation in biotic assemblage attributes; 3) quantitatively define the reference condition for these attributes; 4) demonstrate relationships of indicators with disturbance; and 5) evaluate the importance of potentially confounding environmental and biological factors. These are important considerations for minimising Type I and Type II error rates and hence correct conclusions about river health assessment. I argue throughout this thesis that satisfying these requirements can provide a quantitative basis for the use of fish as indicators of river health that is not only rigorous and scientifically defensible, but more importantly, is crucial in justifying management interventions that may benefit fish and gaining broader acceptance of monitoring and management by the community.

The implications of each of these issues will now be discussed in the context of the development of a river health monitoring program using fish in south-eastern Queensland, Australia. I will also identify critical knowledge gaps and areas of future research that would further strengthen such a monitoring program. Finally, I describe how fish are being used to monitor the health of rivers and stream in south-eastern Queensland.

8.2. River health assessments are only as good as the data that underpins them

The ability to develop an efficient data sampling program without sacrificing accuracy and precision, and hence ability to detect changes through space and time, is a critical requirement of every river health assessment program. In particular, field work may entail the most time consuming and expensive part of an assessment program and therefore the amount of sampling effort required to collect the data necessary to allow construction of reference conditions and to provide data on sites being newly assessed is an important consideration. In Chapter 3 I demonstrated that accurate and precise reach-scale estimates of fish assemblage attributes, such as species richness, species composition and species relative abundances, could be obtained from multiple-pass electrofishing plus seine netting of three mesohabitat units. Given the effects of interspecific variation in fish behaviour and habitat use, spatial variation in environmental conditions, and variation in sampling effort required, I concluded that this was generally a more efficient sampling protocol than less intensive sampling over larger spatial scales. Quantification of the potential sources and magnitude of error associated with raw data collection is critical in the context of river health assessment programs. Failure to detect species during sampling has the potential to bias bioassessments and can result in considerable deviations in expected and observed assemblage attributes and a low sensitivity to detect meaningful changes in space or time (Maher *et al.* 1994, Paller *et al.* 1996, Chapters 5 and 6). This may be particularly important for Australian streams, where local fish species diversity may often be comparatively low (Harris 1995, Harris and Silveira 1999). Nevertheless, fish assemblage data collected using the sampling protocol recommended in Chapter 3 was sufficiently accurate and precise that relatively small differences (e.g. $< 20\%$) in these assemblage attributes could be detected with a high statistical power ($1-\beta > 0.95$). I further demonstrated that relatively few stream reaches (e.g. < 4) needed to be sampled

to accurately estimate assemblage attributes within close proximity (e.g. 20% of the half width of the confidence interval) to the true population means.

The minimum sampling effort required is that which provides the necessary information to achieve the goal of a sampling program, and depends on such factors as the species and attributes of interest, the required accuracy and precision, and the efficiency of the sampling protocol (Sheldon 1984, Andrew & Mapstone 1987, Bohlin *et al*. 1989, Norris *et al.* 1992, Maher *et al*. 1994, Angermeier & Smogor 1995, Chapter 3). Ultimately, the best sampling program is one that simultaneously maximises accuracy, precision and sensitivity, and minimises resource use. Issues of cost-effectiveness and the ability to detect change with a stated degree of confidence and scientific defensibility are critical in the context of convincing environmental managers and funding agencies to invest in river health assessment programs (Maher *et al*. 2004). In this context, I conclude from the results of Chapter 3 that an intensive sampling program over small spatial scales (i.e. three mesohabitat units) is more effective than less intensive sampling over longer stream reaches in that more accurate and precise data can be collected, usually with equivalent efficiency and hence little difference in cost.

8.3. Biotic assemblages vary through space and time, but is variation natural or human induced?

The issue of temporal variation is an important one for river health assessment programs and was examined in Chapters 4 and 5. Attributes of biotic assemblages, from which indicators are derived, typically vary at intra-annual and inter-annual time scales, particularly in environmentally variable environments. In the context of designing temporal sampling strategies for stream bioassessment programs, sampling during periods when extreme natural environmental disturbances (such as low flows and floods) are more likely, may introduce variability sufficient to make the detection of changes associated with anthropogenic impacts more difficult. Furthermore, in locations characterised by variable hydrological regimes and complex disturbance histories, substantially different conclusions from bioassessment of a site could be drawn from different years or times of year. This may occur despite data being collected in identical ways on each sampling occasion and in the absence of changes in human disturbance.

This study showed that fish assemblages were generally highly persistent and some attributes of fish assemblages (e.g. species richness, species composition and to a lesser extent, species relative abundances) were highly stable through time, both on an intra-annual and inter-annual basis, at the majority of sites examined. Such attributes make ideal candidates for bioassessment indicators. In contrast, fish assemblages occurring in streams with highly variable flow regimes were more variable. This variability appeared due to natural impacts associated with low flow disturbance. However, fish assemblages at these sites appeared resilient to these natural disturbances, provided that flow and habitat conditions resembled the pre-disturbance state. Fish assemblage attributes that respond to anthropogenic disturbances but exhibit low natural temporal variability are potentially the most sensitive yet robust indicators of human impacts for use in bioassessment programs (Paller 2002). On this basis, I considered fish assemblage attributes such as native species richness, assemblage composition and species relative abundances (e.g. percentage of alien species) to be ideal indicators of river health in south-eastern Queensland, particularly as they could also be demonstrated to respond to anthropogenic disturbance gradients in the region.

A critical underpinning of bioassessment programs in particular, is the ability to accurately define attributes of the assemblage that are expected in the absence of anthropogenic disturbance (i.e. defining the reference condition – Reynoldson *et al.* 1997, Chapters 1, 4, 5 and 6). Natural spatial and temporal variation in assemblages driven by variation in environmental conditions must be accounted for, to the extent that impacts of human-induced disturbance can be accurately assessed (Resh & Rosenberg 1989, Grossman *et al.* 1990, Chapter 1). Although the ability to detect species associations (Angermeier & Schlosser 1989) and relationships with natural habitat gradients (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 in south-eastern Queensland, I demonstrated in Chapters 5 and 6 that spatial variation in certain attributes of fish assemblages could be accurately predicted using a small number of simple environmental variables. Although the total number of fish species available for prediction was low in comparison to other aquatic faunal and floral indicator groups (such as macroinvertebrates and diatoms, respectively), the accuracy and precision of the models was comparable to outcomes of similar studies on such taxa (e.g. Chapter 5).

I further showed that a 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 that resulted in habitat desiccation and local fish extinctions). 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).

The scope of the predictive models of native species richness and assemblage composition 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, Maroochy, Pine and South Coast drainage basins need to be sampled and incorporated into any updated version of the predictive models (see Figure 2.1). I view the predictive models developed in the present study to be dynamic and recommend 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 are updated periodically.

My results are encouraging for the development and implementation of a river health monitoring program in south-eastern Queensland with the qualification that consideration must be given to antecedent and prevailing hydrological conditions. Sampling needs to be stratified to times of year in which natural environmental disturbances are less likely. Sampling during spring and summer, when extreme natural

environmental disturbances due to low flows or floods are more likely, should be avoided, whereas sampling during winter should minimise the chances of natural disturbances causing changes in fish assemblages that cannot be predicted from simple environmental descriptors (such as those used in the predictive models described in Chapters 5 and 6). This sampling strategy reduces the chances of incorrectly diagnosing a site as impacted by human activity (i.e. committing a Type 1 error). Sampling at a time of year when longitudinal movement by fish is not restricted by low flows and fish are able to assort along preferred environmental gradients also maximises the opportunity to detect relationships between fish assemblages and natural habitat gradients and to construct predictive models of these relationships that account for this source of natural spatial variation in fish assemblages (see Chapters 5 and 6). These are not particularly restrictive requirements for the development of a sampling program in a hydrologically variable region of Australia and should not be impractical for adoption by management agencies (see also Wilcox *et al*. 2002).

8.4. Procedures for defining the reference condition: should accuracy be sacrificed for simplicity?

The use of multivariate predictive models such as described in Chapter 5 for predicting attributes of biotic structure (e.g. assemblage composition) for use 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). Multimetric indices such as the Index of Biotic Integrity (Karr 1981, Karr *et al.* 1986) are advocated on the basis that the methods used to define the reference condition are simple and that the individual metrics are easily understood. Moreover, environmental managers and other non-experts can readily understand the final output: a single index composed of summary metrics encapsulating the complexity of natural communities (Karr *et al*. 1986, Fausch *et al*. 1990, Karr & Chu 1999, Barbour *et al*. 1995, Simon 1999). For example, indicators based on the presence and abundance of alien species have potentially broad appeal because of their practicality (i.e. relative ease of sampling, identification and analysis) and conceptual simplicity (it is easy to communicate results to managers and the wider community). Similarly, biodiversity maintenance (as indicated by maintenance of species richness through time) is a notion that is readily understood by the general community and managers as being desirable. While conceptually simple, I demonstrated in Chapters 6 and 7, respectively, that

metrics based on native species richness and alien species are at the same time, accurate indicators of river health.

The relative merits of multivariate *versus* multimetric approaches have been extensively canvassed elsewhere and will not be repeated here (see Norris 1995, Karr 1999, Karr & Chu 1999, Karr & Chu 2000, Norris & Hawkins 2000). Nevertheless, three key issues are: 1) the complexity of the analytical or statistical methods used to define the reference condition for the biological attribute in question; 2) the type of biotic data from which the indicators are being derived (e.g. biotic composition *versus* summary attributes of biotic structure and function); and 3) the relative complexity of the outputs. Although there is no doubt that the application of multivariate statistical models does require a certain level of expertise, the outputs from predictive models of biotic structure (i.e. 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).

I suggested in Chapter 6 that the accuracy and precision of bioassessment results is of critical importance, irrespective of the complexity of the analytical or statistical procedures necessary to define the reference condition. The choice of simplicity over complexity does have some important consequences for Type I and Type II error rates and hence the ability to detect human disturbance at a given locality and diagnose the potential causes. For example, in Chapter 6 I outlined an approach commonly used for defining the reference condition for univariate metrics comprising the Index of Biotic Integrity, the 'maximum species richness line' (MSRL). Although the method is intuitively attractive and conceptually simple, I showed that the ability of the MSRL approach to accurately define the reference condition for native species richness is inherently compromised by the scoring procedure used and because it is limited to predicting variation in the dependent variable along a single environmental gradient (e.g. stream size). This resulted in substantially higher prediction error in comparison to three alternative regression methods, which incorporate single or multiple

environmental variables as predictors. The MSRL approach led to an increased frequency of Type I errors for least-disturbed reference and validation sites (i.e. incorrectly classing these sites as disturbed). As a consequence of the apparent inability of the MSRL approach to adequately account for natural variation in species richness, the ability of the metric to accurately detect a disturbance 'signal' at the test sites was compromised.

The compounding of classification errors arising from the application of the MSRL to multiple structural and functional metrics is potentially high if scores for individual summary metrics are summed to produce a final index (as is usually the case with integrative multimetric indices such as the IBI) (Suter 1993, Norris 1995, Reynoldson *et al*. 1997). The extent of this potential problem has yet to be fully evaluated. Nevertheless, the increased frequency of Type I errors (incorrectly classifying a site as impaired) has important implications for remediation efforts. A commonly held view is that Type II errors (failure to diagnose an impairment) will have more serious environmental consequences than Type I errors (diagnosing impairment in its absence). If the causes of impairment are not identified and corrected, the damage continues unabated. Moreover, if and when impairment is identified, remediation becomes comparatively more difficult due to long recovery times of ecosystems (and their structural and functional components) subjected to long-term stress (e.g. see Detenbeck *et al.* 1992, Harding *et al.* 1998, Allan 2004). Type I errors, in contrast, usually result in only short-term economic costs (Toft & Shea 1983, Andrew & Mapstone 1987, Peterman 1990, Fairweather 1991, Dayton 1998). Thus, the increased chance of rehabilitation dollars being misdirected to those areas incorrectly identified as being impaired may be seen as less consequential than a failure to correctly identify those areas in more urgent need of rehabilitation. In this regard, it could be argued that the high Type I error rate of the MSRL provides a greater sensitivity to deviation from reference condition. Following the precautionary principle this may be acceptable from an environmental conservation perspective but given that resources for rehabilitation are frequently limited, bioassessment methods in which the expected condition for biotic indices is accurately defined and hence Type I errors are minimised, are highly desirable. Provided that collaboration is undertaken with the relevant expertise of ecologists (as suggested by Karr and Chu 1999), timely investment in the services of a statistician (although possibly initially expensive) who can help with the development of rigorous sampling designs and quantitative methods for defining reference

conditions, offers potentially great savings given the ultimate cost of reversing and restoring rivers already disturbed by human activity.

8.5. Detecting disturbance and diagnosing causes?

The strongly nested and hierarchical organisation of river landscapes suggests that aquatic ecosystems are strongly influenced by their surroundings at a variety of scales (Hunsaker & Levine 1995, Allan 2004, Chapter 1). Consequently, human impacts on local assemblages are likely to be scale dependent, potentially being affected by processes operating at both landscape scales (e.g. agricultural runoff from upstream areas and barriers downstream) and local scales (e.g. riparian and in-stream habitat degradation), a concept demonstrated in practice by many studies (e.g. Roth *et al.* 1996; Allan *et al.* 1997; Stauffer *et al*. 2000, Allan 2004, Chapters 5, 6 and 7). That fish can integrate human disturbances arising from multiple sources at a range of spatial and temporal scales is seen as one of the benefits of using fish as indicators (Chapter 1). However, the existence of multiple, scale-dependent mechanisms, potentially non-linear responses of biota to disturbance, and the difficulties of separating current from historical effects, can make it difficult to establish relationships between disturbance and ecosystem health indicators or to diagnose the specific sources or mechanisms of human impact (Allan 2004).

This study demonstrated strong relationships of ecosystem health indicators based on native fish assemblage composition (Chapter 5), native species richness (Chapter 6), and the presence, abundance and biomass of alien fish species (Chapter 7) with a variety of sources of human disturbance potentially functioning at a range of spatial and temporal scales. These disturbances described impacts associated with catchment land use and associated local riparian, in-stream habitat and water quality degradation. The results of this study indicated that streams and rivers affected by human activity and modification are more likely to be susceptible to invasion by alien fish species and display major differences in native fish assemblage composition and native species richness from that expected by comparison with similar areas not subject to human disturbance. These attributes of fish assemblages can therefore be used as summary indicators of degraded stream conditions and these areas can be given appropriate attention for remediation. In this sense, these indictors may be amenable for inclusion into a broad-scale ambient monitoring program aimed at evaluating ecosystem health and for identifying areas that

may require management intervention. However, their utility in diagnosing sources of disturbance or the mechanisms by which they influence fish is debatable and requires further examination.

Indicators based on deviations in native fish assemblage composition from that expected revealed detailed information about the impacts of each source of disturbance on each native fish species, which, when coupled with knowledge of their life history requirements, could potentially help to further elucidate the causes of disturbance to the aquatic ecosystem. However, *post-hoc* correlative approaches and assumptions of linear relationships (such as in this thesis) have limitations in establishing cause and effect, no matter how explicit the conceptual basis for the linkages are. Ideally, experimental approaches are required, as is greater knowledge of the ecological requirements and environmental tolerances of the biota (Pusey *et al*. 2004). Human activities or the presence of invasive alien fishes that may negatively affect individual native species do so via their influence on specific ecological traits (e.g. morphology, movement, trophic ecology, reproductive biology, environmental tolerances and habitat requirements). In this sense, the underlying metrics that describe the functional traits of assemblages and that are incorporated into the index of Biotic Integrity potentially offer more diagnostic capabilities than interpretation of biotic patterns alone, as metrics such as those based on trophic and habitat requirements can provide a mechanistic basis for understanding cause and effect.

The use of ecological traits of fish communities to develop a quantitative mechanistic understanding of the functional linkages between environmental drivers and fish species distributions or abundance patterns, is not well advanced in Australia, but is gaining increased attention in the US and Europe (e.g. Olden & Poff 2003, Vander Zanden *et al.* 2004, Vila-Gispert *et al.* 2005). An important impediment in Australia has been the lack of quantitative ecological information for many species, and the disparate and inconsistent manner in which existing information has been collected and reported in the past (but see Pusey *et al.* (2004) for a systematic study of the ecological requirements native fishes). To incorporate such functional traits into a monitoring program in south-eastern Queensland will require a much greater understanding of how these attributes of biotic communities vary along natural environmental gradients (i.e. defining the reference condition). This knowledge deficit has reduced the capacity to quantitatively predict the consequences of future catchment management or flow

alteration scenarios on key elements of aquatic biodiversity such as fish (Bunn & Arthington 2002, Arthington & Pusey 2003). Nevertheless, habitat restoration (e.g. flow restoration, introduction of woody debris or riparian vegetation rehabilitation) may help prevent the establishment of alien fish populations, assist in the management of those already present (e.g. by reducing abundances) and benefit native fish populations (Arthington *et al*. 1990, Koehn *et al*. 2000, Marchetti & Moyle 2001, Brown & Ford 2002).

8.6. Assessing river health using fish in south-eastern Queensland

Increasing scientific and community concern over the widespread impacts of human activities on river systems has led to the expressed need for monitoring programs to be able to determine whether a location is impacted or experiencing a decline in health. This thesis has demonstrated that it is possible to use fish as an indicator of river health in south-eastern Queensland and that a bioassessment program incorporating fish is capable of detecting human impacts associated with land use changes, but with the following qualifications:

1) Sampling needs to quantitative and rigorous. Multiple-pass back-pack electrofishing plus supplementary seine netting provides more accurate, precise and efficcient estimates of fish species richness, assemblage composition and species relative abundances in comparison to single-pass electrofishing alone. Furthermore, intensive sampling of three mesohabitat units (equivalent to a riffle-run-pool sequence) is a more efficient sampling strategy to estimate reach-scale assemblage attributes than less intensive sampling over larger spatial scales;
2) The timing of sampling is critical, as is consideration of antecedent hydrologic conditions. Sampling during winter should minimise the chances of natural disturbances causing changes in fish assemblages that cannot be predicted from simple environmental descriptors (as are used in the predictive models described in Chapters 5 and 6) and hence reduces the chances of incorrectly diagnosing a site as impacted by human activity (i.e. committing a Type 1 error). This also maximises the opportunity to detect relationships between fish assemblages and natural habitat gradients; and

3) Indicators based on native species richness, assemblage composition and alien species are potentially powerful indicators of river health. However, accurate and precise definition of the reference conditions expected in the absence of human disturbances is critical. Failure to do so can markedly increase classification errors and lead to failure to detect disturbance signals.

The ultimate objective of a bioassessment program should be to trigger some management intervention (e.g. mitigation, rehabilitation and/or restoration), otherwise it is a waste of limited resources simply to document declines in river health. The fish indicators described in this thesis now form part of a broad-scale monitoring program of the health of aquatic ecosystems in wadeable rivers and streams of south-eastern Queensland. Indicators of ecological processes, biodiversity (fish and macroinvertebrates) and water quality are monitored bi-annually at 120 sites. The indicators are intended to provide early warnings to councils and land managers of declines in the health of rivers and streams, report on the effects of different land uses, and to evaluate the effectiveness of management actions aimed at improving and protecting aquatic ecosystems in the region (Moreton Bay Waterways and Catchment Partnership 2002). I hope that we are successful in this endeavour.

Chapter 9: References

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Appendix 1: Published paper arising from this thesis

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

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

10.1.1 Development and application of a predictive model of freshwater fish assemblage composition to evaluate river health. *Hydrobiologia* (In Press)

10.1.2 Accurately defining the reference condition for summary biotic metrics: a comparison of four approaches.
Hydrobiologia (In Press)

10.1.3 Are alien fish as reliable indicator of river health? *Freshwater Biology* (2005).