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The Role of Hydrology in the Ecology of Cooper Creek, Central Australia:

Implications for the Flood Pulse Concept

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for the Degree of Doctor of Philosophy

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Northwest Branch of Cooper Creek, central Australia

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for photocopying and loan.

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Abstract

Flow is the dominant variable in the ecology of streams and rivers. The Flood Pulse Concept of Junk, Bayley and Sparks asserts that regular overbank flows ("pulses") of river discharge govern the dynamics of lowland river-floodplain systems, because they impose wet and dry phases on the floodplain, maintaining high biodiversity and production. The concept derives principally from work on tropical and temperate floodplain rivers, where variations in the flood pulse are relatively predictable, and it implies that biotic adaptations to flow are precluded where variation is unpredictable. However, flow in dryland rivers is highly unpredictable, yet flood pulses may be ecologically no less important than in the rivers of more humid areas.

This thesis examines the generality of the Flood Pulse Concept as a model for the role of flow in large floodplain rivers of all climatic zones. It reviews the literature on hydrology-biology relations, with particular reference to the ecology of riverine fish. Using techniques of ordination, clustering and analysis of similarities (ANOSIM), it examines the relations between flow variability, ecology and climate in large rivers worldwide. Then, using a five-year database for Cooper Creek in Central Australia, it relates structures of fish, macroinvertebrate and zooplankton assemblages and indices of fish health and behaviour to hydrology at several spatial and temporal scales. These relations are established using multivariate techniques, univariate correlation and regression, and Neural Networks modelling.

The above analyses demonstrate that arid zone rivers are exceptionally variable over a wide range of temporal and spatial scales and in manifold facets of flow , and that the biota of such rivers is adapted to this variability at several levels of biological resolution. They show that individual rivers have distinctive hydrological "signatures" in these facets of flow, and that the relations between hydrology and biological responses are also multi-faceted. In such rivers low or zero flows particularly are associated with distinctive biological community structures, but the clustering (persistence) of large floods also has distinctive biological effects. Predictive models using hydrological inputs are able to

account for a substantial proportion of the variance in the biological assemblages of Cooper Creek.

These results are used to develop the Flood Pulse Concept into a general model more applicable to dryland rivers (the "Flow Pulse Model"). To accommodate the dynamism of dryland rivers, this model redefines the floodplain, encompasses all magnitudes of flow (not only overbank flows), enlarges the range of flow variability and flow complexity considered, and covers a greater range of temporal scales. The final chapter explores the implications of this model for river management and conservation. It concludes that the distinctiveness of dryland rivers is such that concepts of river function and river management for dryland rivers should be developed from studies of these neglected systems, not derived from research on rivers in humid zones.

Cooper Creek

I see through this lens, from 7000 feet,
Parts of the fabric the river has unfurled,
From the Great Divide west into the desert.

Here a quilt of lakes in ochre and cream
Stitched with dark gums,
Here a lace of channels, green on khaki,
Here copper brooches of island dunes,
Creeks plaited with ribbons of sand,
The yellow sash of a long waterhole.

This scarf of life a thousand miles long,
Goanna baking his patterned skin
Across five thousand Strzelecki dunes,
Is mortal as whales to harpoons of greed.

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1. Review of concepts

1.1 Introduction

Development of a comprehensive and widely applicable model of the role of flow in river ecology is a matter of some urgency. Impoundment, water withdrawals and diversions, channelisation and floodplain alienation have degraded large rivers throughout the world (Walker 1985, O'Keeffe *et al.* 1989, Dugan 1990, Welcomme 1992, Dynesius & Nilsson 1994). Despite unequivocal, compelling evidence for the ecological significance of flow, these processes continue.

Flow, or discharge, is the dominant variable in the ecology of streams and rivers (e.g. Ambühl 1959, Junk *et al.* 1989, Poff & Allan 1995, Walker *et al.* 1995), although perceptions of its role vary with the observer's perspective in time and space and the nature of the environment and organisms under study. In arid regions, where stream flows are variable, flood and drought are described as disturbances that govern the structure and dynamics of stream communities (Fisher *et al.* 1982, Fisher 1986, Minckley & Barber 1971, Deacon & Minckley 1974). Yet in the literature on the fish of large river systems, flooding is seen as a driving variable rather than a disturbance. In particular, the magnitude of flooding (Krykhtin 1975, Holcik & Bastl 1977, Quiros & Cuch 1989) and the extent of drawdown (Welcomme & Hagborg 1977, Bayley 1991) are related to recruitment. Flooding is critical for lateral and longitudinal migrations (Goulding 1980, Benech *et al.* 1983, Reynolds 1983, Bonetto 1986) spawning (Lake 1967a, Lowe-McConnell 1987), feeding (Welcomme 1979, Lowe-McConnell 1987) and growth (Dudley 1974). At an evolutionary scale, fish life-histories are linked to hydrology, for example in the dichotomy between "whitefish" and "blackfish"of tropical systems (Welcomme 1979) and in the feeding strategies of Amazonian fish (Goulding 1980).

Elements of a flow-mediated model of river fish ecology therefore exist in the literature, and have been synthesized by Welcomme (1979, 1985) and Lowe-McConnell (1987). However, the model is focussed on a simple flood-drought polarity which has obscured the consequences of variations in flow at all magnitudes and the potential complexity of patterns of flow variation. This may be because it is derived principally from work in tropical and temperate systems.

The Flood Pulse Concept (FPC: Junk *et al.* 1989) is the prevailing paradigm for the role of overbank flows (the "flood pulse") in the ecology of lowland, floodplain rivers. It incorporates the flood-mediated fish-recruitment model cited above. The concept asserts that regular pulses of river discharge govern the dynamics of river-floodplain systems, because they impose alternating wet and dry phases on the floodplain, maintaining high biodiversity and production. The FPC follows from work on tropical and temperate floodplain rivers, where variation in the flood pulse is relatively predictable, and implies that adaptations to flow are precluded where flow variation is unpredictable.

In this chapter I discuss the role of flow in the ecology of large rivers, in the context of existing models, particularly the FPC. I describe the known linkages between hydrology and biology and set the FPC in the context of what is known of the hydrological characteristics of rivers in different climates. I focus particularly on the ecology of riverine fish, and on large rivers of the arid zone. Later chapters investigate the relations between flow variability, ecology and climate in large rivers worldwide, and the role of hydrology in the structures and dynamics of zooplankton, macroinvertebrate and fish assemblages in Cooper Creek, a large arid zone river in Central Australia. Together, these chapters provide for an elaboration of the FPC in which the role of flow variability is made explicit, a more complex model of flow is incorporated, and the concept is extended to accommodate the characteristics of large floodplain rivers in arid zones. In considering the biological implications of flow variability, I distinguish the terms *flow pulse* (as above), *flow history* (the sequence of pulses before any point in time) and *flow regime* (a long-term, statistical generalisation of the hydrograph) (Walker *et al.* 1995). My focus is on the *meso* (flow history) scale of temporal variability and the *meso* (river reach and waterbody) scale of spatial variability (*sensu* Walker *et al.* 1995, Table 1).

1.2 Hydrology in Lotic Ecology

1.2.1 RCC, SDC, RPM

The River Continuum Concept (RCC: Vannote *et al.* 1980, Minshall *et al.* 1985) proposed that there is a gradient of physical conditions between the headwaters and mouth of a river, and that the composition and dynamics of biological communities change in response to this gradient. Allochthonous carbon, entering the headwaters as litter (coarse particulate organic matter CPOM), is processed by heterotrophic organisms as it is carried downstream, and rendered into finer particles (FPOM). The proportion of instream production increases downstream (to a point), based on utilization by autotrophic organisms of this increasingly autochthonous carbon. The RCC therefore considers principally a spatial, longitudinal axis of environmental variation, although the role of lateral linkages has been acknowledged (Sedell *et al.* 1989). It is supported principally by work on invertebrates (Bunn 1986, Lillehammer & Brittain 1987, Minshall *et al.* 1992) but has been applied to fish (Oberdorff *et al.* 1993, Totham & Teugels 1998). It overlooks the significance of flow variability, except in considering floods as a "system reset" phenomenon (e.g. Ward & Stanford 1983).

The RCC is not easily applied to floodplain rivers because lateral linkages there are often more important than longitudinal ones (MacArthur 1988, Junk *et al.* 1989, Sedell *et al.* 1989). Lateral linkages are vital for fish which utilise the floodplain for spawning, feeding and refuge (Welcomme 1979, Goulding 1980). For these species the floodplain development in a river segment or *macrohabitat* (*sensu* Salo 1990) may affect local community structure more than the position of that segment in the river continuum. Variations in the timing and duration of flows also are likely to impede regular longitudinal patterns of succession (Winterbourn 1982). In lotic communities subject to intermittent flow and local flooding, periods of mixing and interaction are punctuated by periods of fragmentation (Fisher 1986, Cambray 1991, Merron *et al.* 1993), favouring development of local assemblages. Longitudinal connectivity therefore is temporally variable. In arid zone rivers with high transmission losses (Knighton & Nanson 1994a) there may be a downstream gradient of diminishing biodiversity (Puckridge *et al.* 1999).

The Serial Discontinuity Concept (SDC: Ward & Stanford 1983) qualifies the emphasis on continuum in the RCC by recognising discontinuities in the river continuum caused by dams or other forms of perturbation. Although the original SDC maintained the longitudinal perspective of the RCC, it has been expanded to consider floodplain-river systems (Ward & Stanford 1995a), and the contributions of allochthonous CPOM from the floodplain. This revision therefore incorporates both lateral linkages and flow variability at the magnitude of overbank flows. It has been extended to include vertical linkages (with the hyporheic zone), giving a four-dimensional view of lotic ecosystems (Ward 1989, Ward & Stanford 1995b). Nevertheless the model still does not consider those rivers (principally in drylands) in which longitudinal connection is naturally intermittent.

The Riverine Productivity Model (RPM: Thorp & Delong 1994) challenges and also supplements the perspective of the RCC by emphasizing the significance of local instream production (benthic algae, aquatic macrophytes), and local riparian inputs of organic material which are partly independent of longitudinal gradients. It considers that local carbon sources are more labile than FPOM from upstream, and are abundant in the littoral zone where most consumers live. The RPM is likely to be most important in large rivers with constricted channels (for example, the Ohio River: Thorp & Delong 1994).

1.2.2 Patch Dynamics

The term "patch" implies a relatively discrete spatial pattern in which one patch exists in some relationship to another patch and to the surrounding matrix, and the term "patch dynamics" emphasizes patch change (White & Pickett 1985). Spatial heterogeneity in rivers has been described in terms of patch dynamics, and has been proposed as one axis of a river habitat templet, the other being temporal heterogeneity (Townsend & Hildrew 1994, Resh *et al.* 1994). But temporal heterogeneity, particularly hydrological variation, also may be viewed as a series of environmental patches in time. A sequence of hydrological events in a river, for example, can be seen as a series of patches between which organisms move via diapause and aestivation (cf. Southwood 1977) and populations move via mortality and recruitment. These patches are also linked and interdependent. Temporal and spatial patchiness also interact; for example, macrohabitats assume different forms at different pulse stages – a billabong at low flow

may become a backwater at higher flow and later an anabranch. This dynamism, compared to the more stable main-channel environment, promotes biodiversity (Crome 1988, Grossman *et al.* 1990) and underpins the significance of floodplain environments for river processes. This thesis examines the movement of fish assemblages between patches in space, in response to hydrological changes, and change in these assemblages (also zooplankton and macroinvertebrate assemblages) between the patches (or events) of hydrological history. It also considers the influences on these assemblages of longitudinal and lateral gradients in hydrological conditions, and degrees of connectivity between spatial and temporal patches.

1.2.3 Scale

River systems are defined by hierarchical (sensu Frissell *et al.* 1986) spatial and temporal scales. Spatial scales are determined in part by geomorphological processes (Salo 1990, Zwolinski 1992), but in interaction with temporal climatic and hydrological processes. Under the influence of flow, small-scale spatial patchiness becomes dynamic, and through large-scale geomorphic patchiness hydrological influences themselves are made patchy. This is particularly true of river floodplains: their dynamism underpins the river-floodplain linkage.

Walker *et al.* (1995) define three divisions of temporal scale, viz. *flow regime*, or the statistical generalisation of flow variability as a model of long-term patterns (cf. Beckinsale 1971, Poff & Ward 1989), *flow history*, or the sequence of flow variations in the immediate past (cf. Fausch & Bramblett 1991) – the temporal extent determined by the lifetime of the organism in question, and *flow pulse*, or the current cycle of rise and fall of discharge or stage. Discrepancies between patterns in *flow regime* and *flow history* indicate the stochasticity in the system. Flow variability at these three scales is related to biological process and response in Table 1.

Aspects of variability in a flow regime are likely to be reflected at the ecosystem scale in such processes as fluxes of nutrients and energy (Howard-Williams 1985, Hill *et al.* 1992, Gibson *et al.* 1992) and in responses such as the evolution of life history strategies (Junk 1984, Boulton & Lake 1988, Schlosser 1990, Robinson *et al.* 1992). Variation in aspects of flow history are likely to be reflected in community and population dynamics through the processes of competition, recruitment and mortality (Kushlan 1976, Holcik & Bastl 1977, Beumer 1980, Boulton & Lloyd 1992). Variation

in instantaneous features of a given flow pulse are likely to operate principally at the level of the individual organism, evoking physiological and behavioural responses like spawning and migration (Welcomme 1979, Lowe-McConnell 1987).

Table 1 Flow variability related at various scales to biological features, biological processes and biological responses (after Walker *et al.* 1995).

Feature			Process	Response	Scale	
Geomorphic	Hydrological	Biological	Biological	Biological	Space (m^2)	Time (y)
Macroform	Flow regime	Ecosystem	Fluxes of nutrients and energy	Evolutionary: life-history strategies	$>10^5$	$>10^2$
Mesoform	Flow history	Community, population	Competition, mortality, recruitment	Ecological: changes in community structure	10^3-10^8	1-10^2
Microform	Flow pulse	Organism	Life-history strategies	Physiological, behavioural: diapause, migration, reproduction	$<10^4$	<1

This thesis deals with the role of hydrological variation at different scales. Chapters 2 and 3 consider the flow regime temporal scale and whole river spatial scale, and Chapters 4 and 5 consider the flow history temporal scale, the river reach and waterbody spatial scales. The emphasis is on scales relevant to fish assemblages.

1.2.4 Disturbance and Variability

Disturbance has been defined as "a discrete, punctuated killing, displacement or damaging of one or more individuals that directly creates an opportunity for new individuals to become established" Sousa (1984 p. 356) and as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett 1985 p. 7). In relation to streams, disturbance has been defined as "any relatively discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystem, community or population structure and changes

resources or the physical environment" (Resh *et al.* 1988 p. 433). Floods (spates) are regarded as key disturbances responsible for structuring plant and animal communities—particularly fish communities—in streams (e.g. Fisher *et al.* 1982, Fisher & Grimm 1988, Poff & Ward 1989, Clausen & Biggs 1997). This idea has been extrapolated to large rivers (cf. Resh *et al.* 1988, Junk *et al.* 1989, Reice *et al.* 1990, Sparks *et al.* 1990, Bayley 1991, Ward 1998). Thus, the FPC suggests that the flood pulse is akin to an "intermediate disturbance", promoting diversity when the pulse is "regular" rather than "unpredictable" (Junk *et al.* 1989: p122). The Intermediate Disturbance Hypothesis (IDH: Connell 1978) suggests that species diversity and productivity will be highest at intermediate levels of disturbance, and has been invoked to explain high diversity in small streams (Ward & Stanford 1983).

There are at least four difficulties in using the term "disturbance" to describe the role of flow variability in large rivers:

1. There are many definitions of the term (e.g. Sousa 1984, Pickett & White 1985, Resh *et al.* 1988, Sparks *et al.* 1990, Poff 1992a), depending on whether a disturbance is necessarily a discrete event, what distinguishes a disturbance from "normal" variation, and whether a disturbance is necessarily unpredictable.

2. The term "disturbance" applied to large rivers tends to imply that flood events are discrete and can be considered in isolation. In fact, such events are embedded in a hydrological history which strongly affects their outcome. The thresholds of biological responses to a given event depend on prior events.

3. "Objective measures are needed to identify events that satisfy the criteria provided in the Sousa (1984) or Pickett and White (1985) definitions" (Poff 1992a, p. 87). Yet many measures are framed in terms of biological, ecological or evolutionary responses that are organism-specific, so are arguably tautological, hence untestable.

4. The application of the term *disturbance* to flood and drought events has diverted attention from the fact that riverine biota can be adapted to such events (cf. Junk *et al.* 1989, Bayley 1991).

"Any theory of succession relevant to lotic ecosystems probably should be derived from the study of lotic ecosystems rather than by extrapolation of ideas generated elsewhere" (Fisher 1990: p733). The same could be said of disturbance. Rather than attempting *a priori* to partition flow variability into "normal" and "disturbance" regimes, this thesis relates biological responses to hydrological variation over the full spectrum of that variation (cf. Molles *et al.* 1992).

1.2.5 Environmental Adversity

Adverse habitats have been defined as "those that pose a particular cost for the maintenance of normal protoplasmic homeostatis and the integrity and normal functioning of membranes and enzymes" (Southwood 1988 p. 12). In this sense, rivers with extreme but constant flow conditions (e.g. torrential flows) and rivers with extremely variable flows could both be adverse. This thesis is concerned only with adversity in the latter sense - the temporal heterogeneity of habitat (*sensu* Southwood 1977). Hydrological variability can cause extensive mortality of organisms in arid lotic systems (Fisher 1990, Grimm & Fisher 1992), and it could be argued that such systems are therefore environmentally adverse. Because this view shares some of the drawbacks of the categorisation of "disturbance" events, this thesis avoids the definition of disturbance or adversity thresholds, and considers biological response to hydrological variability at all magnitudes relevant to riverine fish.

As argued above, in highly variable environments like arid zone streams, physical conditions commonly have a dominant influence on ecology – a finding in support of the Harsh-Benign Hypothesis (Peckarsky 1983). However, it is also likely that at certain times, for example during the recession of a flood, biotic interactions play an important role (Lowe-McConnell 1964, Bishop 1987). Although changes in zooplankton and invertebrate assemblages are discussed in Chapter 5 in relation to fish assemblage and population dynamics, the major concern of this thesis is with abiotic influences on all these assemblages.

1.2.6 The Flow Templet

A framework for considering abiotic influences on biota is the 'habitat templet' (*sensu* Southwood 1977). In small streams combinations of flood frequency, flood predictability and overall flow variability have been suggested as the axes of a 'flow

habitat templet' (Minshall 1988, Poff & Ward 1989). As argued above, the situation may be more complex in large rivers (cf. Bayley & Li 1992), where many facets of hydrological variability have biological significance (Richter *et al.* 1996, 1997, Puckridge *et al.* 1998). If so, an overall measure of flow variability is likely to mask ecologically significant aspects of a river's hydrology. The flow templets of large rivers may therefore need to be multi-dimensional, consisting of many components of flow variability and central tendency, determined at spatial and temporal scales appropriate to the question. This thesis will contribute to the development of a flow habitat templet for large rivers, but its focus is on extending the Flood Pulse concept.

1.3 The Flood Pulse Concept

Temporal flow patterns received little attention in the original RCC, but it is widely accepted that floods play a vital role in rivers, particularly those with extensive floodplains. They promote exchanges of water, nutrients and biota between the channel and the floodplain, and they sustain floodplain refuges, feeding and spawning areas (e.g. Welcomme 1979, Brinson *et al.* 1983, Amoros & Roux 1988, Neckles *et al.* 1990), and have particular relevance for fish production (Bayley 1991). The FPC (Junk *et al.* 1989) arose partly from these apparent deficiencies of the RCC. It proposes that regular pulsing of river discharge (the "flood pulse") is the key variable affecting the biota, and thereby emphasises lateral exchanges between river and floodplain and nutrient cycling within floodplain environments, rather than the downstream linkages and nutrient spiralling emphasised by the RCC (cf. Newbold *et al.* 1981, Minshall *et al.* 1985). According to the FPC, the channel receives most of its nutrients from the floodplain and is mainly a corridor for dispersal of biota. The flood pulse imposes alternating wet and dry phases on the floodplain, maintaining high productivity. The flood pulse has been described as an "intermediate disturbance" phenomenon that promotes ecological diversity (Ward & Stanford 1983, Junk *et al.* 1989), in part through imposing a dynamic connectivity between diverse waterbodies (Ward & Stanford 1995b, Ward 1998).

The FPC adds a lateral dimension to the longitudinal spatial variation recognised by the RCC, and explicitly includes temporal variation. It does not, however, analyse the scale and complexity of hydrological fluctuations (Junk *et al* 1989), nor does it pursue their implications for ecosystem function. Perhaps because they are based on evidence from temperate and tropical rivers, both FPC and the RCC pay scant regard to

stochasticity in the dynamics of rivers. In fact the FPC assumes that regularity is typical of large rivers, and that unpredictable pulses impede the adaptations of organisms (Junk *et al.* 1989). Yet life-history attributes like opportunism, flexibility and trophic generalism arguably are adaptations to unpredictable hydrological regimes (Kodric-Brown 1981, Winterbourn *et al.* 1981, Robinson *et al.* 1992, Poff & Allan 1995, Walker *et al.* 1995).

The RPM, although it applies particularly to large rivers with constricted channels, also questions the dominance of inputs from the floodplain in floodplain rivers, and the role of the flood pulse in mediating local autochthonous production. In large floodplain river food webs, the importance of carbon from the Aquatic Terrestrial Transition Zone of the floodplain (ATTZ, Junk *et al.* 1989), is challenged also by preliminary findings of Bunn & Davies (1999) in a large arid zone floodplain river, Cooper Creek (see Chapters 2 & 3). They found that at low water a "bathtub ring" of filamentous algae in the shallow littoral zone of channel waterholes and floodplain pools was the dominant net producer of carbon, and that this algal carbon was the dominant signature in the food webs of these waterbodies. Despite the extensive and vegetated floodplains and braided channels of this river, contributions of carbon from floodplain and riparian litter were small. If this pattern is found to be similar during flooding, the applicability of the FPC to this arid zone floodplain river must be substantially qualified.

1.4 Biologically Significant Facets of Flow Variability

Although the FPC is concerned only with variation in overbank flows (the flood pulse), in-channel flows also have biological significance. Thus, variations in discharge of any magnitude (*flow pulses*) are likely to be significant for at least some organisms. For example, a brief spate in a dry channel may produce a biological response (Stanley *et al.* 1997), small stage-fluctuations may affect littoral biofilms (Sheldon 1994), low-amplitude flows may be important for the maintenance of fish populations (Walker *et al.* 1995) and upwelling hyporheic flows may be critical in providing refuges during drought (Boulton *et al.* 1992). This point could be accommodated within the FPC if perceptions of the pulsing of river discharge (or stage) were made scale-dependent. Defining the flow pulse in terms of magnitude (e.g. overbank flow) is appropriate only for problems at those scales (cf. Poff & Ward 1989). A generally applicable concept

should systematically address the range of temporal or spatial scales over which river flow may vary (Table 1), particularly in arid regions.

A flow pulse is also a four-dimensional phenomenon, extending laterally across the floodplain, longitudinally along the axis of flow, vertically into the hyporheos, and temporally (Ward 1989, Sedell *et al.* 1990, Smock *et al.* 1992). If the full range of potential flow pulse variation is considered across the four dimensions of the pulse, then at least eight phases of a flow pulse are likely to be significant for some riverine species or life-stage (Table 2). These phases include periods of zero and subsurface as well as surface flow. The period around peak flow should also be distinguished because the balance between erosion, transport and accumulation changes markedly during this time (Zwolinski 1992), and physico-chemical variables also show a distinct phase (Boulton & Lake 1990).

Table 2 Ecologically significant phases of a hypothetical flow pulse

1	Dry	
2	Hyporheic Rising	subsurface flow rising within riverbed
3	Channel Rising	surface flow rising within channel
4	Overbank Rising	surface flow inundating marginal land
5	Near Flood Peak	minimal rate of change of stage
6	Overbank Receding	surface flow receding from marginal land
7	Channel Receding	surface flow receding within channel
8	Hyporheic Receding	subsurface flow receding within riverbed

Although the FPC recognises that "the system responds to the rate of rise and fall and to the amplitude, duration, frequency, and regularity of the pulses" (Junk *et al.* 1989: p 122), it is likely that, even for overbank flows, the range of *facets* of flow regime (*sensu* Ch. 2) which is significant for fish ecology is greater than this (Ch. 2). Table 3 is a summary of the literature on linkages between fish biology and flow variability (Puckridge *et al.* 1998).

Table 3. Biological responses to facets of flow variability, from Puckridge *et al.* 1998.

The biological responses are from research on fish in streams as well as rivers, since much of this work has yet to be done in large rivers (Walker *et al.* 1995). What is presented does not necessarily apply to all river fish species (Davies 1989), and is qualified by the integrated nature of river hydrology, which makes separation of the biological effects of particular facets of flow variability difficult. The table is subdivided into three temporal scales: (a) Variations in the *flow regime* may be reflected in the evolution of life-history strategies, (b) variations in *flow history* may be reflected in community and population dynamics, and (c) variations in the features of a given *flow pulse pulse* may affect populations, as in (b), but within the time-frame of the pulse will be apparent in physiological and behavioural responses.

(a)

Long term patterns (flow regime)	**Life history responses**
Highly variable timing	Long breeding season (Cambray 1991), bet-hedging reproduction (Lloyd *et al.* 1991a), flexible spawning strategies (Welcomme 1985)
Highly variable duration	Brief life-cycles, early maturity in floodplain species (Welcomme 1979)
Highly variable amplitude	Mobility (Minckley & Barber 1971), colonising ability (Deacon & Minckley 1974)
Long periods of zero flow	Wide physiological tolerances (Glover 1982, Benech *et al.* 1983)
High spatial variability	High mobility (Winemiller 1989)
Low predictability	Flexibility (Winemiller 1989), variable breeding systems (Kodric-Brown 1981)

(b) Recent hydrological events (flow history)	Community and Population Responses
Extensive surface drying	Local extinction (Deacon & Minckley 1974)
Protracted zero flows	More large carnivores (Kushlan 1976), dominance of physiologically tolerant (Benech *et al.* 1983) and small species (Bishop 1987), mortality from predation (Lowe-McConnell 1987)
Repeated low flows	Low abundance (Quiros & Cuch 1989), more in-channel spawners (Welcomme 1979)
One extreme flood	One dominant year-class and high population densities, particularly of floodplain-dependent species (Krykhtin 1975, Welcomme & Hagborg 1977)
High amplitude variation	Increase in colonizing species (Benech *et al.* 1983), irregular age-class strength (Schlosser 1985, Davies *et al.* 1988), dominance of small omnivorous species (Kushlan 1976), variable juvenile recruitment and assemblage composition (Schlosser 1985)
Sustained high water levels	High production (Quiros & Cuch 1989), increased species richness and biomass (Kushlan 1976), reduced abundance of small species (Bishop 1987).
Highly variable duration	Variable production (Bayley 1991), variable recruitment (Geddes & Puckridge 1989)
Rapid flood recession	Less recruitment of floodplain spawners compared to channel spawners (Welcomme 1989)
Reduced flow pulse frequency	Reduced species richness (Puckridge & Walker 1995)
Series of increasing flow pulse peaks	Less proportional recruitment response (Welcomme 1989)
Highly variable amplitude of the falling limb	Variable migration intensity (Welcomme 1985), variable mortality and yearclass strength (Quiros & Cuch 1989)
Unpredictability	Assemblage instability (Ross *et al.* 1985), reduced community complexity (Bain *et al.* 1988)
High multi-annual flow variation	Major variations in assemblage structure (Benech *et al.* 1983)
Repeated high flows	High production (Quiros & Cuch 1989)

(c)

Features of the present flow pulse	Behavioural and Physiological Responses
Extreme flow pulse peak	Strong growth (Welcomme 1989), high body condition (Junk & Welcomme 1990), intense migration (Welcomme *et al.* 1989)
Short-lived flow pulse	Weak growth (Welcomme 1989)
Steep rising limb	Fall in migration intensity of young fish (Mallen-Cooper & Brand 1991)
Steep falling limb	Weak growth (Welcomme 1985), stranding of floodplain spawning species (Welcomme 1985)
Extreme drawdown	High mortality (Junk & Welcomme 1990), reduced feeding except in piscivores (Welcomme 1989)
Atypical flow pulse timing	No reproduction in seasonal spawners (Welcomme 1979)
Low flow pulse peak	Low incidence of floodplain spawning (Welcomme 1989), weak growth (Welcomme 1979)
Extensive surface drying	Refuge-seeking (Minckley & Barber 1971), increased predation (Larimore *et al.* 1959),
Cessation of flow	Vertical redistribution of intolerant species in response to stratification (Puckridge & Drewien 1988), increased disease (Awachie 1981)

Many of the facets of flow variability in Table 3 can be grouped in the categories of "annual timing" and "rate of rise and fall, amplitude, duration, frequency, and regularity of the pulses" (Junk *et al.* 1989: pp116-122), but some fall outside these categories. Some, particularly those relating to *cessation of flow* and *surface drying*, are outside the scale of overbank flows with which the FPC is concerned. This suggests that the concept needs to be extended to accommodate hydrological events which appear to be biologically significant in some rivers. There are also a number of facets, for example *highly variable amplitude of the falling limb*, *high multi-annual flow variation*, *repeated low flows*, and *a series of increasing flow pulse peaks* at the flow history scale (Table 3b), and *extreme drawdown* and *extreme flow pulse peak* at the flow pulse scale (Table 3c), which appear to have distinct biological linkages that would be obscured by grouping them all as *amplitude variation*. Finally, *spatial variability* (Table 3a) is a distinct facet relevant to the full range of flows, including overbank flows.

A primary task of this thesis is to test and develop a model which extends the Flood Pulse Concept in terms of the range of magnitudes and the temporal and spatial

scales of hydrological events, defines the floodplain in hydrological terms and relates hydrological features (including "flow history") at various scales to biological processes and responses. The model must incorporate the characteristics of all large floodplain rivers, particularly those presently neglected by the FPC, the large floodplain rivers of the arid zone.

1.5 Climatic Influences

In temperate arid and semi-arid regions (*sensu* Beckinsale 1971), rainfall is prone to vary widely according to erratic temporal climatic cycles, including seasonal and diel factors and long-term influences like the El Niño–Southern Oscillation (ENSO: Nicholls 1989, Molles *et al.* 1992). Spatial variability also is conspicuous, illustrated in the localised flooding produced by intense, short-lived local downpours (Farquharson *et al.* 1992). As a consequence (at least in part) of these climatic factors, arid zone streams show high temporal and spatial variability of flow (McMahon 1979, Falkenmark 1989). In Australia flow patterns of the dryland rivers are reputedly more variable than elsewhere in the world (Finlayson & McMahon 1988, McMahon & Finlayson 1991). Such systems provide an opportunity to test our models of lotic ecosystem structure and function under a range of conditions beyond the generally mesic ones under which they were framed (Fisher 1986).

The following features may be exceptionally pronounced in dryland rivers:

1.5.1 Variability in pulse timing

In arid zones, seasonal changes in temperature are predictable and extreme (Comin & Williams 1994), but patterns of flow pulse timing vary geographically (Beckinsale 1971). Rivers in some arid regions have seasonally defined hydrological cycles, rivers in others do not (Rodier 1985). For those arid zone rivers where hydrological events are uncoupled from season, particularly from temperature cycles, organisms face complex and even contradictory environmental cues. It is suggested (Bayley 1991) that in such a situation fish production will be lower than in systems having more predictable pulse timing, or than in tropical rivers, where seasonal variations in temperature are less pronounced and hydrological events can be considered the principal driving factors (Junk *et al.* 1989).

1.5.2 Variability in Pulse Amplitude

Rivers with arid zone climatic influences may have extended periods of zero flow, when sections become lentic (Rodier 1985, Knighton & Nanson 1994b). In such rivers, the beginning or end of an in-channel flow event may, especially after long periods of drought, be as significant as the overtopping of the banks (Bishop 1987). In-channel flows, like overbank flows, may cause "changes in the physico-chemical environment that biota react [to] by morphological, anatomical, physiological or ethological adaptations, or by a change in community structure" (Junk & Welcomme 1990: p. 492), and the progress of the water's edge (the "moving littoral": cf. Junk *et al.* 1989) up and down within the channel may be as important as its passage across the floodplain during overbank flows (Thorp & Delong 1994, Sheldon & Walker 1993). Overbank flows may simply increase the area available for these processes. Such rivers may also have periods in which some reaches dry completely at the surface (Rodier 1985, Kotwicki 1986). The river channel will therefore function only intermittently as a "highway" (*sensu* Junk *et al.* 1989), and some reaches can be considered part of the floodplain.

1.5.3 Long-Term Variation

Even in rivers which vary little over extended time-scales, particular events in flow history may have pronounced effects on assemblage composition and ecological processes (Welcomme & Hagborg 1977, Benech *et al.* 1983, Quiros & Cuch 1989). In dryland rivers which are highly variable in the long-term, single events or event clusters in their flow history, perhaps governed by ENSO cycles (Molles *et al.* 1992) may dominate their geomorphology (Graf 1988, Kresan 1988, Pickup *et al.* 1988), assemblage composition and ecological processes (Puckridge *et al.* in press).

1.5.4 Spatial Variation

Spatial hydrological variation is a feature of all lotic systems, and may be due to spatial patchiness of rainfall or local topography, channel form or the longitudinal summation or attenuation of the flow pulse (Schick 1988, Fausch & Bramblett 1991, Knighton & Nanson 1994a). Where it is pronounced, as in some dryland rivers, location may be significant in determining patterns of inundation and physico-chemical features. For example, in low-gradient dryland systems such as Cooper Creek and the Diamantina River, there may be high transmission losses (Kotwicki 1986, Falkenmark 1989,

Knighton & Nanson 1994a), producing a downstream gradient of diminishing flooding frequency and amplitude, and a corresponding gradient in physico-chemical and hence biological characteristics (Allan 1988). In such rivers, data on local hydrology will be be important for the prediction of ecological features such as community structure (Horwitz 1978, Pearson *et al.* 1992).

1.5.5 Unpredictability

Dryland rivers reputedly are the least predictable (e.g. Farquharson *et al.* 1992). But models of the ecology of large rivers have been based on studies in tropical and temperate regions, where rivers exhibit less hydrological variability (e.g. Vannote *et al.* 1980, McArthur 1988, Junk *et al.* 1989). The FPC focuses on systems where "the pulse is regular and of long duration" (Junk *et al.* 1989: p 122). Further, Bayley (1991: p 84) stated that "a predictable annual flood pulse is essential for the survival of the system". Junk *et al.* considered that regularity is typical of large rivers, and that unpredictable pulses impede biological production and the adaptations of organisms. This is too narrow a view of biotic adaptation and ecological response, because life-history attributes like opportunism, flexibility and trophic generalism arguably are adaptations to unpredictable hydrological regimes (Kodric-Brown 1981, Winterbourn *et al.* 1981, Robinson *et al.* 1992, Poff & Allan 1995, Walker *et al.* 1995).

Chapter 2 will explore the biologically significant patterns of flow variability in a selection of large rivers from major climate zones worldwide, and whether the Flood Pulse Concept and the flow habitat templet should be extended to accommodate these patterns.

1.6 A Hydrology - Fish Ecology Model

Much work on the habitat requirements of lotic fish has emphasized vegetation structure, channel and floodplain morphology, substrate, water physicochemistry and hydraulics (Angermeier & Karr 1983, Copp 1989, Cellot *et al.* 1994, Copp *et al.* 1994, Fjellheim & Raddum 1996, Heggenes *et al.* 1996) and central tendencies in the flow regime at thresholds considered ecologically significant (Baran *et al.* 1995, Sutton *et al.* 1997). Where variability of flows has been considered, it has been at restricted scales and in relation to few aspects of flow (Horwitz 1978, Davies 1989). These approaches have been formalized to assess and protect habitat threatened by increased water

resources development, and so to provide managers with quantities which can be built into river engineering and manipulation (Nestler *et al.* 1989, Gore *et al.* 1991, Ubertini *et al.* 1996). This work has principally been sited in streams rather than rivers, or in highly regulated temperate rivers, or in unregulated but relatively invariant tropical rivers, and has often focussed on salmonids. It has nevertheless had considerable influence on thinking about abiotic determinants of fish ecology, and diverted attention from the hydrological variability of many lotic systems.

This thesis follows another line of thinking about determinants of lotic fish ecology, which predates the articulation of the FPC, but has been incorporated into it. This view emphasizes the roles of flooding and the floodplain in the fish ecology of large floodplain rivers (Welcomme & Hagborg 1977, Welcomme 1979, Junk *et al.* 1989, Bayley 1991, Bayley & Li 1992). The model (which we will term the Flood/Floodplain Fish Ecology Model) derives principally from studies of large tropical floodplain rivers, although research on streams has also made important contributions (Poff & Ward 1989, Poff & Allan 1995). The model proposes that flooding, through inundation of the floodplain, enlarges and diversifies available habitat and releases nutrients which fuel microbial, algal, zooplankton and macroinvertebrate blooms (Maher & Carpenter 1984, Crome 1986, Lowe-McConnell 1987, Crome & Carpenter 1988, Boulton & Lloyd 1992, Hirst & Ibrahim 1996). This sequence of events evokes fish migration, spawning and feeding responses leading to recruitment (Welcomme 1979, Lowe-McConnell 1987, Culver & Geddes 1993, Merron *et al.* 1993). The subsequent withdrawal of floodwaters initiates reverse migrations, a period of diminishing habitat and food supply, and consequent mortalities.

The model is supported by studies of hatching of invertebrate resting stages from inundated floodplain soils (Boulton & Lloyd 1992), invertebrate blooms on newly inundated floodplain (Maher 1984, Maher & Carpenter 1984, Crome 1986), flow pulse-cued feeding and spawning migrations (Northcote 1978, Reynolds 1983, Welcomme 1985, Bonetto 1986, Kwak 1988), flow pulse-induced spawning (Lake 1967a, Cambray 1991), dependence of fish larval survival on high densities of appropriate sized zooplankton (Arumugam & Geddes 1992, Geddes & Puckridge 1989, Rowland 1992), movement of fish onto newly inundated floodplain (Goulding 1980, Benech *et al.* 1983), lag correlations between historical flow pulse magnitudes and fish catch (Holcik

& Bastl 1977, Quiros & Cuch 1989) and between fish yield and floodplain area (Awachie 1981). Characteristic "flow regimes" have been related to fish adaptation, particularly on a regional basis (Poff & Ward 1989, Poff & Allan 1995) and variation in many facets of the flow regime has been related to fish responses - principally in streams - at all of the temporal scales defined above (Table 3 above).

However there are several qualifications of this model.

1. There has been debate on the importance of high zooplankton densities to fish larvae (Frank 1988, Post & McQueen 1988, Gehrke 1991). If critical zooplankton densities are not required, the importance of flow pulse-induced zooplankton blooms is less obvious.

2. The timing, extent and pattern of responses to flow pulsing vary greatly within and between fish assemblages. For example, there may be a variety of migration responses to a flow pulse in the fish assemblage of a given river (Welcomme 1985, Bonetto 1986, Bishop 1987). There may also be a variety of spawning strategies among fish in a given river (Welcomme 1985, Lloyd *et al.* 1991a). In the Murray-Darling for example, strategies range from the obligate flow pulse-dependency of *Macquaria ambigua*, which does not spawn in the absence of flows, to the flow pulse-independent spawning of *Maccullochella peelii* (Lake 1967a). In species like the latter, a flow pulse may still affect the level of recruitment resulting from a given reproductive effort.

3. That fish recruitment does not always depend on flow pulse magnitude alone is suggested by the correlation of fish production in a given year with the proportion of floodwaters remaining in the system after flood recession (Welcomme & Hagborg 1977, Bayley 1991). This finding suggests an important role for drought-phase mortality in fish recruitment.

4. The model tends to neglect the variety and complexity of floodplain habitats. These vary greatly in their suitability for fish spawning, feeding and shelter, and their utilisation varies accordingly (Gehrke 1990, 1991). On Cooper Creek in South Australia, utilization of the floodplain may be diurnal, perhaps dependent on temperature cycles (Geddes & Puckridge 1989). Utilisation of the floodplain also varies between species in a given system. In tropical rivers, there is a strong

distinction between "blackwater" species which remain on the floodplain, sheltering in permanent refuges, and "whitewater" species which do not leave the main channel (Welcomme 1985). The latter still are dependent on flooding, because the main channel habitat is replenished by inflow of nutrients and biota from the floodplain during flood recession. However, the variety of strategies in relation to floodplain use and in response to flooding is more complex than this simple distinction implies (Welcomme 1979, Goulding 1980)

5. The model may underestimate the complexity and the range of temporal and spatial scales of hydrological cycles. For example, it focuses on the phenomenon of "flooding", or the "flood pulse" and gives less attention to hydrological events over the full range of discharge magnitudes (the "flow pulse"), or to the variety of biologically significant facets of flow variability (Table 3), or to antecedent hydrological events ("flow history" and persistence). A more complex picture of hydrological patterns may be necessary, particularly in dryland rivers.

In large rivers, the spatial scale of movements of individual fish may extend for hundreds of even thousands of kilometres (Reynolds 1983). The timing and pattern of movements, distribution, reproduction and feeding of all age-classes over this scale need to be understood in relation to past and present hydrological events. Manipulation at the above spatial scale is impracticable, but this thesis attempts to supplement comparisons above and below impoundments in regulated rivers, and experimental studies based on pond systems, with observations in an unregulated river of fish responses to hydrological events over appropriate spatial and temporal scales. Within the larger task of testing, reviewing and extending the FPC, the thesis will test the applicability of the Flood/Floodplain Fish Ecology Model to a large arid zone floodplain river.

1.7 Outline

1.7.1 Aims

1. To test the applicability of the FPC's assumptions about flow variability to large river systems worldwide (Chapter 2).

2. To test the applicability of the flood/floodplain fish ecology model to the fish assemblage of Cooper Creek, an extremely variable arid zone river (Chapters 3-5).

3. To test the applicability of the Flood Pulse Concept to the fish, zooplankton and macroinvertebrate assemblages of Cooper Creek (Chapters 3-5).

4. To extend the the Flood Pulse Concept in terms of the range of magnitudes and the temporal and spatial scales of hydrological events it accomodates, and the range of facets of hydrological variation it relates to biological processes and responses. (Chapter 6).

5. To discuss the management implications of the extended Flood Pulse Concept (Chapter 6).

1.7.2 Approach

1. At the flow regime temporal scale and the whole river spatial scale, to:

   - Compare patterns of flow variability between large rivers from different climatic zones (Chapter 2).
   - Identify the facets of flow variability necessary to characterize these rivers, particularly in terms of their fish ecology (Chapter 2).

2. At the flow history, flow pulse and flow regime temporal scales, the river reach and individual waterbody spatial scales, and in a dryland river system (Cooper Creek) in which flow variability is extreme, to:

   - Describe patterns of temporal and spatial variation in overall assemblage structures of fish, zooplankton and macroinvertebrates, and relate these patterns to facets of flow history and flow pulse at the spatial scales of waterbody and river reach (Chapter 4).
   - Relate patterns in assemblage characteristics - abundance, evenness, richness, and (for fish) overall spawning intensity, migration intensity, exotic/native abundance ratio and disease incidence - to facets of flow history, flow pulse and flow regime (Chapter 5).
   - Describe patterns in individual fish species recruitment, and relate these patterns to flow history, flow pulse and persistence in flow regime (Chapter 5).

3. Modify accordingly the Flood Pulse Concept and the flood/floodplain fish ecology model, and discuss the management implications (Chapter 6).

1.7.3 Hypotheses

Relevant hypotheses from this overview are listed in the introduction to each chapter. Note that some are tested in several chapters.

1. At the flow regime temporal scale and the whole river spatial scale:

1.1. Large rivers with major arid zone climatic influences are no more variable than rivers influenced primarily by other climates (Ch. 2).

1.2. For the purpose of determining the ecological significance of hydrological variability in large rivers, variability may be summed in a single measure (Ch. 2).

1.3. The facets of the flood pulse listed by Junk *et al.* (1989) are adequate to characterize large rivers by their biologically significant patterns of flow variability (Ch. 2).

1.4. Large arid zone rivers do not exhibit multi-annual hydrological persistence (Ch. 2)

1.5. Large arid zone rivers are not exceptionally variable in the seasonal timing of their flow pulses (Ch. 2.).

1.6. Large arid zone rivers are not exceptionally hydrologically unpredictable (Ch. 2).

1.7 Large arid zone rivers are not outstandingly variable in their flow pulse amplitude (Ch. 2).

1.8. Fish assemblages of hydrologically unpredictable rivers have predominantly:

(a) K-selected life histories

(b) precocial reproduction

(c) high parental investment in offspring (Ch. 3).

1.9. The biota of hydrologically unpredictable rivers is not adapted to the flood pulse (Junk *et al.* 1989, Bayley 1991) (Chs. 3,5).

2. At the flow history and flow pulse temporal scales and the river reach and waterbody spatial scales in Cooper Creek:

2.1. The overbank phases of the flow pulse are biologically more important than the in-channel phases (Ch. 4).

2.2 Variations in fish, zooplankton and macroinvertebrate assemblage structures are independent of flow history (Ch. 4).

2.3. The facets of the flood pulse listed in Junk *et al.* (1989) are adequate to describe the influence of hydrology on overall structure of fish, zooplankton and macroinvertebrate assemblages (Ch. 4).

2.4. Hydrological events at the magnitude of overbank flows are sufficient to describe biology-hydrology interactions in floodplain rivers (Chs 4, 5)

2.5 When season and flow pulse are out of synchrony, fish production falls (Bayley 1991) (Ch. 5).

2.6 Fish recruitment is not related to flow pulse magnitude (Ch 5).

2.7 Health of fish assemblages (disease incidence, exotic/native species ratio) is independent of hydrology (Ch. 5).

3. At the flow history and flow pulse temporal scales and the river reach spatial scale in Cooper Creek:

3.1 Variations in indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are independent of hydrology (Ch. 5).

3.2 Most of the seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are redundant, and could be replaced by fewer, summary measures (Ch. 5).

3.3 The seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages account for a trivial amount of the variance in these indices (Ch. 5).

3.4 The facets of the flood pulse listed in Junk *et al.* (1989) are adequate to describe the influence of hydrology on indices of structure, health and behaviour of fish

assemblages, and structures of zooplankton and macroinvertebrate assemblages (Ch. 5).

3.5. Relations between flow history measures and indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages have the same sign throughout flow history (Ch 5).

4. At the flow regime and flow history temporal scales and the river reach spatial scale in Cooper Creek:

4.1. (a) Fish spawn primarily in response to seasonal, not hydrological cues (i.e. follow a 'double or nothing' spawning strategy, *sensu* Lloyd *et al.* 1991a) (Chs 3, 5)

(b) Fish migrate primarily in response to seasonal, not hydrological cues (Chs.3, 5).

4.2 Indices of structure of fish, zooplankton and macroinvertebrate assemblages are not related to waterbody permanence (Ch 5).

4.3. Indices of fish assemblage health and behaviour are not related to waterbody permanence (Ch 5)

2. Climate, flow variability and the ecology of large rivers

2.1 Introduction

Predictability and changes in flow (Minshall 1988) and "flood frequency, flood predictability and overall flow variability" (Poff & Ward 1989: p1810) have been proposed as elements of a "habitat templet" for streams. Variations in amplitude, frequency, timing, duration, drawdown and rate of change also are biologically significant (Walker *et al.* 1995, Richter 1996, 1997). For example, Poff and Allan (1995) correlated daily flow predictability and base-flow stability with the functional traits of fish. Thus, flow variability underpins river ecosystem function.

The Flood Pulse Concept (FPC: Junk *et al.* 1989) asserts that regular pulses of river discharge are a key factor in the dynamics of river-floodplain systems. The concept acknowledges the significance of the variability and predictability of the duration, amplitude, frequency, timing and rate of rise and fall of the pulse, but deals only with pulses that overflow the banks, i.e. "flood pulses". However the FPC's focus on overbank flows limits its applicability. This chapter suggests a wider perspective and defines a "flow pulse" not in terms of a threshold, but as a rise and fall in discharge (or stage) at scales of space and time appropriate to the observer's frame of reference.

The FPC is based on large tropical rivers (e.g. McArthur 1988, Junk *et al.* 1989, Thorp & Delong 1994) where variations are said to be "predictable" (Junk & Welcomme 1990). It appears to understate the significance of spatial and temporal flow variability and predictability in rivers of other climatic regions. In the arid zone, for example, the coefficient of variation of annual flows far exceeds that for continental areas as a whole (McMahon 1979), and the average skew of annual flows and peak annual discharges is higher in arid than in humid regions. Some of these attributes are most pronounced in arid Australia and southern Africa (McMahon & Finlayson 1991) and their implications must be considered if the FPC is to have global applications.

In most regional or global comparisons of river regimes, flow variability has been described by statistics such as the slopes of flood-frequency curves (Farquharson *et al.* 1992), seasonal distribution of mean monthly flows (Haines *et al.* 1988), coefficients of

variation (CV) of daily and maximum and minimum mean annual flows, and differences between mean and median flows (Jowett & Duncan 1990, Clausen & Biggs 1997). Others have employed the CV and skew of monthly and annual flows and peak discharges, flow and flood frequency and duration curves and time series of annual discharge (McMahon 1979, McMahon *et al.* 1992). Poff & Ward (1989) and Poff (1996) classified streams in the United States using 12-15 measures that they presumed were ecologically significant, but only three measured variability in the sense of deviations from a central tendency. However, Richter *et al.* (1996, 1997) considered deviations from central tendency for 13 measures over intervals from a day to a year. This simple approach may be the most useful in a biological context. Large rivers may reveal more complexity because their catchments often overlap climatic zones and flow variations occur at different scales. Thus, existing regional generalizations may be too simplistic (Haines *et al.* 1988).

This chapter considers flow regimes at monthly, annual and multi-annual scales. Although the analysis compares several gauging stations for each river, this does not represent a comprehensive analysis of spatial variation (Schick 1988, Fausch & Bramblett 1991). In considering the biological implications of flow variability, this chapter distinguishes the terms *flow pulse* (as above), *flow history* (the sequence of pulses before any point in time) and *flow regime* (a long-term, statistical generalisation of the hydrograph) (Walker *et al.* 1995). The focus of this chapter is on the *mesoscale* of temporal variability and the *macroscale* of spatial variability (Walker *et al.* 1995). A *facet* of a river's flow regime denotes a feature of biological significance, and a *measure* is the quantification of a facet at a given scale. The *variability* of a measure is indicated by the frequency and magnitude of departures from its central tendency (Townsend & Hildrew 1994). Biologically-meaningful measures of flow variability were chosen for a multivariate analysis designed to characterise 52 rivers worldwide and to seek climatic groupings (e.g. "arid zone" and "tropical" rivers).

Results of these analyses are used to test the following hypotheses from Chapter 1:

At the flow regime temporal scale and the whole river spatial scale:

1.1 Large rivers with major arid zone climatic influences are no more variable than rivers influenced primarily by other climates.

1.2 For the purpose of determining the ecological significance of hydrological variability in large rivers, variability may be summed in a single measure.

1.3 The facets of the flood pulse listed by Junk *et al.* (1989) are adequate to characterize large rivers by their biologically significant patterns of flow variability.

1.4 Large arid zone rivers do not exhibit multi-annual hydrological persistence.

1.5 Large arid zone rivers are not exceptionally variable in the seasonal timing of their flow pulses.

1.6 Large arid zone rivers are not exceptionally hydrologically unpredictable.

1.7 Large arid zone rivers are not outstandingly variable in their flow pulse amplitude.

2.2 Methods

2.2.1 Hydrological Measures

Twenty-three hydrological measures were chosen (Table 4), based on a number of facets of flow variability likely to be biologically significant (Table 3, Ch. 1). With two exceptions (MSKEW and ASKEW), these measures correspond to five key facets (Richter *et al.* 1996, 1997): timing, frequency, duration, rate of change and magnitude. An indicator of skew based on the difference between mean and median (cf. Jowett & Duncan 1990) was used. Colwell's indices (Colwell 1974) were not used as their suitability for hydrological analysis is suspect (Gan *et al.* 1991, Walker *et al.* 1995, Poff 1996).

Table 4 Measures of hydrological variability

Measures derived from hydrology-biology links in Table 3, Chapter 1, with additional measures added to extend the range of temporal scales. "Variability" in all cases calculated as range/median (S100), interquartile range/median (S50), or 90th-10th percentile range/median (S80)

Code	Flow variability measure
ASKEW	((mean - median)/median) of all annual flows.
ANTF	variability between years of each year's variability between months.
ATOT	variability of all annual flows
FALA	variability of amplitude of all falling limbs.
FIVE	variability of sums of every five years' total annual flows.
FLDR	variabililty of the duration of all falling limbs (for zero flows duration calculated to end of continuous zero flows).
PSFR	variability of number of pulses (peak to peak or trough to trough) in each year.
FLRT	variability of discharge fall per month for all falling limbs.
LSEA	inverse of variability between months of number of pulse troughs in each month.
MDAN	median between years of each year's variability between months.
MDMF	median between months of each month's variability between years.
MSKEW	((mean - median)/median) of all monthly flows.
MNTF	variability between months of each month's variability between years.
MTOT	variability of all monthly flows.
PEAK	variability of all peak discharges.
PSEA	inverse of variability between months of number of pulse peaks in each month.
RSAM	variability of amplitude of all rising limbs.
RSDR	variability of duration of all rising limbs
RSRT	variability of discharge rise per month for all rising limbs.
SEVN	variability of sums of every seven years' total annual flows.
THRE	variability of sums of every three years' total annual flows.
TRGH	variability of all minimum discharges.
ZEROF	% of all months in record with zero flow.

Hydrological data were obtained from the Murray-Darling Basin Commission, SA Water, UNESCO (1971) and the database of McMahon *et al.* (1992). The latter two sources are restricted to monthly and annual discharges. Rivers with catchments of 100–500,000 km^2 were selected to reduce the effects of catchment size on variability, and the earliest available 20 years of continuous record were used to minimise effects of regulation. Simulated pre-impoundment data were substituted for gaugings for the Vaal River, South Africa (SA Cooperative Centre for Water Research, unpubl.). For five rivers, 20 years of record were not available, but in these cases the time span was not less than 15 years. The final database includes approximately equal numbers of rivers with gauging stations in arid, temperate, tropical or continental/polar climatic regions (Köppen-Geiger classification *sensu* Geiger 1954). The data are for one station on each of 52 rivers (Table 5).

Table 5 Rivers, gauging stations and catchment areas upstream of stations

Data from UNESCO 1971, McMahon *et al.* 1992, and unpub. data from the Murray-Darling Basin Commission, South Australian Engineering and Water Supply Department, and the South African Cooperative Centre for Water Research.

Code	River	Station	Catchment (km^2)
AMU	Amu-Darya	Chatly	450000
ARK	Arkansas	Little Rock	409740
ASS	Assinboine	Headingley	162000
AUX	Aux	Outardes Power Plant	189000
BAH	Bahr	Mongalla	450000
BAN	Bani	Douna	101600
BUR	Burdekin	Burdekin Falls	114000
COL	Colorado	Lees Ferry	279500
COO	Cooper	Innamincka	240000
DAN	Danube	Nagymaros	183262
DAR	Darling	Bourke	386000
DIA	Diamantina	Birdsville	115000
DNI	Dniepr	Dniepr Hydroelectric Power Plant	463000
DON	Don	Razdorskaya	378000
FIT	Fitzroy	Riverslea	132000
FRA	Fraser	Hope	203000
GOD	Godavari	Dowlaishwaram	299320
HUA	Huai He	Bang Bu	121330
IND	Indigirka	Vorontsovo	305000
KOL	Kolyma	Sredne-Kolymsk	361000
KRI	Krishna	Vujayawada	251355
KUR	Kura	Surra	178000
LIM	Limpopo	Beit Bridge Pump Station	195742
LOI	Loire	Montjean	110000
MEK	Mekong	Mukdahan	391000
MIS	Mississippi	Alton	444200
NEV	Neva	Novosaratovka	281000
NIG	Niger	Dire	340000
NIL	Blue Nile	Roseires	210000
NTH	Nth Saskatchewan	Prince Albert	119500
ODE	Oder	Gozdowice	109365
OGO	Ogooue	Lambarene	203500
OUB	Oubangui	Bangui	500000
PET	Petchora	Ust-Tsilma	248000
REDA	Red	Alexandria	175000
REDE	Red	Emerson	104000
RHI	Rhine	Lobith	180000
RIO	Rio Grande	Laredo	352180
SAN	Sanaga	Edea	135000
SAO	Sao Francisco	Juazeiro	490770
SEV	Severnaya-Dvina	Ust-Pinega	348000
SNA	Snake	Clarkston	267300
SON	Songhau Jiang	Harbin	390526
STH	Sth Saskatchewan	Saskatoon	139500
SYR	Syr-Darya	Tyumen-Aryk	219000
TIS	Tisza	Szeged	138408
URA	Ural	Kushum	190000
VAA	Vaal	Douglas Weir	193842
VIS	Vistula	Tczew	193865
WIN	Winnipeg	Slave Falls	124000
XIJ	Xi Jiang	Wu Zhou	329705
YAN	Yana	Dzanghky	216000
Multiple stations per river			
COO2	Cooper2	Currareva	150220
DAN2	Danube2	Orsova	578300
DAN3	Danube3	Central Izmail	807000
DAR2	Darling2	Louth	489300
DAR3	Darling3	Wilcannia	569800
MIZ1	Missouri1	Yankton	723900
MIZ2	Missouri2	Herman	1368000
NIG2	Niger2	Koulikoro	120000
NIG3	Niger3	Mopti-Nantaka	281600
PAR1	Parana1	Guaira	806000
PAR2	Parana2	Corrientes	1949813

In a second analysis to validate the assumption that a single gauging station can be taken to represent a river, data were obtained for several stations on each of six rivers, including four from Table 5. As only three rivers in the database had overlapping records, this analysis unavoidably confounds spatial and long-term variability. To investigate the influence of climate on flow variability, climatic measures for gauging stations were derived by scoring the presence in their catchments of the major zones of a modified Köppen classification (Tanke & Gulik 1989). Ten zones are represented (Table 6).

Table 6 Köppen climate zones and codes (after Tanke & Gulik 1989).

Code	Climate type
Af	tropical rainy
Aw,As,Am	tropical wet and dry monsoon
Bs	dry steppe
Bw	desert
Cs	mid-latitude rainy with dry summer
Cw	mid-latitude rainy with dry winter
Cf	mid-latitude rainy with precipitation in all seasons
Df	continental, precipitation in all seasons
Dw	continental with dry winter
Ef,Eh	polar, snow climate

2.2.2 Descriptive and Exploratory Analysis

Non-parametric statistics were used (except for means in MSKEW and ASKEW) because many of the data were non-normal and not readily transformed. Following Richards (1989, 1990), the *spread* is less responsive to the length of record than other measures of dispersion. This is indicated by three measures of the scope of departures from the median, namely S50 ([75–25 percentiles]/median), S80 ([90–10 percentiles]/median) and S100 (range/median). These were calculated for each of the measures in Table 4 (except ZEROF, MSKEW, ASKEW). Spearman rank correlations between measures were tested for significance ($\alpha = 0.05$) using Bonferroni-adjusted probabilities in SYSTAT 6.0 (Wilkinson & Hill 1994). Other analyses employed PATN

3.6 (Belbin 1993) unless otherwise indicated. The following procedures were repeated independently using S50, S80 and S100 and for the climatic data (the latter are binary scores and so were not range standardized). Finally, the data from 11 stations replicated on rivers were added to the 52-station matrix and subjected to ordination and clustering (see below).

Variability measures were derived from raw monthly and annual data. The resulting matrix (columns by measures) was range standardized, converted to a Bray-Curtis dissimilarity matrix and subjected to semi-strong hybrid multidimensional scaling (SSH) (Belbin 1991a). The minimal stress configuration (i.e. minimum mismatch beween interpoint distances in ordination space and those predicted from the dissimilarity matrix) was identified from 100 random starts. Finally, hydrological or climatic measures were fitted to the corresponding ordination space as vectors of best fit, using multiple linear regression (PCC), and goodness of fit was examined by 100 Monte Carlo randomized re-runs (MCAO) (Belbin 1991b).

Although separations or groupings of vectors in the ordination space are usually determined by eye (Faith & Norris 1989), for this analysis with 23 vectors a protocol had to devised. It was assumed that if the angle of separation between a pair of vectors was 0-20° or 160-180° for all three 2-dimensional projections, those vectors were "interdependent". Choice of the angle of separation was not wholly arbitrary because the number of facets of hydrology that the literature suggests are biologically meaningful (Table 3, Ch. 1) were also considered .

Cluster analyses employed flexible agglomerative hierarchical fusion (flexible UPGMA) (Sneath & Sokal 1973) on the Bray-Curtis matrix. The dendrogram was cut at a level of dissimilarity which gave the most easily interpreted number of clusters. It was then re-plotted with this number of groups, and the significance of the model was tested using ASIM (cf. ANOSIM: Clarke & Warwick 1994). ASIM uses a Monte Carlo process to allocate the original dissimilarity values randomly to the chosen groups, and uses the *F*-ratio to compare the average within-group and average between-group dissimilarities. The contributions of measures to within- and between-group dissimilarity were determined by the SIMPER routine in PRIMER (Clarke & Warwick 1994).

2.2.3 Hypothesis Testing

The relationship of hydrology and climate initially was explored by fitting the climatic measures into the ordination space as vectors of best fit (PCC) and testing the fit for statistical significance ($\alpha = 0.05$) (MCAO). The climatic measure vectors best correlated with the ordination then were superimposed on the ordination plots.

The groups of rivers indicated by the climatic analysis were compared to those from the hydrological analysis using PRIMER (Clarke & Warwick 1994). Data based on S100 and S50 were range standardised, fourth-root transformed and used to compute a Bray-Curtis dissimilarity matrix. The climatic groups were then imposed on the matrix and ANOSIM was applied with 10,000 Monte Carlo simulations. River groups of five, seven and nine divisions were used. Statistical significance was determined for the overall groups and for the differences between groups, subject to Bonferroni correction (Sokal & Rohlf 1995, p 240). In this case, probabilities considered significant were <1.25 times the adjusted significance level (which differed with the numbers of comparisons) (Neter *et al.* 1985).

2.3 Results

Although results are attributed to rivers, they strictly relate to gauging stations. For brevity, the results of the analyses based on the S90 data are not presented here, because they were consistent with those from the analyses based on the S100 and S50 data.

2.3.1 Correlations of Flow Variability Measures

There appear to be five independent measures of flow variability. For the S100 data only one measure, PSFR (variability of pulse frequency) is not significantly correlated ($P > 0.05$) with any other measure. For the S50 data, four measures (PSFR, MNTF, RSDR, FLDR) are statistically independent. Two (PSEA, LSEA) are correlated only with each other and may be considered together as a fifth independent measure.

2.3.2 Flow Variability Ordinations

The three-dimensional MDS ordination for the S100 data (Fig. 1a) separates rivers with catchments mainly in dry steppe and/or mid-latitude rainy climates (*Group A* (arid): Cooper, Diamantina, Limpopo, Darling, Vaal, Burdekin, Fitzroy and marginally

the Oder and Tisza) from a group of rivers with catchments mainly in regions with tropical rainy climates (*Group T* (tropical): Oubangu, Sanaga, Bani, Ogooue, Niger and Blue Nile, and surprisingly also the Mekong, Indigirka and Kolyma, which overlap regions with continental and/or snow climates). On axes two and three, the polarity of groups A-T is less clear. Only one hydrological measure (MNTF) is not significantly correlated with the ordination.

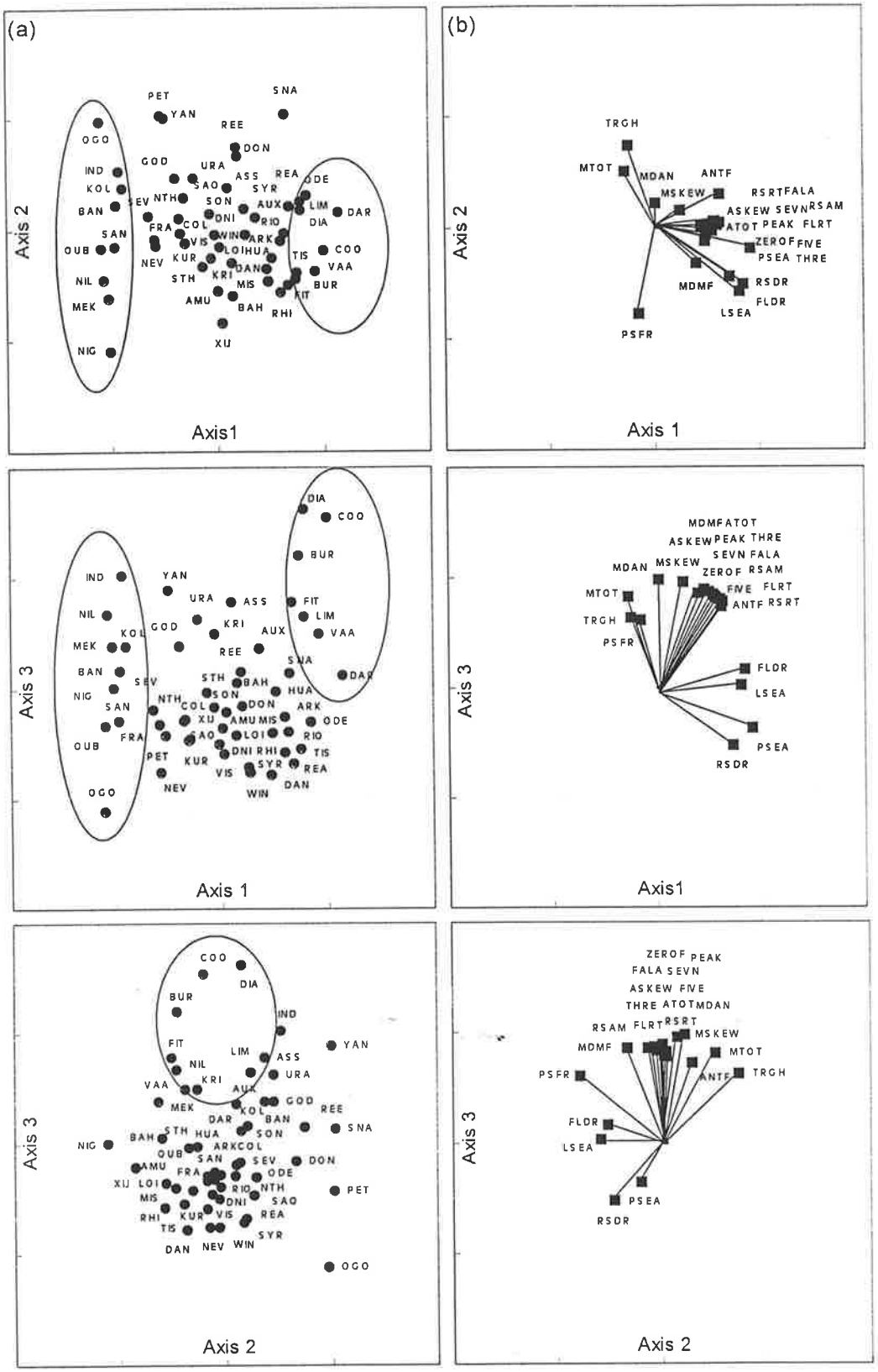


Figure 1 Semi-strong hybrid MDS ordination of 52 gauging stations by 23 measures of hydrological variability. Stress 0.12, ratio/ordinal cut point 1, measures based on range/median (S100). (a) Gauging stations labelled by river. Most strongly polarized groups enclosed. (b) Hydrological measures significantly correlated with the ordination are plotted as projections of equal-length vectors in the 3D space onto the 2D plots.

The ordination for the S50 matrix (Fig. 2a) also separates groups A and T. As before, several rivers in each group have parts of their catchments in regions of continental climates. All hydrological measures are correlated ($P < 0.05$) with the ordination.

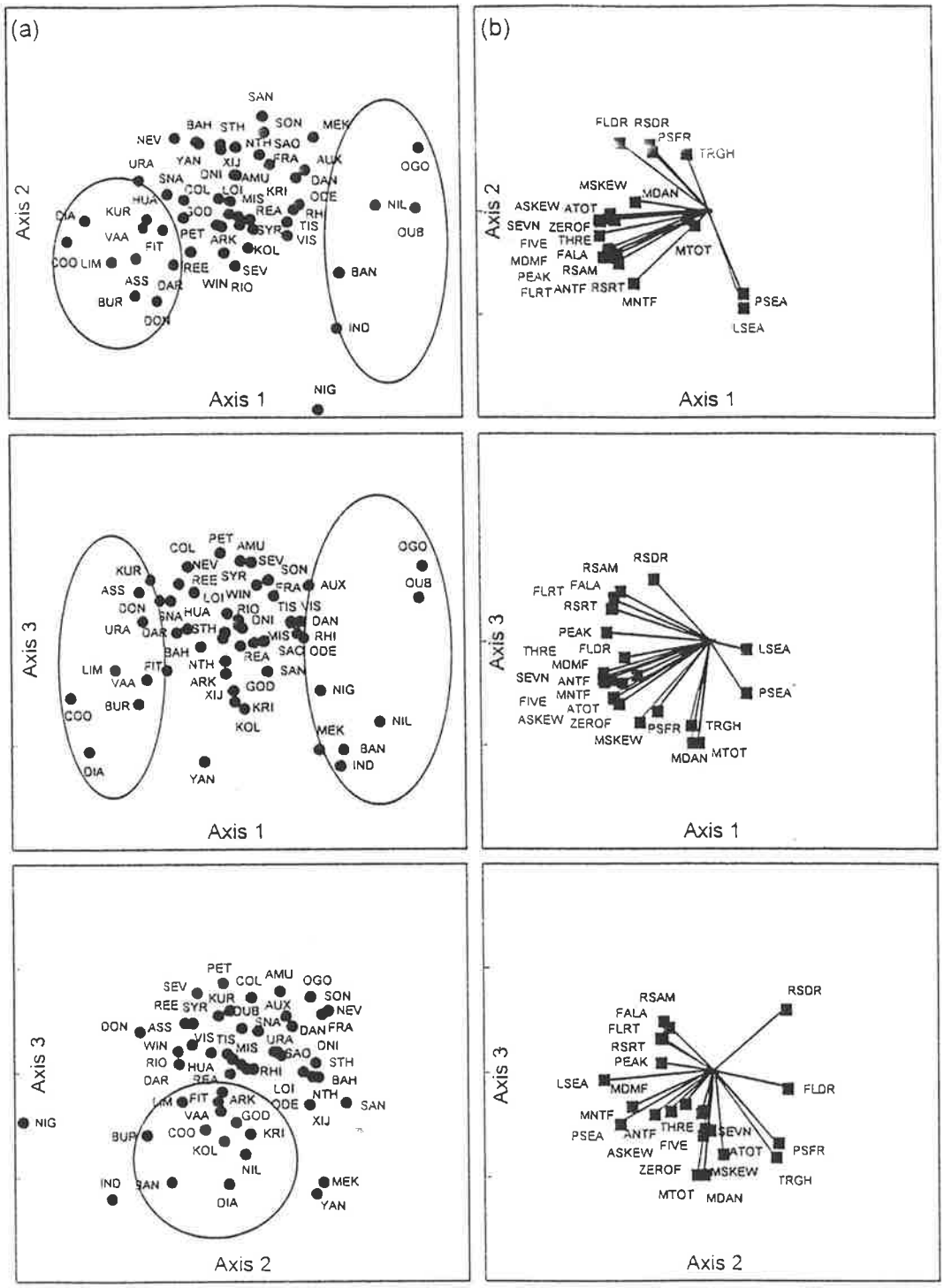


Figure 2 Semi-strong hybrid MDS ordination of 52 rivers by 23 measures of hydrological variability. Stress 0.14, ratio/ordinal cut point 0.82, measures based on interquartile range/median (S50). (a) Gauging stations labelled by river. Most strongly polarized groups enclosed. (b) Hydrological measures significantly correlated with the ordination are plotted.

2.3.3 Independent Flow Variability Vectors

When hydrological measures correlated with the S100 ordination are overlaid on the ordination (Fig. 1b), the Group A–T polarity is associated with vectors representing variability of pulse amplitude (RSAM, FALA, PEAK, ZEROF, ANTF, ATOT, THRE, FIVE, SEVN), rate of change (RSRT, FLRT) and predictability (MSKEW, ASKEW).

When the hydrological measures correlated with the S50 ordination are plotted as vectors in the ordination space (Fig. 2b), the Group A–T polarity again is associated with vectors representing variability of pulse amplitude (ZEROF, MDMF, ANTF, ATOT, THRE, FIVE, SEVN) and predictability (MSKEW, ASKEW). In the combined S100 and S50 results, there are 10 relatively independent hydrological measures, representing variability of pulse timing (LSEA, PSEA), pulse frequency (PSFR), pulse duration (FLDR, RSDR), magnitude at various temporal scales (MDAN, MNTF, MDMF) and extreme magnitudes (TRGH, PEAK).

2.3.4 Flow Variability Clusters

Flexible UPGMA cluster analysis for the S100 data (Fig. 3) supports the ordination groupings. The three-group dendrogram (Fig. 3a) separates groups that match Groups A and T, but with added rivers from continental climatic zones and some *allogenic* rivers (i.e. rivers with flows from more than one climatic zone). The seven-group dendrogram shows the same pattern, but splits the Diamantina and Cooper from Group A and divides Group T into four (Fig 3b). ASIM indicates that the groupings in both dendrograms are significant (P <0.001).

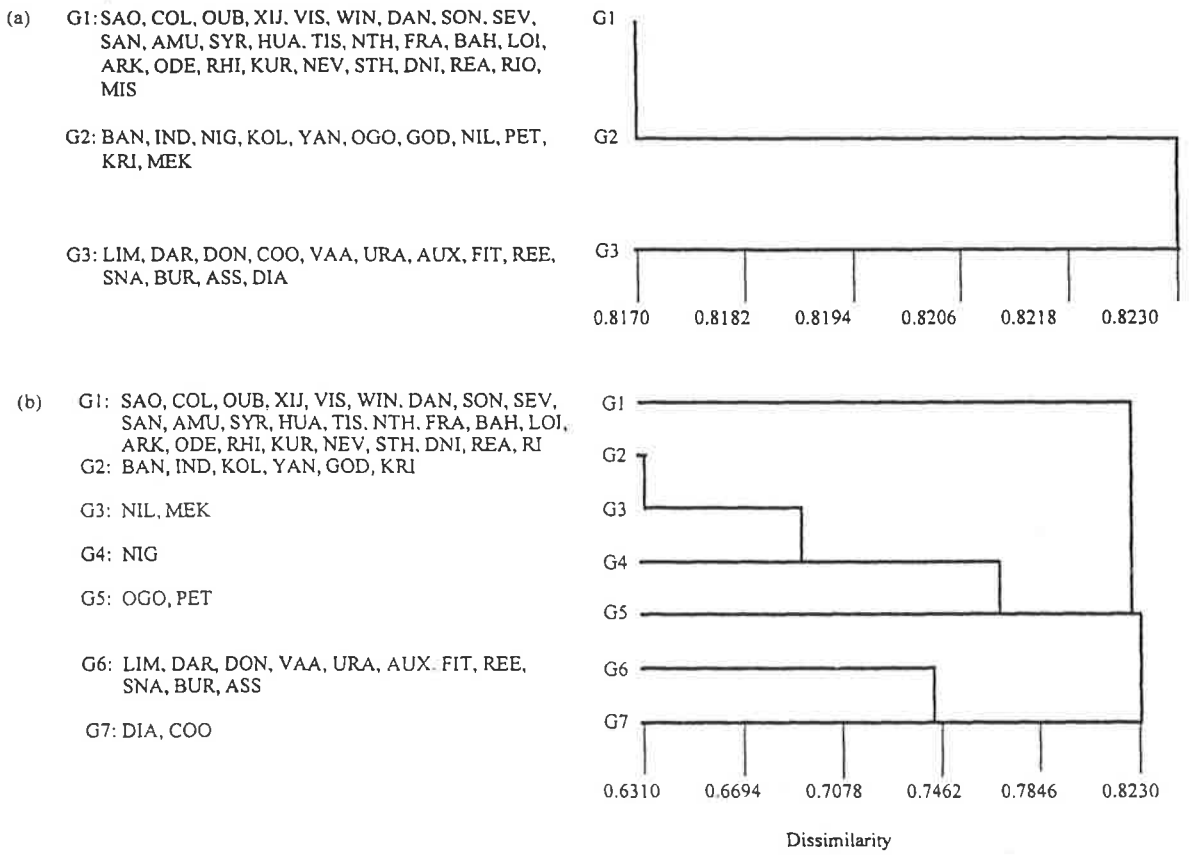


Figure 3 Dendrograms of flexible UPGMA cluster analysis of 52 gauging stations by 23 measures of hydrological variability. Measures based on range/median (S100). Members of groups labelled by river. For both dendrograms, ANOSIM *P*-values < 0.001. (a) Three-group dendrogram. (b) Seven-group dendrogram.

Cluster analysis of the S50 data produces a three-group dendrogram different to that based on the S100 matrix. Group T is divided into two subgroups, and the Mekong and Group A rivers are grouped with the remainder. The seven-group dendrogram restores Group A as in the ordination but with two added continental climate rivers, and the Diamantina and Cooper are removed to their own group. The Group T rivers are divided into four subgroups. Overall, however, the clusters confirm the Group A–T polarity in the ordinations. From ASIM, the groupings in both dendrograms are significant (P <0.001).

2.3.5 Overall Variability per River

When the medians of all range/median (S100) measures per river, and the medians of all interquartile range/median (S50) measures per river are plotted (Fig. 4), the extreme variability of Australian and southern African rivers is obvious. In the S50 plot

(Fig. 4b) there is a clear discontinuity between the Cooper and Diamantina, other Australian and southern African rivers, and the remainder. The rivers with the lowest variability scores are mainly central African rivers from tropical rainy climates, but there are also several rivers (Neva, Fraser, Indigirka) with continental and/or snow climatic influences.

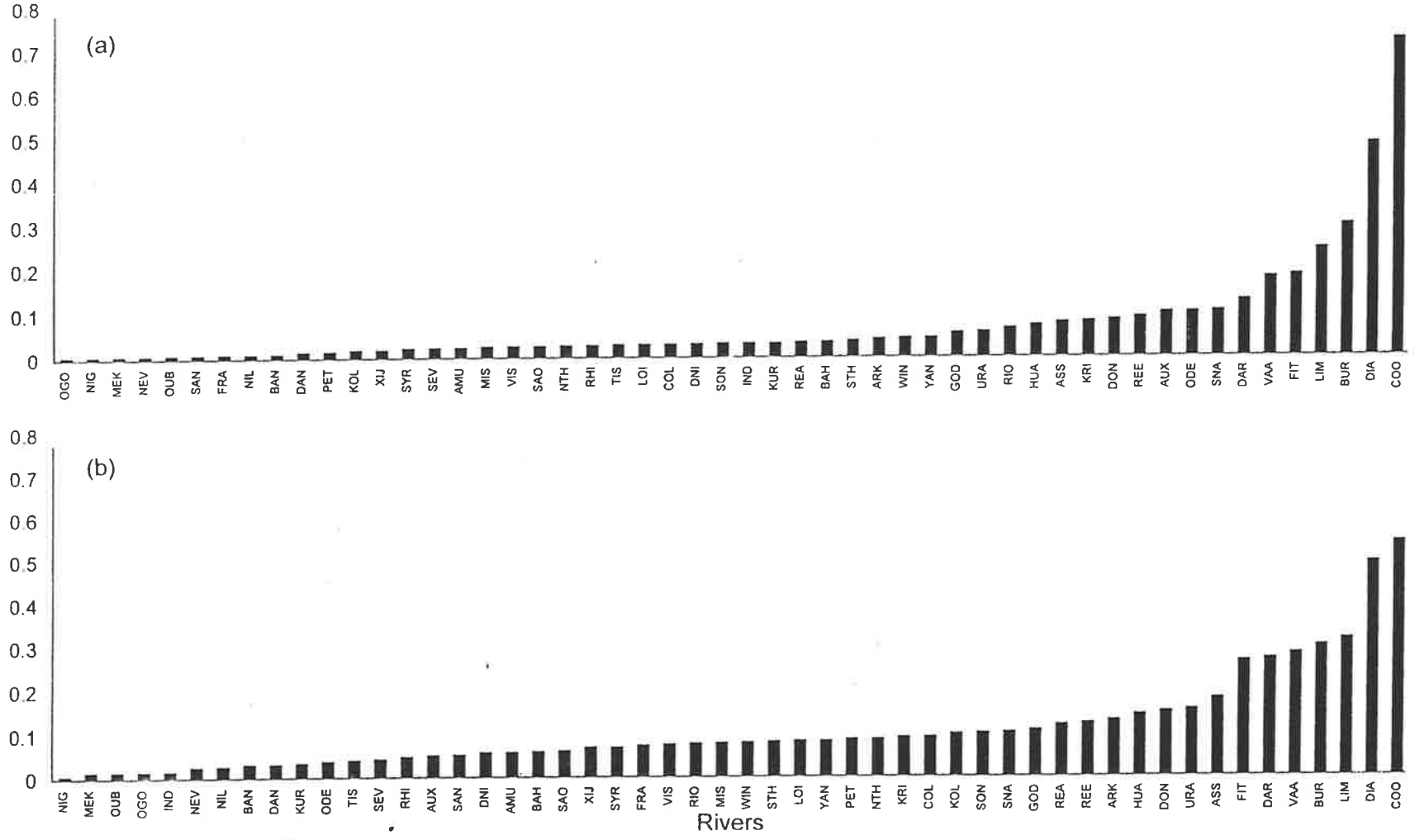


Figure 4 Summary medians of all hydrological measures for each of 52 gauging stations, labelled by river. (a) Medians of measures based on range standardized range/median (S100). (b) Medians of measures based on range standardized interquartile range/median (S50).

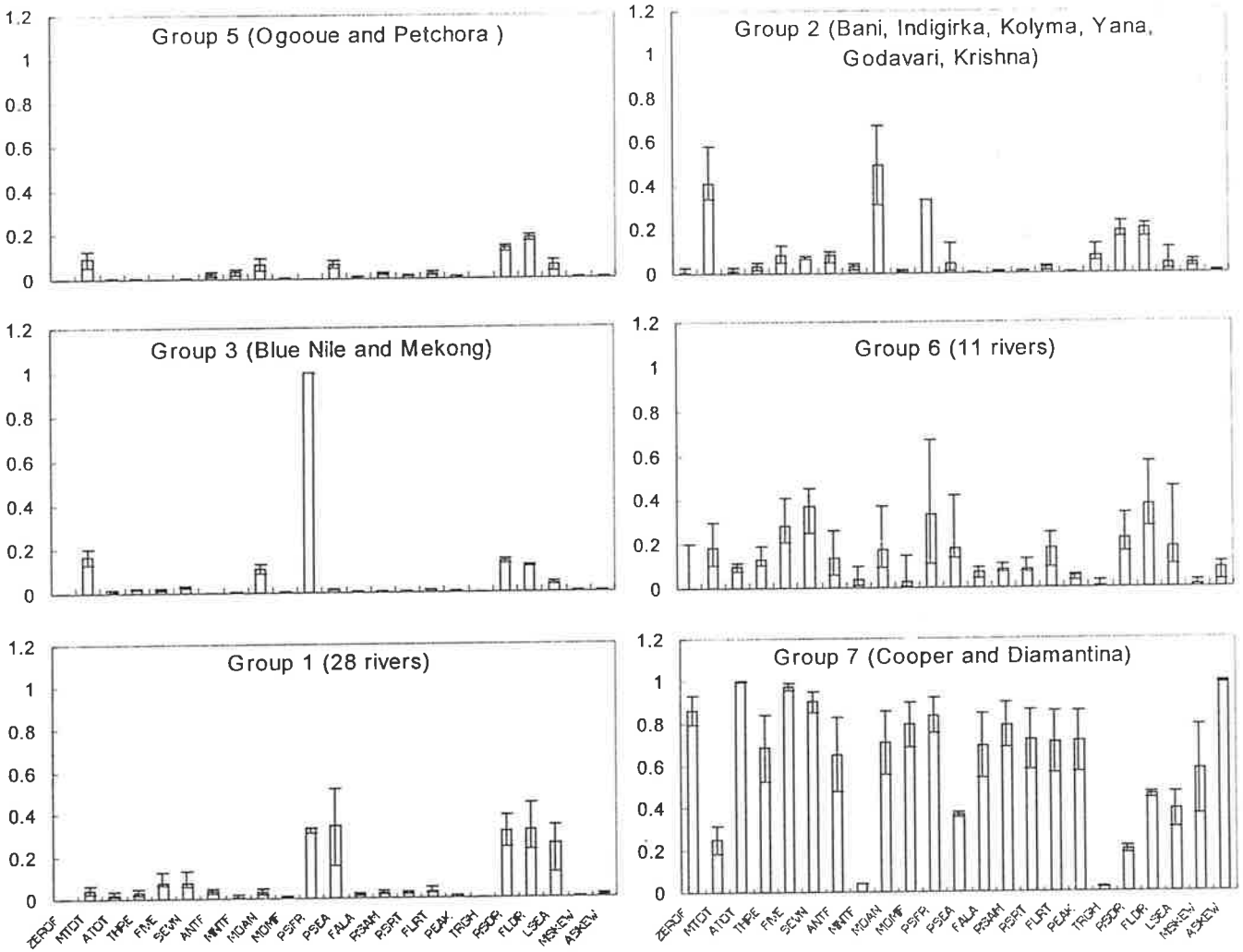


Figure 5. Summary medians and interquartile ranges of all hydrological measures for each of 6 groups of gauging stations labelled by river. Groups are 6 of the 7 from the dendrogram of flexible UPGMA cluster analysis based on range/median (S100).

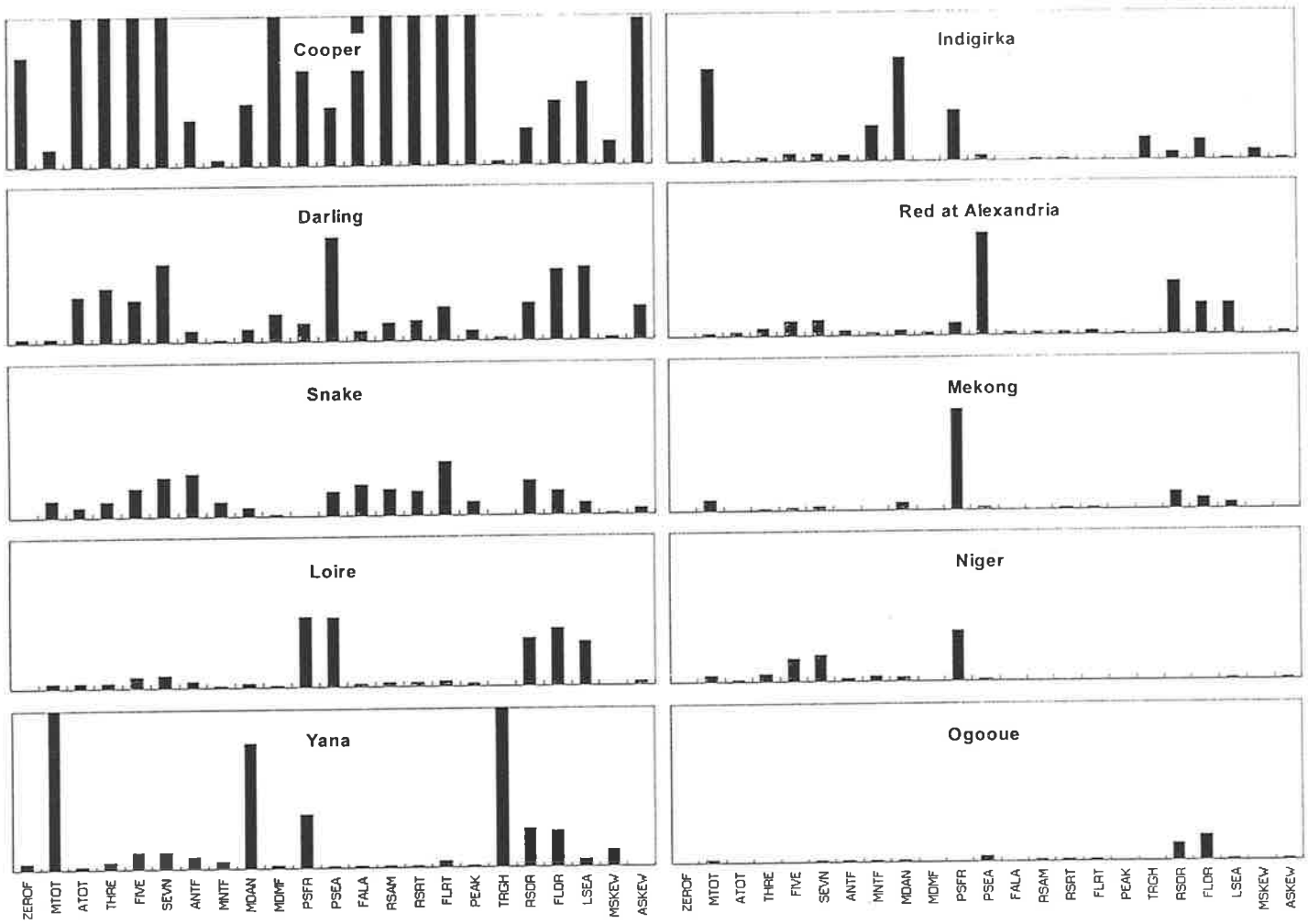


Figure 6. Values of 23 hydrological measures, based on range standardized range/median (S100), for individual gauging stations labelled by river. All charts to the same scale.

2.3.6 Patterns of Variability

The spectra of median scores on measures of variability for each group from the seven-group dendrogram show distinctive patterns (Fig. 5). For the S100 and S50 data, Australian arid zone rivers the Diamantina and Cooper show high or highest values for most measures. At the other extreme of the S100 data, the Ogooue and Petchora have low values on all measures. The Blue Nile and Mekong have the maximal score on the flow frequency measure (PSFR) yet very low scores on all other measures.

The patterns of these values (based on range/median) for individual rivers are illustrated in Figure 6. For both river groups and individual rivers, there is a striking variety in patterns of scores on variability measures which is not apparent in the overall values shown in Figure 4. This is apparent also for the scores on the S50 measures (not shown).

2.3.7 Flow Variability Measures Distinguishing Groups of Rivers

On the S100 three-group dendrogram, the measures of variability contributing >5% to dissimilarity between any of the three groups are PSFR, SEVN, FIVE, FLDR, MDAN, LSEA, PSEA, RSDR, FLRT and MTOT. For the corresponding S50 dendrogram they are PSEA, FLDR, PSFR, MDAN, MTOT, RSDR, RSAM, RSRT, LSEA, ANTF, FLRT and PEAK. Groups A–T in the S100 three-group dendrogram are separated by variability in pulse frequency (PSFR), variability in monthly amplitude (MTOT), median of variability in annual amplitude (MDAN), variability of amplitude of total multi-annual flows (FIVE, SEVN), variability of duration of falling limb of the pulse (FLDR), and variability of timing of minimum flows (LSEA).

There were eight independent measures that contributed to distinctions among groups in the above dendrograms. These are variability in pulse frequency (PSFR), median of variability in annual flow magnitude (MDAN), variability of duration of falling and rising limbs (FLDR, RSDR), variability of timing of minimum and maximum flows (LSEA, PSEA), and variability of peak flows (PEAK). To this group should be added a measure of multi-annual flow magnitude variability (a combination of FIVE and SEVN); this is

characteristic of the dissimilarity between groups A and T, and could represent the cluster of correlated vectors aligned with the A-T polarity.

2.3.8 Replicate Stations Analysis

The three-dimensional MDS ordinations based on the S100 and S50 data for the replicate stations rivers-hydrology matrices (63 stations, stress 0.13, 0.14, ratio/ordinal cut point 1) (not shown) retain the overall configurations of the 52-station ordinations. There is clear separation between replicate stations for a given river, and particularly for rivers in the middle of the space (some stations are as far removed from each other as those on different rivers). However, the replicate stations remain within the original broad groups. Cluster analyses for the replicate stations S100 (Fig. 7a) and S50 data (Fig. 7b) confirm the results from the ordinations, and suggest that the analyses of data from one gauging station per river reflect outcomes for river groups, if not always for individual rivers.

(a) G1:12 + Niger 2
G2: 8
G3: 2
G4: Niger1, Niger 3
G5: 2
G6: 2
G7: 17 + Danube 1, Danube 2, Danube 3, Parana 1, Parana 2, Missouri 1, Missouri 2
G8: 3 + Darling 1, Darling 2, Darling 3
G9: 2 + Cooper 1, Cooper 2

(b) G1: 12 + Parana 1, Parana 2, Danube 1, Danube 2, Danube 3
G2: 2
G3: 13 + Missouri 1, Missouri 2
G4: 1 + Darling 1, Darling 2, Darling 3
G5: 4
G6: 4
G7: 4
G8: 1 + Cooper 1, Cooper 2
G9: 2
G10: 1
G11: 2
G12: 4
G13: Niger 1
G14: Niger 2, Niger 3

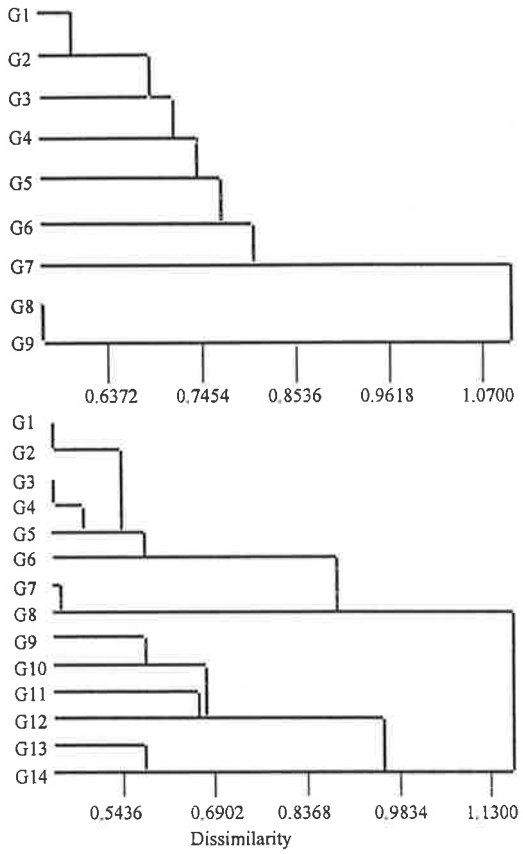


Figure 7 Dendrograms of flexible UPGMA analysis of 63 gauging stations (on 54 rivers) by 23 measures of hydrological variability, stations labelled by river. For both dendrograms, ANOSIM P<0.001: (a) nine-group dendrogram, measures based on range/median (S100); (b) fourteen –group dendrogram, measures based on interquartile range/median (S50).

2.3.9 Climate Ordination and Clusters

Eight of the 10 climate measures (Af, Aw/As/Am, Bs, Cw, Cf, Df, Dw and Ef/Eh: Table 6) are correlated with the three-dimensional ordination (P <0.05) (Fig. 8a). The other climatic zones (Bw and Cs) are present only in the catchments of five and two rivers, respectively. The correlated measures plotted as vectors on the ordination are aligned approximately with five climatic groupings of the rivers: continental climates with precipitation in all seasons (Df), continental climates with dry winter and/or snow climates (Dw, Ef/Eh), mid-latitude rainy climates with precipitation all seasons (Cf), tropical rainy climates (Af, Aw/As/Am), mid-latitude rainy climates and/or dry steppes climate (Cw, Bs). The clusters in the five-group dendrogram (ASIM: P <0.001) for the climatic data resemble the groups on the climate ordination plot.

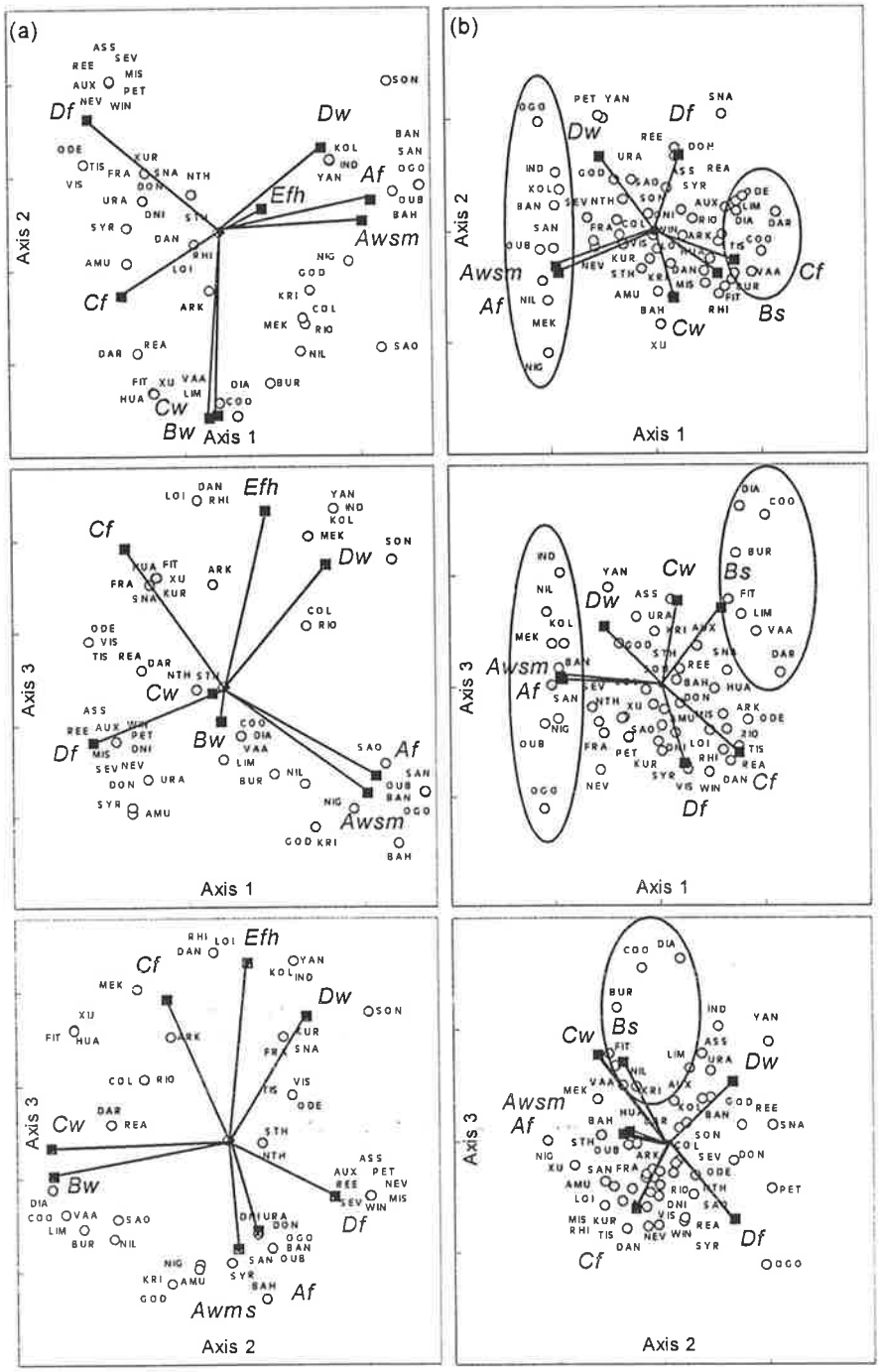


Figure 8 Semi-strong hybrid MDS ordination of 52 gauging stations (labelled by river). (a) Ordination by 10 measures of climate zones in the catchments, stress 0.15, ratio/ordinal cut point 1. Significantly correlated climate measures plotted. (b) Ordination by 23 measures of hydrological variability. Significantly correlated climate measures plotted, and most strongly polarized groups enclosed. "Aw,As,Am" and "Ef,Eh" (Table 6) abbreviated to "Awsm", "Efh".

2.3.10 Correspondence of Climate Measures with Flow Variability

Seven of the climate vectors (Af, Aw/As/Am, Bs, Cw, Cf, Df, Dw) are significantly correlated (P <0.05) with the S100 ordination of rivers (Fig. 8b). In the S100 ordination space, Af and Aw/As/Am are closely correlated, whereas the other five are relatively independent. The alignment of the vectors generally corresponds with the overall separation between Group A and Group T rivers. Five of the seven climate vectors correlated with the S100 ordination are correlated also with the S50 ordination (P<0.05) (not shown). The climatic vectors again correspond with the separation between Group A and Group T rivers, and there is also a separation of rivers with "continental climate" influences along the Df vector. Both ordinations suggest a strong climate-hydrology correspondence that is confirmed by ANOSIM.

2.3.11 Tests of Climate-Flow Variability Correspondence: Group Pairs

ANOSIM results for the between-groups comparisons (Table 7) show that for both S100 and S50 data the highest frequencies of significant differences are between predominantly Group A rivers and rivers in all other climate groups. This reinforces the hydrology ordinations, indicating that Group A is the most distinctive of the groups.

Table 7 ANOSIM between-groups analysis of the range/median and interquartile range/median hydrology dissimilarity matrices grouped by climate. (a) Definitions of climate group codes. (b) Analysis results. Only intergroup differences less than 1.25 of the Bonferroni adjusted threshold significance level are included.

(a)

Code	Definition
Aw/As/Am+	rivers with major catchment areas in tropical wet and dry monsoon climates, but usually in other climates as well.
Cw,Bs	rivers with major catchment areas predominantly in mid-latitude rainy climates with dry winters, and in dry steppes.
C,Bs	rivers with major catchment areas predominantly in mid-latitude rainy climates, and in dry steppes.
Bs+	rivers with major catchment areas predominantly in dry steppes, but usually in other climates as well.
Cf	rivers with major catchment areas in mid-latitude rainy climates with precipitation in all seasons.
Cf+	rivers with major catchment areas in mid-latitude rainy climates with precipitation in all seasons, but usually in other climates as well.
C+	rivers with major catchment areas in midlatitude rainy climates, but usually in other climates as well.
Dw	rivers with major catchment areas in continental climates with dry winters, and usually in snow climates as well.
Df	rivers with major catchment areas only in continental climates with precipitation in all seasons.
Cf,Df	rivers with major catchment areas in both or either Cf and Df

(b)

Variability statistic	No. groups in dendrogram	Climate group	Climate group	ANOSIM significance level (%)	Bonferroni adjusted significance threshold (%)
Range/median	5	Aw/As/Am+	Bs+	0.6	0.5
	5	Aw/As/Am+	C+	0.2	0.5
	7	Aw/As/Am+	C,Bs	0.0	0.238
	7	Aw/As/Am+	Cf+	0.3	0.238
	9	Aw/As/Am+	Cw,Bs	0.0	0.139
	9	Cw,Bs	Df,Bs	0.1	0.139
	9	Cw,Bs	Cf,Df	0.0	0.139
	9	Cw,Bs	Df	0.1	0.139
Interquartile range/median	5	Aw/As/Am+	Bs+	0.1	0.5
	7	Aw/As/Am+	C,Bs	0.1	0.238
	7	C,Bs	Cf+	0.2	0.238
	7	C,Bs	Dw	0.1	0.238
	7	Cf+	Dw	0.3	0.238
	9	Cw,Bs	Df,Bs	0.1	0.139
	9	Cw,Bs	Cf,Df	0.0	0.139
	9	Cw,Bs	Df	0.1	0.139

2.4 Discussion

2.4.1 Climate and Flow Variability

Multivariate analyses of hydrographs separate groups of mainly central African tropical rivers (Group T) from Australian and southern African rivers with catchments in dry steppe and/or mid-latitude rainy climates (Group A). The "dry steppe/mid-latitudes rainy climates group" is highly variable, particularly the Cooper and Diamantina, whereas rivers of low overall variability belong mainly to the "tropical rainy climates" group. This implies that "tropical" and "dryland" rivers (*sensu* Walker *et al.* 1995) represent extremes of a spectrum of hydrological variability, and accords with results of global comparisons between streams (McMahon 1979). The dichotomy may also reflect inter-continental differences (McMahon & Finlayson 1991). Australian dryland rivers in particular show positive correlations between variability and catchment area (McMahon *et al.* 1992). By these criteria, large Australian dryland rivers (Cooper and Diamantina) might be considered the most variable in the world.

2.4.2 Facets of Flow Variability

The continuum of variability described above, of course, is a simplification. While it is true that all but four of the 23 hydrological measures used in this analysis are inter-correlated (c.f. Clausen & Biggs 1997), many more facets of hydrological variability are likely to be biologically significant. Ten of the 23 vectors of flow variability measures are relatively independent in the hydrology ordinations, and the remainder are oriented toward Group A. This remainder was considered an eleventh vector. Eight of these measures also distinguished the major river groups. These results understate the diversity of important measures, because pairs and larger groups of interdependent vectors (like those associated with the A-T polarity) could represent influences independent of the individual measures cited here. The literature also suggests a diversity of measures of biological importance (Table 3, Ch.1).

Different groups of rivers vary widely in patterns of median values of hydrological measures, particularly for the relatively independent measures. For example, in the S100

three-group dendrogram, multi-annual flow variability (FIVE, SEVN), which probably incorporates an ENSO signal (Allan 1985, Molles *et al.* 1992), is characteristic of the dissimilarity between the "mid-latitudes rainy climates and dry steppe" and the "tropical rainy climates" group. This result implies that large dryland rivers may show characteristic long-term persistence in flow magnitudes (Puckridge *et al.* in press).

The results also demonstrate that individual rivers may have distinctive patterns of values (*signatures*) on hydrological variability measures. If these measures are biologically significant, the rivers should also be ecologically distinctive. Thus, although there are ecological differences between hydrologically "variable" and "regular" rivers (Poff & Allan 1995), this simple dichotomy may obscure other important differences. To characterise the hydrological variability of a river in an ecologically meaningful way, at least eight and probably 11 measures of hydrological variability may be necessary (in addition to measures of central tendency). This assumes that measures characterising variability exclusively in the middle (S50) range of hydrological events are needed in addition to those in the extreme (S100) range (Gaines & Denny 1993). For comparison, Poff & Ward (1989) and Poff (1996) used only three measures of variability in the sense used here, and Richter *et al.* (1996) used 13 (but did not consider their independence).

2.4.3 Biological Significance of Flow Variability

The eight measures cited above can be related to particular features of fish biology (Table 3, Ch. 1). The variability of pulse-timing (LSEA, PSEA) has been linked with length of breeding season, spawning periodicity and reproductive strategies, variability of duration (RSDR, FLDR) with length of life-cycles and age at maturity, variability of flow magnitude (MDAN, PEAK) with colonising ability and general mobility, variability of pulse frequency (PSFR) with species richness, and multi-annual variability of flow magnitude (FIVE, SEVN) with major variation in assemblage structure.

Even interdependent measures may have different biological linkages. For example, ASKEW (predictability of annual flows) is aligned with ZEROF (the proportion of months with no flow). Predictability of flows has been linked with mobility and colonizing ability, and the frequency and duration of zero flows have been linked with variation in the

proportions of large carnivores, physiologically-tolerant species and small species in the assemblage, and variation in mortality through disease (Table 3, Ch 1). These correlations are not necessarily causal, and may be specific to taxa and particular scales. However, they provide a framework for an expanded model of hydrology-biology linkages (cf. Poff 1992b, Poff & Allan 1995.

2.4.4 Constraints of Spatial and Temporal Replication

This analysis assumed that data from a single gauging station suffice to characterise a large river. The above test of this assumption indicates that it is valid at the global scale of river groups. These results are constrained however by the temporal scale of the data; the measures of variability used are surely scale-dependent (Poff 1996). When sufficient daily discharge data become available, the analysis should be repeated. For the present, it is considered that the temporal scales used here are adequate for fish and other organisms with comparable life-spans.

2.5 Summary

Hypothesis 1.1, that *large rivers with major arid zone climatic influences are no more variable than rivers influenced primarily by other climates*, **Hypothesis 1.2**, that *for the purpose of determining the ecological significance of hydrological variability in large rivers, variability may be summed in a single measure*, and **Hypothesis 1.3**, that *the facets of the flood pulse listed by Junk et al. (1989) are adequate to characterize large rivers by their biologically significant patterns of flow variability*, are all rejected.

Hypothesis 1.4, that *large arid zone rivers do not exhibit multi-annual hydrological persistence* is not tested by the above analysis (see Puckridge *et al.* in press), but Group A rivers are exceptionally variable at multiannual scales, so multiannual cycles are likely to exist.

Hypothesis 1.5, that *large arid zone rivers are not exceptionally variable in the seasonal timing of their flow pulses* is rejected, because the Cooper and Diamantina show high values of variability of flow pulse timing (LSEA, PSEA), and LSEA contributes to the

A-T distinction in the S100 dendrogram. That LSEA, PSEA are not consistently aligned in ordinations with the A-T polarity qualifies this conclusion, however.

Hypothesis 1.6, that *large arid zone rivers are not exceptionally hydrologically unpredictable* is rejected, because not only are the measures of skew (MSKEW, ASKEW) aligned in the ordinations (Figs 1b, 2b) with Group A-Group T polarity, but the most variable rivers of Group A (the "dry steppe/mid-latitudes rainy climates group"), the Cooper and Diamantina, show extremely high values of annual skew (ASKEW) and to a less extent monthly skew (MSKEW).

Hypothesis 1.7, that *large arid zone rivers are not outstandingly variable in their flow pulse amplitude*, is rejected.

These results at the flow regime and whole river scales suggest that the FPC should be extended to encompass the complexity and diversity of hydrological patterns in large rivers, and the biological implications of more measures of flow variability relevant to overbank flowpulses. It should be adapted to accommodate the characteristics of rivers in arid zones, particularly their unpredictability, their multiannual variability and the roles of instream flow pulses and drought in their ecology. Chapters Three to Five will examine further the need for modification of the FPC by testing its applicability to flow-biology relations in a large arid zone floodplain river, Cooper Creek in central Australia.

3. The Lake Eyre Basin, Cooper Creek and Coongie Lakes: physical and biological outline, and the characteristics of the fish assemblage.

3.1 Introduction

The last chapter placed the hydrological variability of the lower Cooper Creek and lower Diamantina River into the context of large river systems worldwide. This chapter sets the geomorphology, limnology, biology and hydrology of Cooper Creek in the context of arid zone lotic systems in general. It briefly describes the Lake Eyre Basin in central Australia through which this river flows, and in more detail Cooper Creek itself and particular regions on its lower reach. Finally, to provide a background for the analyses that follow, it discusses the life-history characteristics of the fish assemblage of the lower Cooper.

The characteristics of the fish assemblage are then used to test the following hypotheses from Chapter 1:

1. At the flow regime temporal scale and the whole river spatial scale:

1.8. Fish assemblages of hydrologically unpredictable rivers have predominantly:
(a) K-selected life histories
(b) precocial reproduction
(c) high parental investment in offspring.

1.9. The biota of hydrologically unpredictable rivers is not adapted to the flood pulse (Junk *et al.* 1989, Bayley 1991).

4. At the flow regime and flow history temporal scales and the river reach spatial scale in Cooper Creek:

4.1. (a) Fish spawn primarily in response to seasonal, not hydrological cues (i.e. follow a 'double or nothing' spawning strategy, *sensu* Lloyd *et al.* 1991a).
(b) Fish migrate primarily in response to seasonal, not hydrological cues.

3.2 Arid Zone Surface Waters - General

3.2.1 Arid Zone Rivers

3.2.1.1 Hydrology and geomorphology

Streams in the arid and semi-arid zones (i.e. those with catchments confined to these zones, *sensu* Farquharson *et al.* 1992) are characterized by strongly skewed distributions of flow and large transmission losses downstream (Rodier 1985). McMahon (1979), in a worldwide comparison of hydrological variability, illustrates some aspects of the variability of discharge of arid zone streams, although over a narrow range of time-scales. However, arid zones differ in their degree of variability on McMahon's criteria, and the above characteristics are much more pronounced for the arid zone rivers of Australia and South Africa, as Chapter 2 demonstrated (see also Alexander 1985, McMahon & Finlayson 1991). Topographic, vegetation and evaporation characteristics of arid zones in these continents tend to amplify rainfall variability in its translation to runoff.

Such rivers - i.e. with catchments confined to the hot arid and semi-arid - should be distinguished from rivers like the Senegal, Nile, Chari, Niger and Orange-Vaal of Africa, the Columbia and Colorado of North America, the Indus of Asia and the Murray-Darling in Australia, all of which flow through arid zones but derive most of their discharge from remote, humid catchments, and retain the hydrological characteristics of those catchments (Rodier 1985, Comin & Williams 1994). Similarly, rivers such as the Ob and Lena in the CIS and the McKenzie in Canada have dry catchments, but because their climates are sub-arctic, their flow patterns are different from those of hot, semi-arid catchments (Farquharson *et al.* 1992). These distinctions are borne out in Chapter 2.

Arid zone rivers have complex channel morphologies, in which a single channel operates at low flow conditions and a wider, often braided channel or channel of complex cross-section operates at high flows (Graf 1987, Nanson *et al.* 1986). Rare, large floods play a dominant role in shaping these morphologies (Pickup *et al.* 1988). The geomorphology of arid zone rivers also tends to be more dynamic than that of humid zone rivers (Graf 1987, Kresan 1988).

3.2.1.2 Limnology and Biology

Arid zone rivers are characteristically more turbid and more variable in physico-chemistry than humid zone rivers (Comin & Williams 1994, Williams 1987a). The biotas of arid zone streams are generally tolerant of extreme environmental conditions (Williams 1987a, Comin & Williams 1994), spatially and temporally patchy in community composition and abundance (Comin & Williams 1994, Puckridge & Drewien 1988), flexible in life-history strategies (Kodric-Brown 1981), opportunistic in response to flow variation (Deacon & Minckley 1974), and dependent on drought refugia (Shmida *et al.* 1986, Stafford Smith & Morton 1990, Morton 1990, Briggs 1992).

3.2.2 Lakes

Most arid zone lakes are shallow, intermittent or episodic (*sensu* Comin & Williams 1994), variable in depth, strongly affected by wind action, turbid, variable in temperature, dissolved oxygen concentrations and salinity, and subject to diel thermal stratification (Comin & Williams 1994).

3.3 Lake Eyre Drainage Basin

Cooper Creek and the Diamantina River are the largest rivers in the endorheic arid zone Lake Eyre Basin of central Australia. The following description of the Basin provides a context for the study of lower Cooper Creek in Chapters 4 and 5.

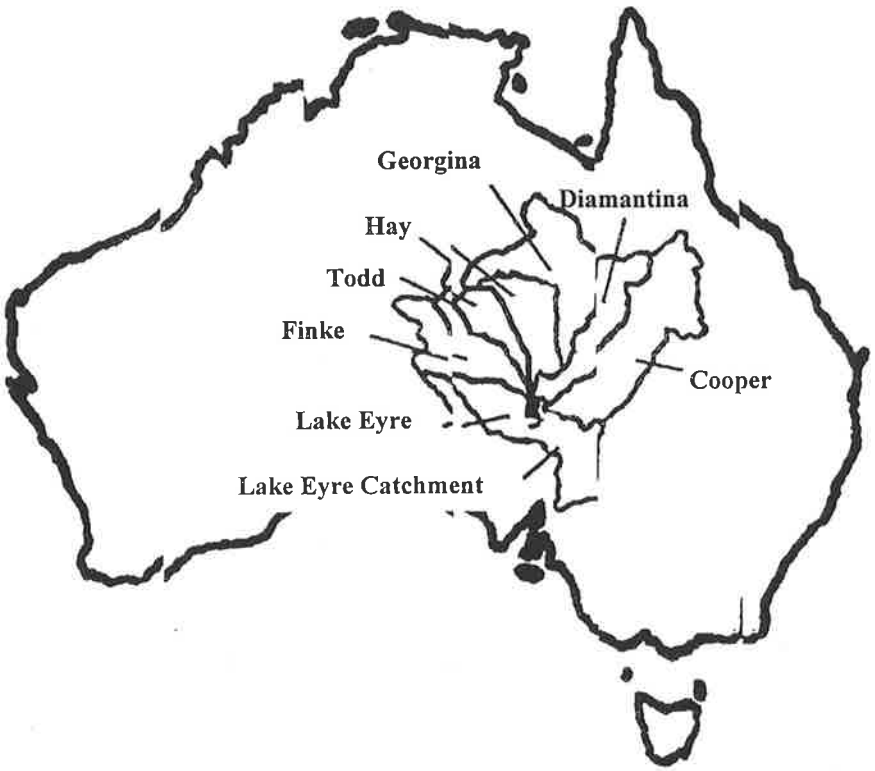


Figure 9 The Lake Eyre Basin, showing major catchment areas

3.3.1 Geomorphology

(Adapted from Kotwicki (1986), except where otherwise indicated).

The basin (Fig. 9) is bounded in the east by the Highlands of Queensland, in the north by the MacDonnell Ranges, in the west by the Musgrave, Everard and Stuart Ranges and in the south by the Flinders Ranges, and has an area of 1,140,000 km^2. Its topography is mostly flat, with only 30% of the basin above 250m ASL, and the headwaters of the Diamantina and Cooper at only 230m. The lowest point in Lake Eyre is 15m below SL. Its stream gradients are very low, yet it is one of the largest areas of coordinated internal drainage in the world, despite its position in the driest part of the continent. An

anastomosing flow pattern at low flows and a braided flow pattern during floods is a characteristic of some of the major floodplains in the basin (Nanson *et al.* 1986, Rust & Nanson 1989). Multiple benched channel forms, reflecting rare exceptional flood events, are a feature of those river reaches with confined channels (Pickup *et al.* 1988).

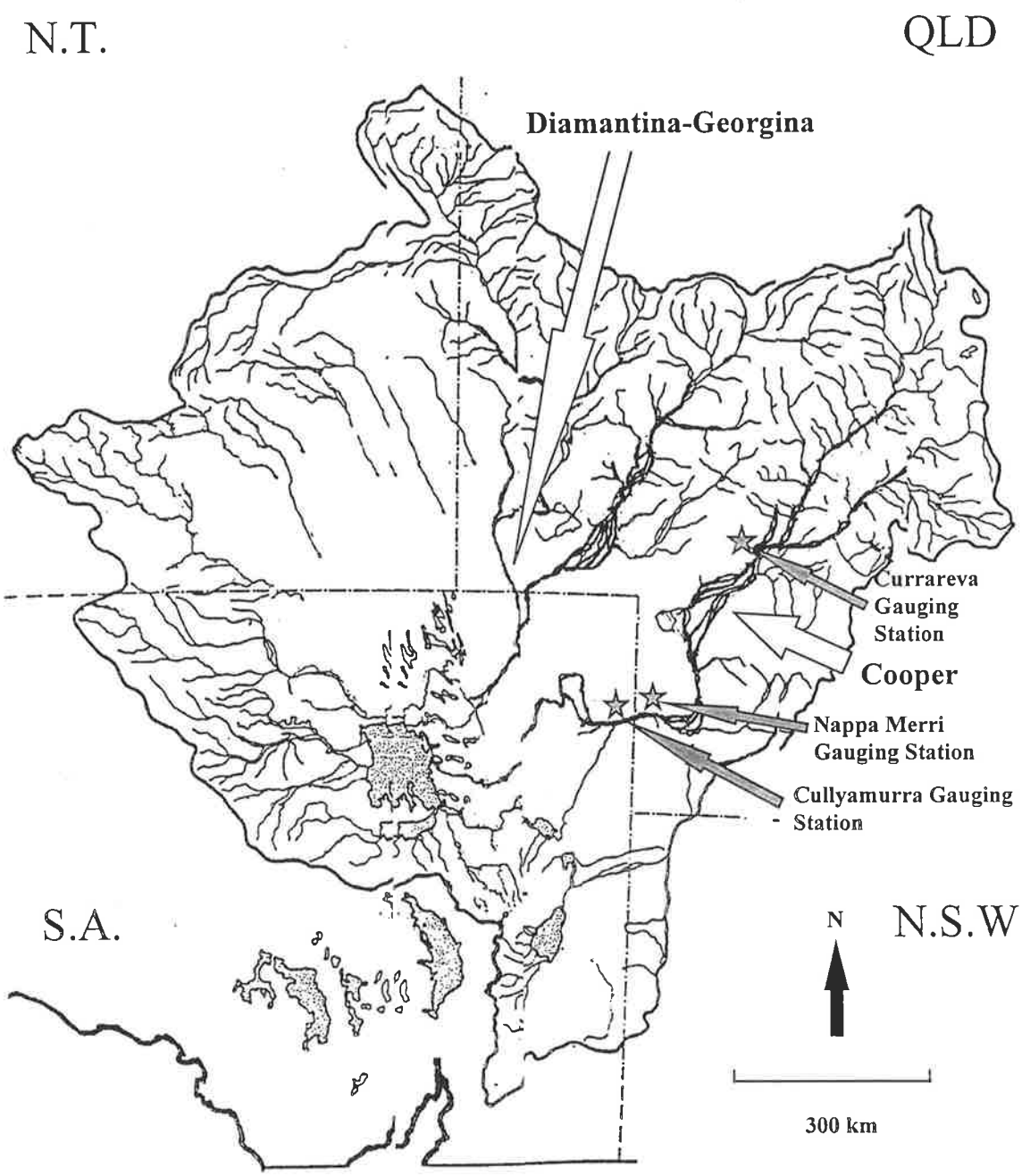


Figure 10 The Lake Eyre Basin, showing major river courses and Cooper Creek gauging stations

Because of their low gradients and relief and the exceptional range of their flow amplitudes, most rivers in the basin have large areas of floodplain (Fig. 11). The Cooper

and Diamantina/Georgina have floodplain soils occupying 1/5 (for the Georgina) to 1/3 (for the Cooper) of their total catchment areas (Graetz 1980).

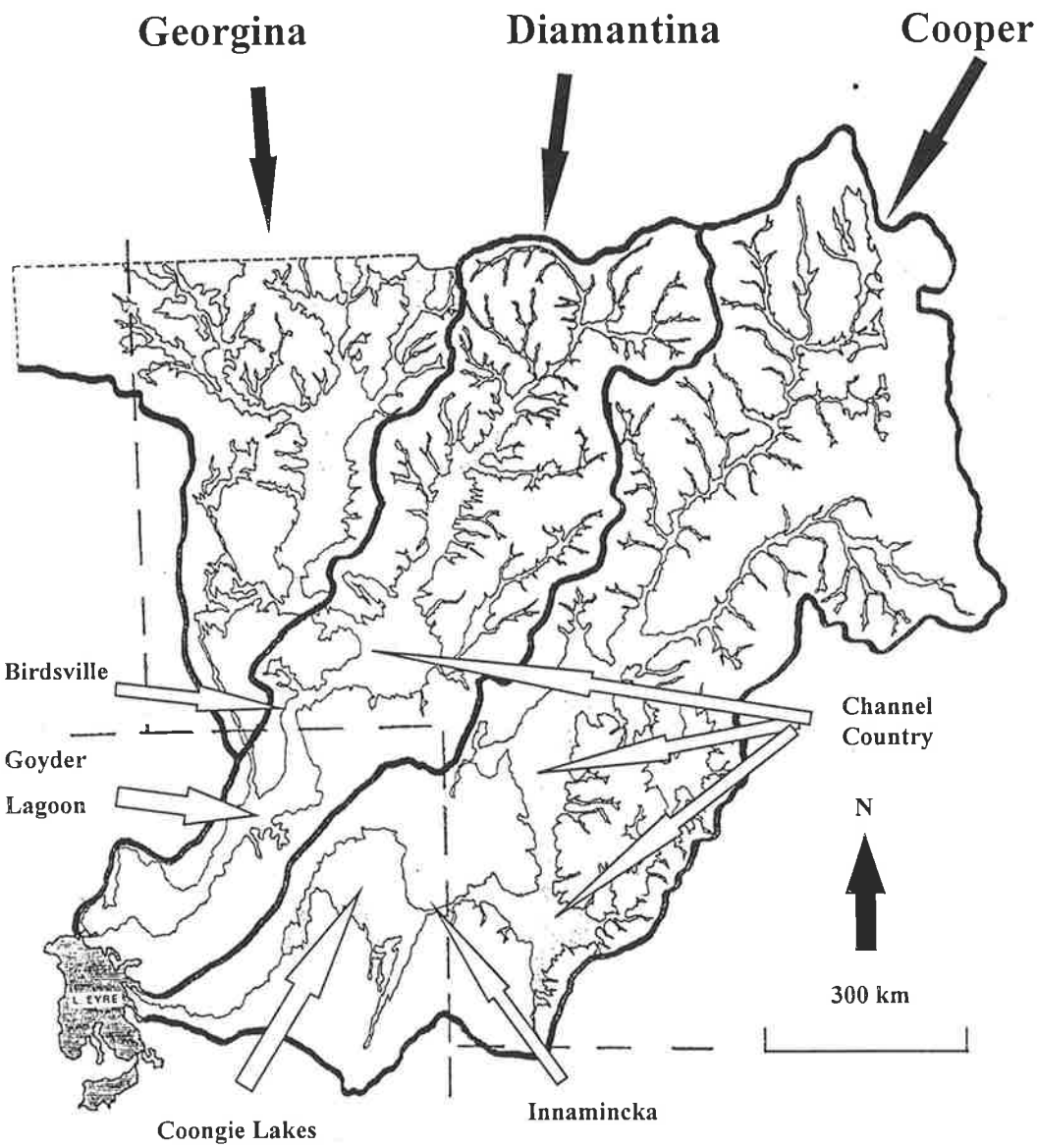


Figure 11 Cooper, Diamantina and part of the Georgina catchments showing areas of floodplain soils (after Graetz 1980)

3.3.2 Hydrology

Rainfall in the Lake Eyre Basin averages less than 400mm annually, and at least half of the basin averages less than 200mm (Kotwicki 1986). All rivers in the basin, including the largest, the Cooper and Diamantina/Georgina, have the majority of their catchments in the arid to semi-arid zones (Kotwicki 1986). Major flow events usually derive from southerly penetrations of the north Australian monsoon in late summer (Knighton & Nanson 1994a). Individual flow events differ in the relative contributions of arid and more humid areas of the catchments, but given the spatial variability of arid zone rainfall, most rivers derive substantial inputs from local falls in the arid zone (Kotwicki 1986, Allan 1985). Mean annual evaporation from a Class A pan is greater than 3m for all but the eastern margins of the basin. Mean annual runoff is only 2.8 mm in depth over the basin, or 1% of the mean annual runoff of all the land areas of the world (Kotwicki 1989).

The index value of variability of annual rainfall in the basin ((90th percentile-10th percentile)/50th percentile) is the highest in Australia (1.5-2.0, Kotwicki 1986), although there is a long-term pattern related to the ENSO cycle (Allan 1985). All streams are characterized by variation in discharge and flow duration (Kotwicki 1986), which Chapter 2 demonstrated is exceptional in a world context.

Transmission losses mean most rivers in the Lake Eyre Basin decline in discharge in their lower reaches (Knighton & Nanson 1994a) - the opposite to patterns in temperate and tropical systems (Falkenmark 1989). The Cooper and Diamantina/Georgina systems have the largest catchments in the basin, and have the largest and most sustained discharge (Kotwicki 1986). The Cooper and Diamantina/Georgina also appear to have the lowest overall gradients of the major Lake Eyre Basin rivers (Tetzlaff & Bye 1978).

None of the major rivers in the basin has been substantially modified hydrologically by impoundments, flow diversions, artificial levees or channelisation (Dayton 1994, Puckridge 1998), in contrast to the Murray-Darling (Walker *et al.* 1992, Cadwallader 1978, Sheldon & Walker 1993), and in fact to the majority of large rivers in Australia (Walker 1985). Hydrological patterns in the basin are therefore relatively unaltered.

3.3.3 The Fish Assemblage

The native fish assemblage of the Lake Eyre Basin (20 spp, 9 endemics) is not as rich as the Murray-Darling (approx. 33 spp., depending on how many estuarine species are included) (Merrick & Schmida 1984, Allen 1989, Glover 1990, McDowall 1996a). In the present state of taxonomic knowledge, the two basins share only five species, viz. *Hypseleotris klunzingeri*, *Retropinna semoni*, *Nematalosa erebi*, *Leiopotherapon unicolor* and *Neosilurus hyrtlii*. The Lake Eyre basin *Macquaria* populations were, until recently, considered to lie within the *M. ambigua* species of the Murray-Darling, but are now likely to be described as a distinct species (Musyl & Keenan 1992). Of the Lake Eyre Basin species, four -*Chlamydogobius* sp. nov., *Neosilurus* sp. nov. *Craterocephalus dalhousiensis* and *Scaturiginichthys vermeilipinnis* (Glover 1990, Ivantsoff *et al.*1991) - are confined to artesian springs. Glover (1990) describes 19 native species from the northeast deserts but one more - viz. *Ambassis mülleri* - must be added in the light of recent work (Allen 1989). The Lake Eyre hardyhead *Craterocephalus eyresii* appears to be confined to the more saline lower reaches of the rivers, *Amniataba percoides* has only been recorded in the western section of the Lake Eyre Basin, and a recent revision of the neosilurid group (Allen 1989) places *Neosilurus glencoensis* in synonomy with *N. hyrtlii*. Two introduced species - the mosquitofish, *Gambusia holbrooki* and the goldfish *Carassius auratus* are established in the Cooper (Puckridge & Drewien 1988), but in 1989, the Murray cod *Maccullochella peeli*, which is exotic to the Lake Eyre Basin, was introduced into the Thompson River in the headwaters of Cooper Creek in Queensland (Pierce 1990). The outcomes of this introduction have yet to become apparent.

The taxonomic status of many of the Lake Eyre Basin fish must be considered uncertain. The assemblage includes a number of putative cosmopolitan species, which may on further study be recognized as endemic. *Hypseleotris* in the Murray-Darling is now recognized as a species complex (Larson & Hoese 1996), and the same may be true of the Cooper Creek representatives. The Cooper neosilurids are still under revision (Allen 1989).

3.4 Cooper Creek

3.4.1 Geomorphology

The Cooper rises on the northern slopes of the Warrego Range, Queensland, and terminates in Lake Eyre (Fig 10). Its total length is 1523km, and total catchment area 306000 km^2. Even for a Lake Eyre Basin river, the Cooper has a very low stream gradient - 5.2 x 10^{-4} from the headwaters to the Barcoo-Thomson junction, and 1.7 x 10^{-4} from there to Lake Eyre.

The macromorphology of the river has five major features - the higher gradient headwaters drained by the principal tributaries, the Thomson and the Barcoo, which have relatively narrow floodplains (Figs10, 11), the anastomosing and braided system of the Channel Country, the constrained, high gradient channel through the silcrete tablelands upstream of Innamincka, the extensive, complex floodplain of the lower Cooper as it spreads through the dunefields of the Strzelecki Desert, and the terminal phase of river where the floodplain again contracts and the channel meanders across the low dunes of the Tirari Desert to Lake Eyre. A major distributary, Strzelecki Creek, splits from the Cooper immediately downstream of Innamincka, and flows south through the Strzelecki dunefields to its terminus in the Lake Blanche - Lake Callabonna complex (Fig. 12). Although flooded in large events by the Cooper, the Strzelecki can also flow from local rainfall (Drewien & Best 1992).

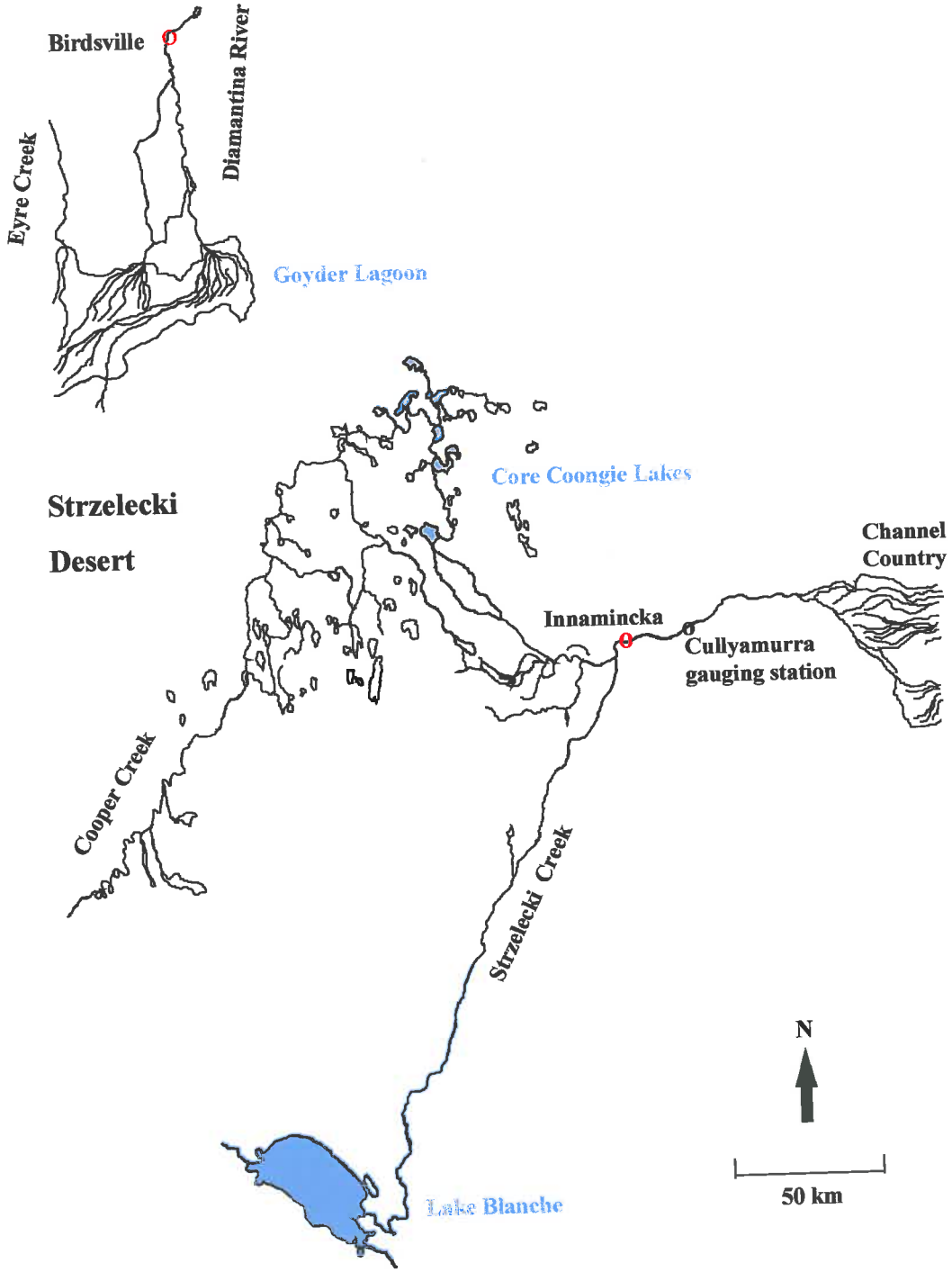


Figure 12 Major waterbodies on lower Cooper Creek and the Diamantina river.

Constriction of the Cooper as it flows through the tablelands at Innamincka (Figs 11, 12) sharply divides the Queensland Channel Country upstream from the complex floodplain in the Strzelecki and Sturt's Stony Deserts downstream. This floodplain is "interlaced with channels, billabongs and lakes, and intersected by lines of north-south dunes" (Kotwicki 1986 p.32). Braiding is also characteristic of some floodplain areas during high flows.

3.4.2 Hydrology

There are only three gauging stations with substantial records on the Cooper system - at Currareva, Nappa Merri and Innamincka (Fig. 10), and the first two were inactivated in 1988. Chapter 2 describes the discharge variability of the lower Cooper at Innamincka, where variability exceeds that upstream (Knighton & Nanson 1994a). Flow velocities are very low, at 3.1km/day being ¼ that of the Diamantina (Kotwicki 1986), and flow transmission times tend to be long, amounting to several months (Knighton & Nanson 1994a). Late summer is the main period of discharge maxima. Transmission losses are very high. Average annual flow at Currareva (catchment area 150,220 km^2) is 3.35 km^3 (SD 3.45), and at Cullamurra (catchment area 236,700 km^2) 2.06 km^3 (SD 3.63). Approximately 6km^3 of water was retained on the floodplain between Innamincka and Kopperamanna in 1974 (Kotwicki 1986), and for threshold flows above 25% duration, transmission losses exceed 75% over the Currareva-Nappa Merrie length (Knighton & Nanson 1994a). This is principally due to the area of floodplain inundated at such flows, since there is little infiltration loss (Rust & Nanson 1986).

3.4.3 Limnology

Table 8 Physico-chemistry of Cooper Creek at Cullyamurra waterhole over July 1978 to June 1983 (Glatz 1985)

Parameter	Temp (°C)	Conductivity (µS/cm at 25 °C)	pH	Dissolved Oxygen (ppm)	Turbidity (NTU)	Total Kjeldahl N	Total P
Mean	22.6	200	7.9	8.2	226	0.93	0.42
Range	13-30	70-820	7-8.9	5.8-10.8	110-360	0.72-1.12	0.25-0.91

The results in Table 8 were recorded in a permanent channel reach, probably the most physico-chemically stable habitat in the river, at intervals of 1-3 months (depending on the parameter measured). The results illustrate that even at this site, physico-chemical factors are highly variable. In the shallower, more ephemeral waterbodies typical of the Cooper catchment, waters are similarly warm, fresh, turbid, alkaline and nutrient-rich, but variability is more pronounced (see Coongie Lakes below).

3.4.4 Fish

The fish assemblage recorded for Cooper Creek consists of 15 native species in 10 families, and two exotics (Table 8, S.A. Museum records, Glover 1986, Puckridge & Drewien 1988, Ivantsoff *et al.* 1991, Glover 1990). Of the native species, the record for the leathery grunter *Scortum hillii* is doubtful (Glover 1990, Allen 1989), and the endemic red-finned blue-eye *Scaturiginichthys vermeilipinnis* has been recorded only from artesian springs (Unmack & Brumley 1991). The Cooper Creek tandan, *Neosilurus* sp., is endemic to the Cooper system. The records for the Channel Country in Queensland, which includes the middle and upper catchments of both the Cooper and Diamantina, give thirteen native species and two exotics (McFarland 1992). Of the native species in the Channel Country, four (the pennyfish *Denariusa bandata*, the barred grunter *Amniataba percoides*, the desert goby *Chlamydogobius eremius*, and the flathead goby *Glossogobius giurus*) do not appear to be present in the Cooper assemblage. To this list should be added the redfinned blue-eye *Scaturiginichthys vermeilipinnis*. However, the pennyfish, leathery grunter and flathead goby are not listed for the Lake Eyre Basin by either Allen (1989) or Glover (1990).

Table 9 Fish species recorded for the Cooper Creek system

Family	Taxon	Code
Native species		
Clupeidae	*Nematalosa erebi*	Neme
Retropinnidae	*Retropinna semoni*	Rets
Plotosidae	*Neosilurus hyrtlii*	Neoh
	Neosilurus argenteus	Neoa
	Neosilurus sp.	Neos
Atherinidae	*Craterocephalus eyresii*	Crae
Melanotaeniidae	*Melanotaenia splendida tatei*	Mels
Pseudomugilidae	*Scaturiginichthys vermeilipinnis*	
Ambassidae	*Ambassis mulleri*	Ambm
Percichthyidae	*Macquaria* sp.	Macs
Terapontidae	*Bidyanus welchi*	Bidw
	Leiopotherapon unicolor	Leiu
	Scortum barcoo	Scob
	Scortum hillii	
Gobiidae	*Hypseleotris* sp.	Hypk
Exotic species		
Cyprinidae	*Carassius auratus*	Cara
Poeciliidae	*Gambusia holbrooki*	Gamh

From the species distributions given in Allen (1989), one species (the bony herring *Nematalosa erebi*) is cosmopolitan, six species (the callop *Macquaria* sp. , Welch's grunter *Bidyanus welchi*, the silver tandan *Neosilurus argenteus*, the Cooper Creek tandan *Neosilurus* sp., the redfinned blue-eye *Scaturiginichthys vermeilipinis* and the desert rainbowfish *Melanotaenia splendida tatei*) are confined to central Australia, four species (the spangled perch *Leiopotherapon unicolor*, Hyrtl's tandan *Neosilurus hyrtlii*, Mueller's

glassfish *Ambassis mülleri*, the Barcoo grunter *Scortum barcoo*) have a tropical to central Australian distribution, and three taxa (the Australian smelt *Retropinna semoni*, the Lake Eyre hardyhead *Craterocephalus eyresii*, and the western carp gudgeon *Hypseleotris* sp.) have a central to temperate distribution.

There are at least two exotics established in the Cooper system: the mosquitofish *Gambusia holbrooki* and the goldfish *Carassius auratus*. Neither of these species yet forms a dominant element in the fish assemblage, and their ecological effects are probably small (Puckridge & Drewien 1988, Reid & Puckridge 1990).

3.4.5 Macroinvertebrates and zooplankton

The most intensive collections have been made in the Coongie Lakes system, and will be discussed below.

3.5 Lake Blanche

3.5.1 Hydrology and Geomorphology

The maximum flooded area of the lake is 73,333 ha, and its bed profile is shallow and uniform, but hundreds of low islands appear at low water levels (Drewien & Best 1992). Inundations of Lake Blanche derive principally from flows in Strzelecki Creek (Fig. 12). Flows reaching Lake Blanche from the Cooper probably occur only once every 10 - 15 years on average (Drewien & Best 1992), which makes Lake Blanche an extreme outlier of the Cooper system. The lake held water for at least 12 months after the 1990 flooding (Drewien & Best 1992). The Strzelecki also flows from local rainfall, and the frequency of fillings of Lake Blanche from this source and other local catchments is not known. However, "even minor flooding of the lake may create reasonably large areas of wetland" (Drewien & Best 1992 p. 18).

3.5.2 Limnology

The only data available are from brief surveys in August 1990 and February 1991, at the mouth of the Strzelecki. In August 1990, approximately two months after inundation, the lake was about 0.5m deep. The pH was 8.5, salinity 300-400 ppm. In February 1991, Lake Blanche was only a few centimetres deep. The Strzelecki mouth was still 1.3m deep,

but there was no flow except for transient seiche effects. The pH in the Strzelecki mouth at Lake Blanche had risen to 9.2 and salinity to 1870 ppm. The water column was weakly stratified and well oxygenated (10.4ppm) except for the bottom 0.2m, which was almost anoxic. Transparency (Secchi depth 18cm) was moderate for the Cooper system (Puckridge & Drewien 1992).

3.5.3 Biology

Aquatic vegetation in the Strzelecki mouth in February was limited to *Myriophyllum* sp. in the shallows, but there was considerable inundated floodplain vegetation, principally chenopods. The phytoplankton was not sampled. Fish samples were only taken in February, where the Strzelecki enters Lake Blanche. Seven species were collected: Bony herring *Nematalosa erebi*, Lake Eyre Basin callop *Macquaria* sp., Welch's grunter *Bidyanus welchi*, silver tandan *Neosilurus argenteus*, Hyrtl's tandan *N. hyrtlii*, spangled perch *Leiopotherapon unicolor* and larvae of western carp gudgeon *Hypseleotris klunzingeri*. Catches were dominated by juveniles, but spawning of bony herring and western carp gudgeon had recently occurred because larvae of both were present.

3.6 Coongie Lakes - the Principal Study Area

3.6.1 Climate

Mean monthly maxima at Moomba (130 km south of Coongie Lake) are 38-39°C over December – February and 19°C in July, while mean monthly minima are 22-24°C in December –February and 6°C in July (Mollenmans *et al.* 1984). Mean diurnal temperatures therefore range over approximately 15 °C in winter and summer, but the actual range can be 25°C, with summer temperatures sometimes reaching 50°C, and winter temperatures falling below 0 °C (Reid 1988). Potential evaporation rates reach 3.6m for an isolated class A pan, with a pan coefficient (or conversion factor to approximate evaporation from a real water surface) of 0.6 (Kotwicki 1986). These ranges of temperature and evaporation rates create a dynamic aquatic environment, placing great demands on the physiological tolerances, rates of growth and maturation of aquatic organisms.

3.6.2 Geology and Geomorphology

Two terrestrial units appear in the surficial geology of the study area (SADME Geology 1:250,000 map sheets) - the Strzelecki Dunefield of the core study area (the Coongie Lakes region), and and a broken gibber and boulder duricrust unit of principally Oligocene-Miocene age (Krieg *et al.* 1990) at the extreme downstream and upstream sites of the study area. The Cooper Creek system, interacting with these terrestrial units, has produced a variety of aquatic units at a number of scales relevant to this study. These units can be described as floodplain and permanent channel waterbodies. Those claypans and saltlakes which are at some time inundated by river flow (as distinct from direct rainfall) are most usefully considered part of the floodplain (*sensu* Chapter 1). These landforms are described in more detail below.

3.6.2.1 Stony Tablelands

The stony tablelands, which intrude into the study area upstream of Innamincka (Fig. 12), are remnants of the Mid-Jurassic to Cretaceous Eromanga basin - a silcrete land surface which has been dissected into cuestas and plateaus. The "Innamincka Dome," an Oligocene to early Miocene uplift of these sediments, represents a substantial barrier to the westward flow of the Cooper, and is responsible for the confined, stony, relatively high gradient channel (Cullyamurra Waterhole) upstream of Innamincka, where the river cuts through the dome (Fig. 11). This is the only example of such a channel morphology in the study area.

3.6.2.2.Gibber Plains

The gibber plains interact with the river system only at the northern extreme of the Coongie Lakes region, around Lake Maroopootanie (Fig. 13). The plains are the product of weathering of the Cretaceous silcrete capping of the stony tablelands. Deflation of these weathering products continues until the stony fragments form a protective layer over desert loams. Those shores of Lake Maroopootanie which intersect with the gibber differ from all other lakes shores in the presence of a scattered stony substratum.

3.6.2.3.Dunefields

Lake Eyre basin dune morphology and genesis have been described by Twidale and Wopfner (1990). The dunes of the northern Strzelecki Desert average 12-15m in height, occur at a spacing of 3-6 dunes per kilometre, and may individually extend for hundreds of kilometres. Convergences or Y-shaped junctions are common, usually open to the south. The surface sands, which are primarily of quartz grains, cover a clay core, and the interdunes are predominantly grey cracking clays, with sometimes a sandy veneer. The dunes tend to the NNW in the Coongie area, aligned with the prevailing wind, and so intersect the waterbodies from the SSE, forming serrated shores. The dunes are asymetrical in cross-section, usually with a gentle western - facing slope and a steep eastern flank. Downwind of major waterbodies, (on the NNW), the dunes tend to be low, poorly coordinated and white, and the shores smoother. With distance downwind of such waterbodies, the dunes become higher, more coherent and deeper in colour.

3.6.2.4.Aquatic units

Immediately downstream of Innamincka, a major distributary, the Strzelecki Creek, splits from Cooper Creek and extends 200 km southwest to lakes Blanche, Gregory, Calabonna and Frome (Fig. 12). Thirty km downstream of the Strzelecki bifurcation, a major anabranch, the Northwest Branch, splits from what is called the "Main Branch" of the Cooper, trends 130km to the northwest and then doubles back to the west and southwest in the arc of lakes known as 'the northern overflow', which ultimately rejoins the Main Branch and continues west towards Lake Hope and ultimately Lake Eyre (Reid & Puckridge, 1990). The region within this arc, and extending downstream to Lake Hope - an area of 1,980,000ha. (Gillen & Drewien 1993). - is floodplain (Graetz 1980), and is designated a site ("Coongie Lakes") under the Ramsar Convention.

This floodplain is a mosaic of more than 100 shallow lakes (Gillen & Drewien 1993), several internal deltas, swamps, numerous channels and other wetlands formed by the inundation of the dunefields of the northern Strzelecki Desert (Fig 12). Soils throughout are grey to red cracking clays, overlain on the southern and eastern shores of the lakes by sandy veneers. The clays are so fine as to preclude a significant hyporheos (A. Boulton, University of New England, pers. comm., 1991). Stony and gravel substrates are only extensive

upstream of Innamincka and downstream on the shores of Lake Maroopootanie – at the extremes of the study range.

The channel braiding characteristic of the Channel Country in the middle Cooper is less pronounced, and is replaced by channels often confined by dunes connecting the lakes (Gillen & Drewien 1993, Reid & Puckridge 1990). The "Coongie Lakes" are the more frequently flooded lakes in this mosaic (Reid & Puckridge 1990).

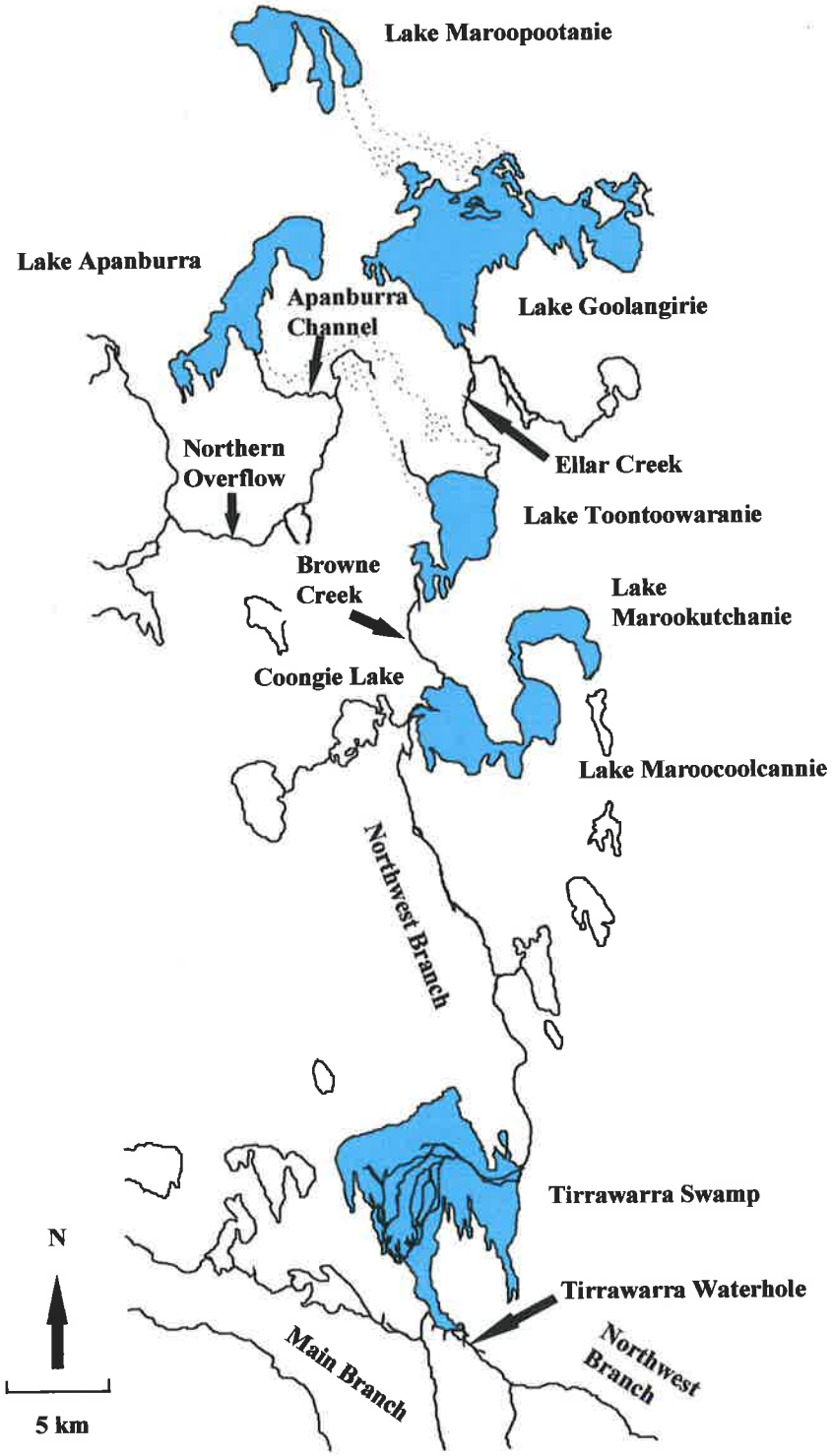


Figure 13 Coongie Lakes system core waterbodies

Within this floodplain, at the scale of reaches, geomorphic variety can be seen in the contrasts between the deep clay channel of the Northwest Branch (Frontispiece), the internal delta of Tirrawarra Swamp (Fig. 14), the string of channels of varying definition (Coongie Crossing Waterhole, Browne Creek, Ellar Creek, Apanburra Channel) connecting the floodplain lakes, the lakes themselves, e.g. Coongie (Fig. 15), Toontoowaranie (Fig. 16), Goolangirie (Fig. 17), Apanburra (Fig. 18), and Maroopootanie (Fig 19), and the mouth-deltas where the channels meet the lakes.



Figure 14. Tirrawarra internal delta.



Figure 15. Coongie Lake southern shore.



Figure 16. Lake Toontoowaranie western shore



Figure 17. Lake Goolangirie western shore



Figure 18. Lake Apanburra western shore



Figure 19. Lake Maroopootanie western shore

There is a strong interaction between the morphology of the dune system and river morphology. At the temporal scale of flow history, large floods may erode dunes, cut new channels through them and re-route the river. Dunes are also eroded where they intersect southeastern lake shores. On the other hand, floodplain flows may be channelled into interdune corridors, and lake profiles are strongly influenced by dune intersection. Characteristic lake profiles comprise a jagged south-eastern shore where mature dunes are migrating into the lake, and a smooth north-western shore where prevailing winds create strong wave action, and wind deflation prevails during dry phases.

This is a complex floodplain landscape, varying in attributes such as frequency, timing and duration of inundation, flow rates, balance of rainfall and river inputs, shoreline development, vegetation density and structure and water chemistry. The intricacy of inundation pattern and the dune topography provide for a high degree of landscape patchiness and density of edge or riparian effects/ecotones (Walker *et al.* 1995, Salo 1990, Gregory *et al.* 1991), which contribute to diversity of habitat (Reid & Puckridge 1990, Gillen & Drewien 1993). The numerous flow ponding areas provided by this landscape are likely to act as nutrient traps (*sensu* Stafford Smith & Morton 1990, Morton 1990), and

therefore as sites of high productivity and as drought refugia (Gillen & Drewien 1993, Briggs 1992, Morton *et al.* 1995).

The core sites in this study (with the exception of Lake Maroopootanie) are the more frequently inundated lakes, wetlands and associated channels in the Coongie Lakes system, but the study also extends upstream to channel sites immediately downstream and upstream of Innamincka.

3.6.3 Hydrology

As part of the Cooper floodplain, the Coongie Lakes region is subject to the exceptionally variable flow regime of Cooper Creek, described above. The closest station to the sampling area is at Cullyamurra Waterhole (Fig. 12). This record is for only 20 years, and has some doubtful data because of incidents of equipment failure. From the beginning of records at the gauging station at Cullyamurra in 1973 up to 1992, some flow occurred in the Cooper at Cullyamurra in each year (SA Engineering and Water Supply Dept, unpub. data) but not all flows reached the Coongie Lakes system. In most years, flows downstream of Innamincka are absorbed in the floodplain, and the terminus varies with flow volume, local rainfall conditions and waters remaining after previous floods. Because of the high spatial variability of rainfall events, localized flow events are common (e.g. Roberts 1988). The Northwest Branch, rather than the Main Branch, appears to take the bulk of flows, but this depends on shape and amplitude of the flow pulse arriving at the Main Branch - Northwest Branch junction (Allan 1988, Puckridge *et al.* 1999).

Flows into the Coongie Lakes system along the Northwest branch (Fig. 13) have not been reliably documented. Allan (1988), using a combination of historical anecdotes, gaugings from the Cullamurra station, records of flows further downstream in the system and 1987 observations of the discharge volume at Innamincka necessary to produce flows into the lakes, concludes that years in which no flows into the lakes occur at all are "rare indeed". Coongie Lake itself is rarely dry, but frequency of inundation of the lakes by the Cooper decreases along the course of the Northwest Branch (Reid & Puckridge 1990, Puckridge *et al.* 1999). However, inundation may occur in any part of the system from local heavy rainfall, and reaches of the system may flow independently of others (Roberts 1988). The variability of river flows and the erratic inputs from local rainfall make for complex

patterns of inundation in these waterbodies, which is reflected in the variety of their patterns of floodplain vegetation (Gillen & Drewien 1993).

Because of the low gradients and large storage capacity of the floodplain lakes, flows through the system may be very slow. A late summer/early autumn monsoon downpour in the headwaters of the Cooper produces an early winter flow at Coongie (Puckridge *et al.* 1999). In 1987, lags between the commencement of flows at Cullyamurra gauging station and at the Northwest Branch near Coongie Lake varied from one to two weeks, and peak depth in Coongie Lake lagged a further week. Lags between the lakes may be longer, with Goolangirie receiving peak flows up to three weeks later than Toontoowaranie. Peak depth in Goolangirie therefore was not reached until two-three months after the pulse passed Cullyamurra gauging station (Allan 1988, Puckridge *et al.* 1999). The delaying effects of the lake storages are exacerbated by the presence of shallow sills at the downstream margins of the lakes, probably built by prevailing onshore winds during periods of no flow. These sills prevent throughflow in the interconnecting channels until the lakes reach 1.5 - 2.0m in depth (Reid & Puckridge 1990). However the magnitude of timelags is likely to vary considerably with the shape and amplitude of the flow pulse, and with antecedent events in the system (Puckridge *et al.* 1999).

The low gradients and topographic relief in this region mean that shallow floodwaters spread very widely, and channels may be ill-defined, multiple or indistinguishable as geomorphic entities (Reid & Puckridge 1990). In terms of their hydrologic character, at different stages of a flow pulse backwaters become anabranches, swamps become lakes, anabranches become billabongs, lakes become channels. Permanent channel waterbodies are confined to deep reaches of the Main Branch and Northwest Branch, principally upstream of Coongie Lake (Fig. 13). Downstream of Coongie flows may spread in many directions (Puckridge *et al.* 1999).

The lakes system is characterized by great variability in timing, magnitude, frequency and duration of hydrological events within a given waterbody over time and between waterbodies in space at a given time. This situation provides an opportunity to compare the effects of various hydrological histories on fish assemblage ecology. It also presents problems, in that the complexity of the changes may confound interpretation, and the

magnitude of the events means some sites will dry up during any sampling program, making the record patchy.

3.6.4 Limnology

(Note EC = microSiemens/cm @ 25 °C)

The seasonal temperature structure in the lakes is determined by radiation inputs and wind strength. In summer, strong diel stratification occurs, particularly on calm sunny days - a tendency magnified by the high turbidity of the water. In winter, with reduced radiation inputs and more consistent strong winds, the lakes tend to be nearly isothermal (Allan 1988). This pattern is subject to considerable variation due to wind speed variation and cloud cover, and the summer stratification is always temporary. Thermal stratification can be extreme - up to 12°C drop over 1 m in the river channels- with surface temperatures up to 36°C and even 40°C in shallow lake margins (Glover 1982, Roberts, 1988). Winter water temperatures may fall below 10°C (Glover 1982).

In December 1986, physico-chemical measurements were taken in Coongie Lake and in the river channel immediately upstream, after a protracted period of low and zero flows (Roberts 1988). In the river channel, oxygen levels were very low (4 mg/l at the surface, 0.5-3.0 mg/l at the bottom), contrasting with uniformly high levels (8.5mg/l) in the lake itself . The river channel showed strong diurnal oxygen and temperature stratification during windless periods, whereas the lake showed only temperature stratification under similar conditions. In fact the lakes are characteristically better oxygenated throughout the water column than the channels, even during thermal stratification. In the river channels, flooding produces an isothermal water column which is also uniformly low in oxygen, and even brief flow events from local rain destratify the water column (Roberts 1988).

Records taken between July 1978 and June 1983 at Cullyamurra gauging station, 140km upstream of Coongie Lake, show high mean values for turbidity (226 NTU), total Kjeldahl nitrogen (0.93mg/l) and total phosphorus (0.42mg/l) (Glatz 1985). In December 1986 at the Coongie Lake - North-West Branch mouth, turbidities in both the river channel and the lake were very high (490-620 NTU, Secchi depth 4cm) due principally to high densities of fine clays (>1 micron diameter) and the gilvin levels were exceptionally low. In the river channel, conductivity varied from 280 to 190-214 EC, pH from 8.2 to 7.6-7.9, and

chlorophyll-a concentrations varied in the river channel from 9.3 - 26.4 microgm/l, principally in response to a local flow event. In the lake, conditions were more stable, with conductivity around 330 EC, ph 8.5, and chlorophyll-a varying between 20.1 and 18.5 microgm/l. Compared to 5-year mean values for the River Murray at Morgan (Glatz 1985), the river channel at Coongie Lakes in December 1986 had about ¼ of the conductivity, 5 times the turbidity, 3-4 times more total and soluble phosphorus and higher concentrations of all forms of nitrogen. Since the TN:TP weight ratio was 2.0-3.2 , algal production at that time was probably nitrogen limited (Roberts 1988). Although turbidities are high, these are unlikely to limit algal and zooplankton production, at least in the lakes, because of wind-induced turbulence (Roberts 1988, Geddes 1984).

Physico-chemical conditions in the Coongie Lakes system however are likely to be highly variable, particularly in water-bodies isolated from flow. During extended periods of zero flow, salinity and pH values increase overall (Roberts 1988), and gradients in these values also develop from the more to the less frequently flooded waterbodies (Allan 1988). Protracted regional flooding reduces values overall, and also levels all waterbodies to common values.

3.6.5 Aquatic vertebrates

The aquatic vertebrates of the Coongie Lakes region are not diverse compared to tropical systems like Kakadu (Bishop *et al.* 1986). However, compared to other arid zone systems, the assemblage is significant. The region supports eight frog species, including an undescribed species of *Cyclorana* (Reid & Puckridge 1990). The fish assemblage includes at least 12 of the 14 native species recorded for the Cooper catchment (Puckridge & Drewien 1988). Of the two species missing, one is the redfinned blue-eye, *Scaturiginichthys vermeilipinnis*, confined to springs in central Queensland (Ivantsoff *et al.* 1991), and the other is the Lake Eyre hardyhead, *Craterocephalus eyresii*, which in the Cooper is confined to reaches downstream of the Coongie region, often in higher salinity habitats.

3.6.6 Plankton and macroinvertebrates

Little is known of the microflora and microfauna of the Cooper. Twenty-eight samples of zooplankton taken in December 1986 from Coongie Lake and the adjacent

channel contained 41 rotifer species, 12 cladoceran species, 4 copepod species and 3 protozoan species (Roberts 1988), but another 18 taxa were identified only to genus. All taxa had been previously recorded in Australia, and as expected from the geographical position of Cooper Creek, there was strong overlap between tropical and temperate forms (Roberts 1988). The river channel showed a higher species richness than Coongie Lake itself, presumably because of the greater habitat complexity of the channel/backwater environment. Considering that these results were obtained from a single collection date at a restricted location, actual species richness in the Lower Cooper is likely to be high. No studies have been made of the phytoplankton, but high chlorophyll-a content in December 1986 and July 1987 indicated a high phytoplankton biomass at this site and time (Roberts 1988).

No comprehensive list of macroinvertebrate species is available for the Coongie Lakes region. In results of a survey which was not temporally replicated, the macroinvertebrate assemblage of the Coongie Lakes region was comparable in richness to the Murray, Darling and Goyder Lagoon on the Diamantina, but the Diamantina and Cooper had much higher evenness (Sheldon unpub.). A study replicated bimonthly through 1987 identified 46 macroinvertebrate families, but did not include determinations to family from the phylum Porifera or the class Arachnida (Table 9). An earlier survey recorded an additional taxon (Amphipoda) for Embarka Swamp on the Main Branch of the Cooper (Mollenmans *et al.* 1984).

Table 10 Macroinvertebrate taxa identified over 1986-87 in the Coongie Lakes system (Puckridge & Drewien 1988)

CLASS/SUB-CLASS	ORDER/SUB-ORDER	FAMILY/SUB-FAMILY	GENUS	SPECIES
BIVALVIA		CORBICULIDAE	Corbiculina	australis
		VELESUNIONINAE	Velesunio	wilsonii
GASTROPODA		THIARIDAE	Thiara	balonnensis
		ANCYLIDAE	Ferrissia	petterdi
		VIVIPARIDAE	Notopala	sublineata
		LYMNAEIDAE	Austropeplea	lessoni
		SUCCINEIDAE	Succinea	australis
		BITHYNIIDAE	Gabbia	australis
		PLANORBIDAE	Glyptophysa	gibbosa
			Glyptophysa	aliciae
			Isidorella	hainesii
OLIGOCHAETA		TUBIFICIDAE		
HIRUDINEA		GLOSSIPHONIIDAE		
		ORNITHOBDELLIDAE		
ARACHNIDA	ACARINA			
CRUSTACEA	ANOSTRACA	BRANCHIOPODIDAE	Branchinella	sp.
	NOTOSTRACA		Triops	australiense
	CONCHOSTRACA	CYCLESTHERIIDAE	Cyclestheria	sp.
		LIMNADIIDAE	Eulimnadia	sp.
		CYZICIDAE	Cyzicus	sp.
	DECAPODA	PALAEMONIDAE	Machrobrachium	australiense
		PARASTICIDAE	Cherax	destructor
		SUNDATELPHUSIDAE	Holthuisiana	transversa
INSECTA	(ANISOPTERA)	LIBELLULIDAE	Trapezostigma	loewi
			Diplacodes	melanopsis
			Orthetrum	caledonicum
	DIPTERA	CULICIDAE		
		CHIRONOMIDAE		
		STRATIOMYIDAE		
		SYRPHIDAE		
		EPHYDRIDAE		
	ODONATA	AESHNIDAE	Hemianax	papuensis
		GOMPHIDAE	Austrogomphus	australis
		CORDULIIDAE	Hemicordulia	tau
	(ZYGOPTERA)	LESTIDAE	Austrolestes	aridus
	COLEOPTERA	DYTISCIDAE	Cybister	tripunctatus
			Homeodytes	scutellaris
			Eretes	decempunctatus
			Necterosoma	australis
		GYRINIDAE	Dineutus	wollastoni
		HYDROPHILIDAE		
		(HYDROBIINAE)	Limnoxenus	sp.
			Sternolophus	marginicollis
		(HYDROPHILINAE)	Hydrophilus	sp.
		HALIPLIDAE	Haliplus	sp.
	EPHEMEROPTERA	BAETIDAE	Cloeon	sp.
		CAENIDAE	Tasmanocoenis	sp.
	HEMIPTERA	NEPIDAE	Laccotrephes	tristis
		NOTONECTIDAE		
		CORIXIDAE	Agraptocorixa	eurynome

Most widespread and most abundant families in the 1987 survey were the Notonectidae, Hydrophilidae, Dytiscidae, Chironomidae, Corixidae and Palaemonidae. The composition of the assemblage appeared to differ according to two major factors – (a) the duration of inundation by river waters, with rain-filled pools at one extreme and permanent river reaches at the other, and (b) a lotic-lentic axis, distinguishing channel and lake habitats. The less frequently flooded lake habitats further downstream were also less species-rich (Puckridge & Drewien 1988).

Sponges are common throughout the system, colonizing mussel shells and wood debris. Molluscs are also widespread, with *Velesunio wilsonii* particularly common in the lakes, and several gastropods - particularly *Austropeplea lessoni* and *Physastra gibbosa* - are abundant in the littoral zone of the channels. *Macrobrachium australiense* is the dominant crustacean in frequently flooded areas, but *Triops australiense*, *Branchinella* spp. and a variety of conchostracans are characteristic of the rain-filled pools.

3.6.7 Aquatic flora

Aquatic taxa have been given only cursory attention in terrestrial surveys. The variability of conditions is such that long-term collections are necessary. Also the paucity of permanent water, the long intervals of drying, the fluctuations in water level, current speed and channel morphology in those channel reaches which are permanent, and the turbidity of the waters, limit the development of aquatic macrophytes. Only seven strictly macrophyte species were found in a two-week survey of the immediate Coongie Lake environment in December 1986 (Roberts 1988). These included two Charophytes or stoneworts, and five vascular plant species. Seven taxa (*Hydrodictyon reticulatum*, *Spirogyra* sp., *Chara* sp., *Azolla filiculoides*, *Lemna disperma* and *Ludwigia peploides*, *Nitella* sp.) were restricted to the river channels and delta, one (*Cyperus gymnocaulos*) to the lake shore and delta, two (*Cynodon dactylon* and *Pseudoraphis spinescens*) to the delta alone, and one (*Myriophyllum verrucosum*) was found in all habitats. The two large green algae, *Spirogyra* sp. and *Hydrodictyon reticulatum* were mentioned because in parts of the river their abundance made them structurally similar to a bed of macrophytes. This small group of taxa, however, formed five distinct "communities", even though sometimes monospecific -

1) a "medium" (*sensu* Roberts 1988) sedgeland dominated by *Cyperus gymnocaulos*, characteristic of sandy soils in exposed positions, principally on the lake.
2) a short emerging herbfield dominated by *Myriophyllum verrucosum*, found on brown silt in protected areas such as lake embayments.
3) a submerged herb-like community, composed of one or more of the macro-algae, the Charophytes and submerged *M. verrucosum*.
4) a floating mat community, dominated by *Ludwigia peploides*, found on the surface of slow-moving and still water in protected areas.
5) a free-floating community, dominated by one or both of *Azolla filiculoides* and *Lemna disperma*, found on calm water surfaces with little current, forming dense aggregations downwind or amongst other communities.

This result suggests a relatively simplified physical structure underwater (Roberts 1988). However in the river channels, additional structural complexity and habitat diversity are provided by the sometimes dense tangles of fallen wood (Lloyd *et al.* 1991b). Also, another 28 floodplain herbs and forbs in 14 families were found during the same survey on islands and in the delta area of Coongie Lakes (Roberts 1988) and more species with semi-aquatic distributions have been found in the larger northeast region (Foale 1982, Mollenmans *et al.* 1984). These taxa are subject to frequent inundation, and form important aquatic habitat at different phases of flooding.

In fact, cluster analysis of the 28 associations of perennial species identified from the Coongie region over 1986/7 (Gillen & Reid 1988) allocated 16 associations to the floodplain/interdune environment, and 11 to the dune crests. Three of these associations comprise a "riverine complex" (more accurately described as a "riparian complex"), with *Eucalyptus coolabah*, *E. camaldulensis*, *Acacia stenophylla* and *A. salicina* as the dominant overstorey species, and *Muehlenbeckia florulenta*, *Sclerolaena intricata* and *Atriplex velutinella* as the dominant understorey species. The other 13 associations comprise a "floodplain complex", with *Halosarcia indica*, *Sclerolaena intricata*, *S. patenticuspis*, *S. bicornis*, *S. calcarata*, *S. lancuspis*, *Malacocera albolanata*, *Sporobolus mitchellii*, *Marsilea drummondii*, *Muehlenbeckia florulenta*, *Atriplex velutinella*, *A. eardleyi*, *Eragrostis australasica*, *E. dielsii*, *Chenopodium auricomum*, *Maireana coronata*,

Morgania floribunda, *Crinum flaccidum* and *Osteocarpum acropterum* as dominant species. Eucalypts, acacias, chenopods, grasses and *Muehlenbeckia* are the groups characteristic of these perennial riparian and floodplain associations.Ordination of the data also suggested a dominant influence of water relations over floristic composition (Reid & Puckridge 1990). Earlier studies identified six vegetation "components" in a "River Channels and Floodplains" "complex" (Social and Environmental Assessment 1980), and 26 floodplain "land systems", principally determined from vegetation (Mollenmans *et al.* 1984). The floristic complexity of the aquatic environment is therefore by no means limited to the macrophytes recorded above, or even to the phytoplankton assemblage. In fact widespread floodplain and riparian species like lignum (*Muehlenbeckia florulenta*) play a major role in determining aquatic habitat during inundation. The hydrological variability of the system means that water levels are constantly changing, and the whole range of floodplain vegetation therefore contributes at different times to aquatic environment complexity. This is true of all floodplain systems, but is probably more pronounced in those of the arid zone.

Analysis of vegetation associations based on annuals (principally grasses and daisies) unites the floodplain and interdune complexes isolated by the analysis of perennials, (presumably because both complexes are subject to inundation), and separates a complex of "riparian woodland on sand" and a "semi-aquatic" complex characterized by more frequent inundation (Gillen & Reid 1988).

Work specifically targeted at wetland vegetation in the Kanowana region immediately downstream of Coongie Lakes identified two major floristic complexes, one, comprising six associations, characterized dry lake beds and lake margins, the other, comprising eight associations, was located along channels, backwaters and on the floodplain (Gillen & Drewien 1993). This study, which combined annuals and perennials in the analysis, did not sustain the distinction between floodplain and channel complexes made by the analysis of Gillen & Reid (1988), and it introduced a new complex - that of dry lake beds and margins. However, since the Kanowana study dealt with a much larger number of lake sites, the latter result is not surprising. The absence of a channel-floodplain distinction is surprising,

and may be related to the scarcity of permanent or frequently flooded channels in the Kanowana region.

No systematic taxonomic or production studies of phytoplankton in the region have been done. Nutrient levels in the system are high (Glatz 1985, Roberts 1988) and the chlorophyll-a content in the 1986 survey was also high, indicating a high phytoplankton biomass (Roberts 1988). However, a major and perhaps dominant contribution to in-channel production may derive from shallow benthic blue-green algal films around the periphery of waterbodies (Bunn & Davies 1999).

3.7 Distribution, abundance and life-history characteristics of the fish of lower Cooper Creek

The fish of the lower Cooper are a subset of the Lake Eyre Basin assemblage. The taxa present in the Lake Eyre Basin assemblage but not in the Cooper are those principally confined to artesian springs (*Chlamydogobius* sp., *Neosilurus* sp., *Craterocephalus dalhousiensis* , *Scaturiginichthys vermeilipinnis*) and those recorded only in the upper Diamantina/Georgina (*Chlamydogobius eremius, Amniataba percoides).*

The following summary provides a context for the study of fish - hydrology relations pursued in Chapters 4-5, and so focusses on characteristics of the assemblage which are likely to reflect adaptations to hydrological conditions. Since the assemblage is little studied, the summary relies in many cases on information from the species' range outside the Lake Eyre Basin. Where even this is absent, the summary may rely on information about closely related taxa. Nevertheless, the information generates profiles against which some of the findings from Chapters Four and Five can be compared. The species profiles follow, in phylogenetic order, except that exotic species are listed last. Summaries of responses to hydrology, reproductive strategies (*sensu* McArthur & Wilson 1967, Southwood 1977, Greenslade 1983), reproductive guilds (*sensu* Flegler-Balon 1989) and reproductive life-styles (*sensu* Bruton 1989) are then given for all species together.

3.7.1 Distribution, abundance and life-histories of individual fish species.

Table 11 Distribution and life-history characteristics of the bony herring, *Nematalosa erebi*

The bony herring, *Nematalosa erebi* is the most abundant and widespread large species in the region. It combines high fecundity and early maturity with longevity. It is a mobile, colonizing species, tolerant of for high temperatures and salinities and is able to spawn independently of flooding. However, it is susceptible to low temperatures and to severe dermal fungal infections.

species	**Neme**
distribution	All drainages except SE coast, Tasmanian and SW coast drainage divisions (Merrick & Schmida 1984, Allen 1989)
abundance	Characteristically abundant (Bishop 1987, Puckridge & Drewien 1988, Puckridge & Walker 1990, Puckridge & Sheldon 1997)
size	Maximum total length in Murray 400-500 mm, weight 1.8kg (Lake 1967c, Puckridge & Walker 1990)
longevity	> 7 years in lower Murray (Puckridge 1988)
	Males may be first mature in Murray at 1 year and between 70 mm length (Lake 1967c) and 126 mm (Puckridge 1988)
spawning patterns	Spawns in lower Murray November - December at water temperatures of 18-20 C, apparently
	independently of flooding (Puckridge & Walker 1990)
ova and fecundity	Ova 0.8mm diameter, initially demersal and adhesive, fecundity up to 900,000 (Puckridge & Walker 1990)
amount of yolk	0.54 mm (Puckridge & Walker 1990)
TL at hatching	2.5-3.5 mm TL (Puckridge & Walker 1990)
TL at first feeding	
parental care	Open substrate spawner, non-guarding (Puckridge & Walker 1990)
maturity	Median total lengths at maturity in lower Murray = 159mm (males) and 199mm (females) (Puckridge & Walker 1990)
movement	Forms schools (Cadwallader 1977), migrates upstream/downstream (Bishop 1987, Puckridge & Drewien 1988,
	Mallen-Cooper & Brand 1991, Harris *et al.* 1992), diel inshore/offshore in Coongie Lakes (Reid & Puckridge 1990)
habitat	Warm, turbid, slow-flowing rivers or lakes (Llewellyn 1983)
tolerances	Tolerant of salinities in Lake Eyre Basin to at least 39 ppt (Ruello 1976)
	Temperature tolerance range 9-38 °C (Merrick & Schmida 1984), sensitive to low temperatures (Puckridge *et al*. 1989)
	Mean DO concentration at capture 4.0 ppm, minimum 0.2 ppm (Bishop 1987)
	Ph tolerance range 4.8-8.6 (Merrick & Schmida 1984)
diseases	Epidemics of dermal infections of *Saprolegnia parasitica* on the Murray (Puckridge *et al.* 1989),
	Achlya sp. on Cooper Creek (Puckridge & Drewien 1988)
	Gill infections of the protozoan ciliates *Chilodonella hexasticha* in central Australian streams (Langdon *et al*. 1985).

Table 12 Distribution and life-history characteristics of the Australian smelt, *Retropinna semoni*.

The Australian smelt *Retropinna semoni* is the most abundant and widespread small species. It has low fecundity, matures early and is short-lived. It is a colonist, tolerant of high temperatures and salinities, and spawns independently of flooding. It is susceptible to fungal infections and several parasites.

species	Rets
distribution	North-east coast, South-east coast, Murray-Darling and Lake Eyre drainage divisions (Merrick & Schmida 1984, Allen 1989)
abundance	Abundant in Murray-Darling (Llewellyn 1983) and Lake Eyre division (Reid & Puckridge1990)
size	Up to 10cm (Llewellyn 1983)
longevity	May live for 2 or more years (McDowall 1996b)
spawning patterns	Spawns in spring at minimum of 15°C (Lake 1967c) or 18°C (LLewellyn 1983) in the Murray-Darling drainage ,
	apparently independently of flooding (Hume et al. 1983).
ova and fecundity	Fertilized ova diameter 0.95mm, demersal and adhesive (Milward 1966), fecundity 100-1000 (McDowall 1996b)
amount of yolk	Initially fills the ovum (Milward 1966)
TL at hatching	4.6mm (Milward 1966)
TL at first feeding	
parental care	Open substrate spawner, non-guarding (McDowall 1996b)
maturity	Matures in the first year at 50-100 mm length (Cadwallader 1977)
movement	Schools near surface (Lake 1967c), moves upstream/downstream in the Lederderg River (Beumer & Harrington 1982)
	and the Murray (Mallen-Cooper & Brand 1991, Mallen-Cooper et al. 1992)
	Upstream movement October-November (Tunbridge 1988)
habitat preferences	Still and gently flowing waters (McDowall 1996b), lakes in the lower Cooper Creek (Puckridge & Drewien 1988).
tolerances	Salinities up to 35 ppt (Merrick & Schmida 1984), 4 day LC50 59 ppt (Williams 1987b)
	Upper temperature tolerance in the Lake Eyre Basin > 35 °C (Puckridge unpub. data),
	lower temperature tolerance in the Lerderderg River < 7 C (Beumer & Harrington 1982).
	Dissolved oxygen < 5.3ppm (Glover 1982)
diseases	*Saprolegnia* dermal infections (Whitley 1960, Jolly 1967), nematode, trematode and protozoan parasites (Beumer *et al.* 1982)

Table 13 Distribution and life-history characteristics of the silver tandan, *Neosilurus argenteus*.

The silver tandan, *Neosilurus argenteus* is widespread but not often abundant. It has low fecundity and large ova, like *N. hyrtlii*. It is a colonist, probably with high physiological tolerances. Like *N. hyrtlii*, it may migrate and spawn in response to flooding.

species	Neoa
distribution	Lake Eyre, Western Plateau, Bulloo-Bancannia, Timor Sea and Gulf of Carpentaria drainage divisions (Merrick & Schmida 1984).
abundance	Moderately common in lower Cooper Creek (Puckridge & Drewien 1988) less common in
	lower Diamantina (Puckridge & Sheldon 1997)
size	Maximum length >20 cm (Larson & Martin 1990)
longevity	
spawning patterns	
ova and fecundity	
amount of yolk	
TL at hatching	
TL at first feeding	
parental care	
maturity	
movement	Movement onto floodplain during flooding (Reid & Puckridge 1990)
habitat	In lower Cooper Creek system, prefers channel, swamp and backwater habitats rather than lakes (Puckridge & Drewien 1988)
tolerances	
diseases	

Table 14 Distribution and life-history characteristics of Hyrtl's tandan, *Neosilurus hyrtlii*.

Hyrtl's tandan, *Neosilurus hyrtlii* is widespread and sometimes abundant. It has low fecundity, large ova and matures relatively late. It probably has high physiological tolerances, but is subject to several parasitic diseases. It migrates and spawns in response to flooding.

species	**Neoh**
distribution	Lake Eyre, Gulf, Timor Sea, North-east Coast, North-west Cape, Bulloo-Bancannia, possibly northern
	Murray-Darling drainage divisions (Pollard *et al.* 1996)
abundance	Common throughout range (Pollard *et al.* 1996). Patchily abundant in lower Diamantina River (Puckridge & Sheldon 1997),
	relatively uncommon in lower Cooper Creek (Puckridge & Drewien 1988)
size	Maximum total length 240 mm (Bishop 1987), 400 mm (Pollard *et al.* 1996)
longevity	
spawning patterns	Spawning congregations and paired spawning behaviour over sand or gravel substrate during flooding,
	and probable repeat spawning per season with repeated floods (Orr & Milward1984),
ova and fecundity	Ova 2.6mm, demersal, non-adhesive (Orr & Milward 1984), fecundity = 4,000 (Bishop 1987)
amount of yolk	2.0 mm diam (Orr & Milward 1984)
TL at hatching	5.7-6.0mm (Orr & Milward 1984)
TL at first feeding	
parental care	Over gravel spawner, non-guarding (Orr & Milward 1984)
maturity	male 171 mm, female 201mm (Orr & Milward 1984)
movement	Upstream spawning migrations during peak flood flows in Queensland (Orr & Milward 1984), downstream spawning migration
	during early wet season flows in Northern Territory (Larson & Martin 1990)
habitat	In lower Cooper Creek system, prefers channel, swamp and backwater habitats rather than lakes (Puckridge & Drewien 1988)
tolerances	Mean DO concentration at capture 3.5 ppm, minimum 1.0 ppm (Bishop 1987)
diseases	Parasitic flatworm (Beumer *et al*. 1982) 3 species of tapeworms (Mackiewicz & Blair 1980) *Lernaea* spp. (Brown 1992)

Table 15 Distribution and life-history characteristics of the Cooper Creek tandan, *Neosilurus sp.*

The Cooper Creek tandan, *Neosilurus* sp. is uncommon and restricted in range. Like *N. hyrtlii* it probably has low fecundity, large ova and matures late. However, it doesn't appear to migrate during floods.

species	Neos
distribution	Cooper Creek catchment of the Lake Eyre drainage division (Allen 1989)
abundance	Uncommon in the lower Cooper (Puckridge & Drewien 1988)
size	Maximum total length at least 600 mm (Unmack 1996)
longevity	
spawning patterns	
ova and fecundity	Fecundity approx. 1000, ovum diam. 3 - 3.8 mm (Unmack 1996)
amount of yolk	
TL at hatching	
TL at first feeding	
parental care	
maturity	
movement	Sedentary in deep waterholes (Puckridge unpub. data, Unmack 1996)
habitat	Creeks, slow-flowing rivers, springs, bores and reservoirs (Allen 1989)
tolerances	Temperature tolerance range at least 12-32 °C (Unmack 1996)
diseases	

Table 16 Distribution and life-history characteristics of the Lake Eyre hardyhead, *Craterocephalus eyresii*

The Lake Eyre hardyhead *Craterocephalus eyresii* is confined to less frequently inundated river reaches, springs and bores. It may become abundant after large floods. It has small ova. It is a colonist, disperses on floodwaters, and has extremely high high salinity and temperature tolerances

species	Crae
distribution	Lake Eyre drainage division, west of the Flinders Ranges (Crowley & Ivantsoff 1990)
abundance	Not usually abundant (Ivantsoff & Crowley 1996, Puckridge & Sheldon 1997), episodically very abundant
	in extreme habitats (Ruello 1976)
size	Maximum length 96mm (Ivantsoff & Crowley 1996)
longevity	3 years (Merrick & Schmida 1984- probably *C. fluviatilis*)
spawning patterns	January-March (Larson & Martin 1990), *C. fluviatilus* spawns amongst aquatic plants (Cadwallader & Backhouse 1983)
ova and fecundity	Ova 1mm diameter (Llewellyn 1983), fecundity of *C. fluviatilis* 1200-1800 (Llewellyn 1979)
amount of yolk	
TL at hatching	*C. stercusmuscarum* 3.4 mm TL (Merrick & Schmida 1984)
TL at first feeding	
parental care	*C. fluviatilis* spawns amongst vegetation, non-guarding (Cadwallader & Backhouse 1983)
maturity	
movement	Disperse on floodwaters (Glover 1982, Ivantsoff & Crowley 1996)
habitat	Lakes, rivers and man-made bores and springs (Ivantsoff & Crowley 1996), in fresh to saline waters,
	over aquatic vegetation and gravel or sandy substrates (Larson & Martin 1990)
tolerances	Tolerates salinity to 110 ppt (Glover 1982)
	Temperature tolerance range at least 9 °C - 37 °C (Glover 1982)
	Tolerates dissolved oxygen < 6 ppm (Glover 1982)
diseases	

Table 17 Distribution and life-history characteristics of the desert rainbowfish, *Melanotaenia splendida tatei*.

The desert rainbowfish *Melanotaenia splendida tatei* is rarely abundant and has a patchy occurrence. Its fecundity is probably low and it may mature early and spawn repeatedly in a season. It colonizes locally during flooding. Its physiological tolerances are probably moderate. It may be susceptible to low temperatures and fungal infections.

species	**Mels**
distribution	Lake Eyre and Barkly Tableland drainages, including Lake Woods (Allen & Cross 1982)
abundance	Uncommon to moderately abundant in the Cooper Creek system (Puckridge & Drewien 1988)
size	7.5 - 8cm standard length (Allen & Cross 1982)
longevity	1-4 years (Allen & Cross 1982)
spawning patterns	Breeding probably when good rains fall (Larson & Martin 1990) although perhaps seasonally as well (Reid & Puckridge 1990).
	In aquaria, *M.s.inornata* spawns daily throughout summer (Crowley & Ivantsoff 1982).
	M.s.splendida may spawn in the wild throughout the year, although with reduced activity from April to August and an increase
	when temperatures and daylengths are increasing and later with rising waterlevels (Beumer 1979b)
	However, in south-eastern Queensland, spawning of *M.s.fluviatilis* (now a synonym for *M.fluviatilis* (Allen 1989)) is largely
	confined to October-November (Milton & Arthington 1984). Individual spawning events last several days, and rising water levels
	are not necessary (Milton & Arthington 1984)
ova and fecundity	Mature ova of *M.s inornata and M.s.splendida are both* 0.9mm, adhesive to plants by 20-30mm filaments (Beumer 1979b,
	Crowley & Ivantsoff 1982). *M.s.inornata* releases 60-100 ova per spawning (Crowley & Ivantsoff 1982)
yolk	
TL at hatching	3.1-3.7 mm (*M.s.inornata*) (Ivantsoff *et al.* 1988)
TL at first feeding	
parental care	*M.s.inornata* over vegetation spawner, non-guarding (Crowley & Ivantsoff 1982)
maturity	M.s.*splendida* matures at 36-40mm, at an age of < 1year (Beumer 1979b)
movement	M.s.*splendida* migrates upstream 2-3 wks after the onset of flooding (Beumer 1979b), schools >30 just below surface
	(Backhouse & Frusher 1980)
habitat	Rivers, small streams, rocky gorge pools, springs, bores, reservoirs (Allen & Cross 1982)
tolerances	Temperature range at least 12 -26 °C (Larson & Martin 1990)
	LD50s for maximum temperature tolerances of *M. s. splendida* (syn. *Nematocentris splendida*) are 34.4°C for adults, 31.4°C for
	juveniles (Beumer 1979b). *M. s. splendida* tolerates gradual increase in salinity up to 15.2 ppt. (Beumer 1979b).
diseases	*M. fluviatilis* prone to high incidence of protozoan and bacterial infection at low temperatures (Allen 1996a)

Table 18 Distribution and life-history characteristics of Müller's glassfish, *Ambassis mülleri*

Müller's glassfish, *Ambassis mülleri* is uncommon and restricted in occurrence. Its fecundity is moderate and it matures early. It may move into newly flooded areas, but not in large numbers. It tolerates a wide range of temperatures. It is probably susceptible to nematode infestation.

species	**Mels**
distribution	Lake Eyre and Barkly Tableland drainages, including Lake Woods (Allen & Cross 1982)
abundance	Uncommon to moderately abundant in the Cooper Creek system (Puckridge & Drewien 1988)
size	7.5 - 8cm standard length (Allen & Cross 1982)
longevity	1-4 years (Allen & Cross 1982)
spawning patterns	Breeding probably when good rains fall (Larson & Martin 1990) although perhaps seasonally as well (Reid & Puckridge 1990).
	in aquaria, *M.s.inornata* spawns daily throughout summer (Crowley & Ivantsoff 1982).
	M.s.splendida may spawn in the wild throughout the year, although with reduced activity from April to August and an increase
	when temperatures and daylengths are increasing and later with rising waterlevels (Beumer 1979b)
	However, in south-eastern Queensland, spawning of *M.s.fluviatilis* (now a synonym for *M.fluviatilis* (Allen 1989)) is largely
	confined to October-November (Milton & Arthington 1984). Individual spawning events last several days, and rising water levels
	are not necessary (Milton & Arthington 1984)
ova and fecundity	Mature ova of *M.s inornata and M.s.splendida are both* 0.9mm, adhesive to plants by 20-30mm filaments (Beumer 1979b,
	Crowley & Ivantsoff 1982). *M.s.inornata* releases 60-100 ova per spawning (Crowley & Ivantsoff 1982)
yolk	
TL at hatching	3.1-3.7 mm (*M.s.inornata*) (Ivantsoff *et al.* 1988)
TL at first feeding	
parental care	*M.s.inornata* over vegetation spawner, non-guarding (Crowley & Ivantsoff 1982)
maturity	M.s.*splendida* matures at 36-40mm, at an age of < 1year (Beumer 1979b)
movement	M.s.*splendida* migrates upstream 2-3 wks after the onset of flooding (Beumer 1979b), schools >30 just below surface
	(Backhouse & Frusher 1980)
habitat	Rivers, small streams, rocky gorge pools, springs, bores, reservoirs (Allen & Cross 1982)
tolerances	Temperature range at least 12 -26 °C (Larson & Martin 1990)
	LD50s for maximum temperature tolerances of *M. s. splendida* (syn. *Nematocentris splendida*) are 34.4°C for adults, 31.4°C for
	juveniles (Beumer 1979b). *M. s. splendida* tolerates gradual increase in salinity up to 15.2 ppt. (Beumer 1979b).
diseases	*M. fluviatilis* prone to high incidence of protozoan and bacterial infection at low temperatures (Allen 1996a)

Table 19 Distribution and life-history characteristics of the Lake Eyre Basin callop, *Macquaria* sp.

The Lake Eyre Basin callop *Macquaria* sp. is the second most abundant and widespread large species. Like *M. ambigua* it is probably late maturing, with buoyant ova and high fecundity. It tolerates high salinities, but is susceptible to parasitic infections. Juveniles colonize downstream on floodwaters, and adults migrate upstream on rising floods to spawn.

species	**Macs**
distribution	Widespread in Lake Eyre drainage (Musyl & Keenan 1992)
abundance	Usually abundant (Puckridge & Drewien 1988)
size	*M. ambigua* in Murray-Darling to 760mm and 23kg (Lake 1967c)
longevity	*M. ambigua* to 26 years (Harris & Rowland 1996)
spawning patterns	*M. ambigua* in the Murray-Darling spawn at >23°C providing there is an accompanying rise in water level (Lake 1967a).
	Without both of the above stimuli resorption of gonads occurs. Ovulation more complete with larger floods (Lake 1967c)
	Timing of spawning of *M. ambigua* flexible, and may occur between October and April in the Murray-Darling (Lake 1967d)
	M. sp. may spawn in response to inflows from local rains, as well as from regional flooding (Puckridge & Sheldon 1997)
ova and fecundity	Water hardened ova of *M. ambigua* in Murray-Darling 3.9 mm, semibuoyant, nonadhesive, fecundity of 2.3 kg. *M. ambigua*
	= 500,000 (Lake 1967c)
amount of yolk	*M. ambigua* 1.1 mm (Lake 1967b)
TL at hatching	*M. ambigua* 3.5-4.0 mm TL (Rowland 1996)
TL at first feeding	*M. ambigua* 5.2 mm TL (Rowland 1996)
parental care	*M. ambigua open substrate spawner,* non-guarding (Lake 1967a)
maturity	Female *M. ambigua* in the Murray-Darling at 4 years, females usually 1.4 kg (Lake 1967c),
movement	Adult *M. ambigua* in the Murray Darling undertake upstream spawning migrations on a rising flood (Reynolds 1983), Sept.-Dec.
	(Koehn & O'Connor 1990). Adult *M. ambigua* migrate downstream in June-July (Koehn & O'Connor 1990), juveniles migrate
	upstream in large numbers during all flow phases except falling waterlevel (Mallen-Cooper & Edwards 1990, Mallen-Cooper
	& Brand 1991, Harris *et al.* 1992). Larvae/juveniles of *M. ambigua* swept downstream January-April (Koehn & O'Connor 1990).
	Larval floodplain use depends on water quality (Gehrke 1990). Juvenile *Macquaria.* sp. in Cooper Creek colonize waterbodies
	downstream and on floodplain in a rising flood (Reid & Puckridge 1990).
habitat	Warm, turbid, slow inland rivers and floodplain lakes (Puckridge & Drewien 1988, Harris & Rowland 1996)
tolerances	Juvenile *M. ambigua* in Murray-Darling can survive temperatures of 4-37°C (Lake 1967c)
	Salinity tolerance of *Macquaria.* sp. in Lake Eyre Basin > 32 ppt (Glover 1982)
diseases	*M. ambigua* in Murray-Darling parasitized by 3 protozoans, 2 flatworms, nematodes
	and the copepod *Lernaea cyprinacea* (Ashburner 1970, Robinson 1982, Beumer *et al.* 1982)

Table 20 Distribution and life-history characteristics of Welch's grunter, *Bidyanus welchi*

Welch's grunter *Bidyanus welchi* is a moderately abundant and widespread large species . Like *B. bidyanus* it is probably long-lived, late maturing, with buoyant ova and moderate fecundity. It has lower salinity tolerance than *M. ambigua*, and is susceptible to dermal fungal infections. Adults probably migrate upstream on rising floods to spawn

species	**Bidw**
distribution	The Lake Eyre and Bulloo-Bancannia drainage divisions (Merrick & Schmida 1984,
	Puckridge & Drewien 1988, Puckridge & Sheldon 1997)
abundance	Widespread and moderately common in the Lake Eyre drainage (Puckridge & Drewien 1988, Puckridge & Sheldon 1997)
size	Up to 350 mm and 1.5 kg (Merrick 1973, Lake 1978 p.137)
longevity	*B. bidyanus* in the Murray-Darling has been aged to 27yrs (Merrick 1996)
spawning patterns	Spawning is associated with summer flooding (Merrick & Schmida 1984)
ova and fecundity	Water-hardened ova (1.8-2.0 mm diameter) buoyant (pelagic), non adhesive (Merrick & Midgley 1976),
	fecundity up to 100,000 (Lake 1978).
amount of yolk	1.14 mm diam. in *B. bidyanus* (Lake 1967b)
TL at hatching	3.6 mm TL in *B. bidyanus* (Lake 1967b)
TL at first feeding	5.7 mm TL in *B. bidyanus* (Lake 1967b)
parental care	*B. bidyanus* open substrate spawner, non-guarding (Lake 1967a)
maturity	Males mature at approx. 240 mm, females at 280 mm (Lake 1978)
movement	Adult *B. bidyanus* in the Murray Darling undertake upstream spawning migrations on a rising flood (Reynolds 1983),
	September - December (Koehn & O'Connor 1990)
	Juveniles also move upstream (Mallen-Cooper & Brand 1991)
habitat	Warm, turbid lakes and slow-flowing rivers (Puckridge & Drewien 1988, Puckridge & Sheldon 1997)
tolerances	*B. bidyanus* temperature range 2 - 38 °C (Lake 1967c)
	Tolerates salinities up to 10 ppt (Glover & Sim 1978), temperatures down to 10.5 °C (Merrick 1973)
diseases	*B. bidyanus* has a dermal fungus infection in early summer in the Murray-Darling (Lake 1967d)

Table 21 Distribution and life-history characteristics of the Barcoo grunter, *Scortum barcoo*.

The Barcoo grunter *Scortum barcoo* is a relatively uncommon and patchily occurring large species. It is probably long-lived, late maturing and with moderate fecundity. Spawning appears to be linked to flooding. It is tolerant of high temperatures.

species	Scob
distribution	Lake Eyre, Bulloo-Bancannia, Western Plateau and Gulf drainage divisions (Merrick & Schmida 1984)
abundance	Not locally abundant and patchy in distribution (Merrick & Barker 1975, Merrick & Schmida 1984)
size	Up to 350mm (Merrick & Schmida 1984)
longevity	
spawning patterns	After summer flooding with temperature 21-28 °C (Merrick & Schmida 1984)
	after wet season flooding in Northern Territory (Martin & Larson 1990)
ova and fecundity	Estimated at 50,000 (Lake 1978)
amount of yolk	
TL at hatching	
TL at first feeding	
parental care	
maturity	Females mature at 250 mm (Lake 1978)
movement	
habitat	Deep billabongs (Larson & Martin 1990)
tolerances	Temperatures up to 40 °C (Lake 1971)
diseases	

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Table 22 Distribution and life-history characteristics of the spangled perch, *Leiopotherapon unicolor*

The spangled perch *Leiopotherapon unicolor* is widespread but not usually abundant. It is early maturing with small ova and high fecundity. It tolerates high salinities, high temperatures and low oxygen concentrations, but it does not tolerate low temperatures, and may develop fungal infections on exposure to cold. It colonizes widely on even brief flows, and undertakes upstream spawning migrations. However flooding is not essential for spawning.

species	**Leiu**
distribution	South-east Coast, North-east Coast, Gulf, Timor Sea, Indian Ocean, Bulloo-Bancannia, Western Plateau, Lake Eyre
	and northern Murray-Darling drainage divisions (Merrick & Schmida 1984)
abundance	Varies from very abundant (Glover & Sim 1978), common (Bishop 1987) to uncommon (Puckridge & Drewien 1988,
	Puckridge & Sheldon 1997).
size	Maximum fork length 236mm (Bishop 1987), rarely exceeds 340 gm (Lake 1967c), may reach 567 gm (Llewellyn 1973).
longevity	
spawning patterns	Spawning in ponds when surface temperatures reached 26 C, bottom temperatures 20 C. Flooding not essential (Llewellyn 1973).
	Spawning in the Black-Alice system of northern Queensland well-defined in December-February, with increasing temperatures
	and daylength, and perhaps triggered by rising water levels (Beumer 1979b)
ova and fecundity	Ova 0.67-0.81 mm, demersal and non-adhesive, fecundity of 65gm fish 113,200 (Llewellyn 1973), mean fecundity
	for a population 16,000-24,000 (Beumer 1979b)
amount of yolk	0.56 mm diam (Llewellyn 1973)
TL at hatching	1.5-2.4 mm TL (Beumer 1979b)
TL at first feeding	
parental care	No substrate preference for spawning, non-guarding (Llewellyn 1973)
maturity	Males from 34 mm, females from 33 mm at 1 year (Beumer 1979b).
movement	Upstream migration on falling flows (Bishop 1987). Swim rapidly through flash floods over considerable distances in very
	shallow water (Lake 1967c), and so disperses widely in arid environments (Glover 1982).
	In north Queensland, undertakes upstream spawning migration during floods (Beumer 1979b).
habitat preferences	Hydrologically less predictable habitats (Bishop 1987), rivers, springs, bores, dams and reservoirs (Glover 1982).
tolerances	Maximum temperature tolerance 44 °C (Glover 1982), minimum 5 °C (Lake 1967c), LD50 maxima and minima 39 and 5.3 °C
	(Llewellyn 1973) LD50 maxima 41.8 °C for adults, 35.5 °C for juveniles (Beumer 1979a).
	Adults and juveniles survive gradual acclimation to salinity of 35 ppt (Beumer 1979a)
	Mean DO concentration at capture 4.5 ppm, minimum 0.2 ppm (Bishop 1987) minimum 1.0 ppm (Glover 1982)
diseases	Tends to develop fungal infections at temperatures below 10 °C (Lake 1967c)

Table 23 Distribution and life-history characteristics of the western carp gudgeon, *Hypseleotris klunzingeri*

In the Murray-Darling Basin the western carp gudgeon *Hypseleotris klunzingeri* is sympatric with the similar undescribed congeners Midgley's carp gudgeon and Lake's carp gudgeon (Larson & Hoese 1996). Since these congeners have not yet been recorded for the Lake Eyre Basin, this thesis will describe the taxon as *H. klunzingeri*. The western carp gudgeon is the second most abundant and widespread small species in the region. It has high fecundity, early maturity and is short-lived. It tolerates high salinities, but is susceptible to some parasitic infections. Although flooding is not necessary for spawning, it may spawn more intensely (or repeatedly) in response to flooding.

species	**Hypk** *(All data on life history must be qualified by the possibility that small numbers of sympatric Hypseleotris sp. 4 and Hypseleotris sp. 5*
	were present in samples).
distribution	North-east Coast, south-east coast, Murray-Darling and Lake Eyre drainage divisions (Glover 1990, Merrick & Schmida 1984,
	Larson & Hoese 1996)
abundance	Locally common (Puckridge & Drewien 1988, Lloyd & Walker 1986)
size	Reaches 45 mm total length (Larson & Hoese 1996)
longevity	
spawning patterns	Spawns in late spring-early summer (Anderson *et al*. 1971) at temps > 22.5 °C in shallows, ova deposited on plants, flooding not
	necessary (Lake 1967a, c). May spawn more intensely (or repeatedly) when flooding occurs (Lloyd *et al.* 1991a)
ova and fecundity	Water hardened ova 0.44-0.53 mm, fecundity 1000-2000 (Lake 1967c), demersal, transparent (Lake 1967b)
	Ova adhesive (Cadwallader & Backhouse 1983)
amount of yolk	0.26-0.35 mm (Lake 1967a)
TL at hatching	1.94 mm (Lake 1967a)
TL at first feeding	3.4 mm TL (Lake 1967a)
parental care	Vegetation spawner, non-guarding (Lake 1967a)
maturity	Mature at 30 cm total length, age 1 year (Lake 1967a, Hoese *et al.* 1980)
movement	Congregates in large schools below dams and weirs (Merrick & Schmida 1984)
habitat	Turbid slow-flowing river channels and swamps, but also inhabits open water in lakes (Puckridge & Drewien 1988).
	Associated with dense vegetation (Llewellyn 1983, Larson & Hoese 1996)
tolerances	4 day LC50 for salinity 38 ppt (Williams 1987b)
diseases	May be infected by a flatworm and several nematodes (Beumer *et al.* 1982)

Table 24 Distribution and life-history characteristics of the goldfish, *Carassius auratus*.

The introduced goldfish, *Carassius auratus* is widespread but not usually abundant. It is long-lived and early maturing with small ova and high fecundity. It tolerates low oxygen levels and a wide range of temperatures, but is subject to several parasitic diseases. Although it may make upstream movements, spawning appears to be independent of flooding.

species	Cara
distribution	North-east Coast, South-east Coast, Tasmanian, Murray-Darling, South Australian Gulf, Western Plateau, South-west Coast,
	Lake Eyre drainage divisions (Merrick & Schmida 1984, Puckridge & Drewien 1988)
abundance	Locally abundant (Merrick & Schmida 1984), common in quiet backwaters, billabongs and lakes (Cadwallader & Backhouse 1983)
size	Up to 400 mm and 1 kg (Brumley 1996)
longevity	At least 10 yrs in South Australia (Mitchell 1979)
spawning patterns	Spawning November-January in NSW (LLewellyn 1983), October-January (Merrick & Schmida 1984), spring-summer at
	temp. > 15 °C (Lake 1967c)
ova and fecundity	Ova (1mm), dermesal, adhesive, attached to aquatic plants (Lake 1967c, Merrick & Schmida 1984)
	Fecundity 160,000-380,000 (Cadwallader & Backhouse 1983)
amount of yolk	
TL at hatching	
TL at first feeding	
parental care	Spawns in vegetation, non-guarding (Cadwallader & Backhouse 1983)
maturity	1 year at 30-50 mm (Merrick & Schmida 1984)
movement	Migrate upstream in Murray-Darling (Mallen-Cooper & Edwards 1990), increased movements during flooding, without a clear
	directional component (Harris *et al.* 1992)
habitat	Slow flowing rivers, still waters (Lake 1967c), weedy sites (Cadwallader & Backhouse 1983)
tolerances	Can tolerate low DO concentrations, lower critical temperature range 0-16 °C, upper critical range 30-42 °C
	(Cadwallader & Backhouse 1983)
diseases	May be infected with 2 protozoans and several flatworms (Ashburner & Ehl 1973, Beumer *et al.*1982)

Table 25 Distribution and life-history characteristics of the mosquitofish, *Gambusia holbrooki*

The introduced mosquitofish, *Gambusia holbrooki* is widespread and in sheltered habitats sometimes abundant. It is short-lived, ovoviviparous and early maturing. Although numbers per brood are low, there are multiple broods per season. It is tolerant of extreme temperatures, low oxygen concentrations and high salinities. It is subject to a number of parasitic infections. It colonizes newly flooded waterbodies. Spawning is independent of flooding. .

species	Gamh
distribution	North-east Coast, South-east Coast, Murray-Darling, South Australian Gulf, South-west Coast, Timor Sea, Lake Eyre and
	Western Plateau drainage divisions (Merrick & Schmida 1984)
abundance	May develop pest densities (Allen 1982), usually but not invariably abundant (Puckridge & Drewien 1988).
size	Maxima 35 mm (males), 60 mm (females) (McDowall 1980)
longevity	Up to third summer (Lloyd *et al.* 1986).
spawning patterns	Ovoviviparous, up to 9 batches of young per year with peak activity in spring. Breeding season in southern
	Queensland October to April (McDowall 1996c)
Fecundity	50-300 young per brood (McDowall 1996c)
TL at hatching	5-8mm TL (Lloyd *et al*. 1986)
TL at first feeding	5-8mm TL (Lloyd *et al*. 1986)
parental care	Ovoviviparous bearer
maturity	Females mature at 4-6 wks, at 18-20 mm SL, males at 17-23 mm SL at 4 wks (Lloyd *et al*. 1986)
movement	Colonizes downstream during floods (Puckridge & Drewien 1988)
	Merrick & Schmida 1984, Lloyd *et al.* 1986),
habitat	Warm, slow-flowing waters, congregates among aquatic vegetation near banks, particularly disturbed environments
	(Merrick & Schmida 1984, Lloyd *et al.* 1986)
tolerances	Temperature range 0.5-44 °C (Lloyd *et al.* 1986, McDowall 1996c)
	Salinities from freshwater to > 30 mg/l (Chessman & Williams 1974), LC50 58.5 mg/l (Chervinski 1983)
	Even if denied access to the water surface, can survive at oxygen concentration of 1.3 mg/l (Odum & Caldwell 1955)
diseases	Parasites include mussel glochidia (Walker 1981), brain and body-cavity parasites and a protozoan (Lloyd *et al*. 1986)

3.7.2 Reproductive strategies, guilds and life-styles of the Cooper Creek and Magela Creek fish assemblages.

The Magela Creek fish assemblage is chosen to contrast with that of the lower Cooper Creek because Magela Creek, in the wet/dry tropics, has a more predictably varying hydrology. Timing and especially magnitudes of flows fluctuate far less than in the Cooper Creek system (Bishop 1987). Further, the reproductive characteristics and migratory behaviours of the assemblage of Magela Creek have been well studied (Bishop 1987). However, the following discussion is based, for the Cooper Creek system, on incomplete data, and provides only provisional tests of the above hypotheses.

3.7.2.1. Reproductive strategies

The Cooper Creek fish assemblage might be expected to exemplify *r*-selection (*sensu* McArthur & Wilson 1967, Southwood 1977) and *A*-selection (*sensu* Greenslade 1983). However, from estimates of maximum fecundity, maximum length, age at sexual maturity and longevity, and considering the native assemblage alone (Table 26), species with *K*-selected traits are slightly more numerous (39% r-selected, 46% *K*-selected) and there is one species (bony herring, *Nematalosa erebi*) with both *r* and *K*- selected traits. *Nematalosa erebi* is also the dominant large species. The influence of *A*-selection (for example in traits such as ability to aestivate) is not apparent. The latter result may indicate that although Cooper Creek is hydrologically unpredictable, there are sufficient refugia to allow fish to evade adverse conditions.

By comparison, the Magela Creek assemblage might be expected to show a greater proportion of *K*-selected strategies. Data on longevity and maximum fecundity are not available for this assemblage, so data on average fecundity, maximum length and AFM must be used (Table 27). From these data it appears that *K*-selection (36%) does further exceed *r*-selection (23%) for this assemblage, but the most notable difference from the Cooper Creek assemblage is the high frequency of combinations of *r* and *K* selected traits (41%). Overall, the predictably variable Magela Creek system appears to favour a greater frequency of *K* –selection, but the Cooper Creek assemblage does not show the dominance of r-selected traits that theory would suggest for an unpredictably variable system. Inference from these findings must be tentative, given the limitations of

the data (particularly for the Cooper) and the comparison between only two rivers. With these qualifications however, it does appear that **Hypothesis 1.8 (a)**, that *fish assemblages of hydrologically unpredictable rivers have predominantly K-selected life histories,* is not rejected for Cooper Creek.

3.7.2.2. Reproductive guilds

Of the six major reproductive guilds identified for fish (Flegler-Balon 1989), only one (A1) is apparent in the native assemblage of Cooper Creek (Table 25). Low parental behavioural investment in offspring seems to be a typical assemblage trait. For the Magela Creek assemblage, data on yolk diameter, TL at hatch and TL at first feed are not available. However on the basis of the available data, three of the six reproductive guilds are represented, and 39% of the native species make a relatively high behavioural investment in offspring. This contrast between the two assemblages in the frequency of high parental behavioural investment in offspring seems appropriate given that the greater predictability of the Magela Creek environment would provide a more secure recruitment return on such investment. Despite the limitations of these data therefore, it appears that **Hypothesis 1.8 (b),** that *fish assemblages of hydrologically unpredictable rivers have predominantly precocial reproduction* is rejected for Cooper Creek.

3.7.2.3. Reproductive life-styles

Precocial and altricial reproductive life-styles have been related to a specialist - generalist polarity (Bruton 1989). From a comparison of the epigenetic characters associated with precocial vs altricial lifestyles, the native species of the Cooper Creek system appear about equally divided between the extremes (Table 25): altricial 46%, precocial 46%, altricial-precocial 8%. In the Magela Creek system, of those species for which the data justify categorization, altricial life-styles represent 39%, precocial 44%, and altricial-precocial 17%. The Magela Creek assemblage shows a slightly higher incidence of high parental physiological investment in offspring, as would be expected from the result (above) for behavioural investment. However, the difference is small given the disparity in environmental predictability between the two systems. Again the limitations of the data preclude a definitive finding, but it appears that **Hypothesis 1.8 (c),** that *fish assemblages of hydrologically unpredictable rivers have predominantly high parental investment in offspring* is not rejected for Cooper Creek.

Table 26 Reproductive strategies, guilds and life-styles in fish of the Cooper Creek system (AFM = Age at First Maturity, TL = Total Length).

Reproductive strategies (*sensu* McArthur & Wilson 1967, Southwood 1977, Greenslade 1983), reproductive guilds (*sensu* Flegler-Balon 1989) and reproductive life styles (*sensu* Bruton 1989) (1) medians given of range measurements (2) max. length, AFM, longevity given for females where sex is known											
Taxon	Maximum fecundity	Max. length (mm)	AFM (yrs)	Longevity (yrs)	Ovum diam. (mm)	Yolk diam. (mm)	TL at hatch (mm)	TL at first feed (mm)	Reprod. strategy	Reproductive guild	Reproductive life style
Neme	900,000	460	1	>7	0.8	0.54	3		r-k	Non guarding, open substrate (A1)	Altricial
Rets	1000	100	1	2	0.95	approx 0.9	4.6		r	Non guarding, open substrate (A1)	Altricial
Neoa		200		moderate					k?	?	Precocial?
Neoh	4000	240		moderate	2.6	2	5.85		k	Non guarding, open substrate (A1)	Precocial
Neos	1000?	600		long?	3-3.8				k?	?	Precocial?
Crae	1800	96		3	1		3.4		r	Non guarding, open substrate (A1)	Altricial
Mels	100	80	1	4	0.9		3.4		k	Non guarding, open substrate (A1)	Altricial-Precocial
Ambm	2400	80	1	short	0.7		2	2.25	r	Non guarding, open substrate (A1)	Altricial
Macs	500,000	760	4	27	3.9	1.1	3.8	5.2	k	Non guarding, open substrate (A1)	Precocial
Bidw	100,000	350	5	27	1.9	1.14	3.6	5.7	k	Non guarding, open substrate (A1)	Precocial
Scob	50,000	350		long					k	?	Precocial
Leiu	113,000	240	1	moderate	0.74	0.56	2		r	Non guarding, open substrate (A1)	Altricial
Hypk	2000	45	1	1-2 ???	0.49	0.31	1.94	3.4	r	Non guarding, open substrate (A1)	Altricial
										?	
Cara	380,000	400	1	10	1				r-k	Non guarding, open substrate (A1)	Altricial
Gamh	300	60	0.1	2	Ovoviviparous		5.8	5.8	r	Bearer, internal (C.2)	Precocial

Table 27 Reproductive strategies, guilds and life-styles of fish of the Magela Creek. (Data from Bishop 1987, Larson & Martin 1990, Allen 1989)

Taxon	Average fecundity	Maximum length (mm)	AFM (yrs)	Ovum diam. (mm)	Reprod. strategy	Reprod. guild	Reprod. lifestyle
Megalops cyprinoides	10,000	410	1		r-k	non-guarding, open substrate (A1)	altricial
Nematalosa erebi	13,200	340	1	small	r-k	non-guarding, open substrate (A1)	altricial
Scleropages jardini	172	690	3.5	large	k	external bearer (C1)	precocial
Arius leptaspis	140	600	2	large	k	external bearer (C1)	precocial
Arius graeffei	140	395	2	large	k	external bearer (C1)	precocial
Anodontiglanis dahli	8000	490	1		r-k	non-guarding, open substrate (A1)?	?
Neosilurus ater	7890	460	1	medium, demersal	r-k	non-guarding, open substrate (A1)?	precocial
Neosilurus hyrtlii	3630	242	1	large	k	non-guarding, open substrate (A1)	precocial
Porochilus rendahli	900	195	1	small	r-k	non-guarding, open substrate (A1)?	precocial-altricial
Strongylura kreffti	400	640	2	adhesive?	k	non-guarding, open substrate (A1)?	precocial
Melanotaenia splendida inornata	171	98	0.4	adhesive	r	non-guarding, open substrate (A1)	altricial
Ambassis spp.	134	81	0.8	adhesive?	r	non-guarding, open substrate (A1)	altricial
Lates calcarifer	6,000,000	900	4	small, buoyant	k	non-guarding, open substrate (A1)	precocial
Amniataba percoides	125,000	188	1	small	r	non-guarding, open substrate (A1)?	altricial
Hephaestus fuliginosus	500,000	340	2	demersal	r-k	non-guarding, open substrate (A1)?	precocial-altricial
Leiopotherapon unicolor	48,000	236	0.5	small	r	non-guarding, open substrate (A1)	altricial
Syncomistes butleri	27,000	320	2		r-k	non-guarding, open substrate (A1)?	?
Pingalla midgleyi	45,000	120	1		r	non-guarding, open substrate (A1)?	?
Glossamia aprion	250	175	1		k	external bearer (C1)	?
Toxotes chatareus	73,300	307	2	small	r-k	non-guarding, open substrate (A1)?	precocial-altricial
Liza alata	2,000,000	570	3	small, buoyant	r-k	non-guarding, open substrate (A1)	altricial
Oxyeleotris lineolatus	100,000	395	2	small, adhesive	k	nest guarder (B2)	precocial

3.7.3 Strategies of response to hydrological variation in the Cooper Creek and Magela Creek systems.

3.7.3.1 Change in flow as a spawning cue

Among the native species of Cooper Creek, flow-dependency of spawning induction (*sensu* Koehn & O'Connor 1990) slightly exceeds flow-independence (independent 36%, flow-cued 46%) and species for which induction is sometimes flow cued and sometimes not, represent 18% (Table 28). Induction of course is only one phase of the reproductive process, and the intensity or frequency of spawning events in relation to flow will be addressed in Chapter 5.

In the Magela system, because increases in flow are relatively regular in timing, it is difficult to distinguish seasonal and hydrological cues to spawning. However, Bishop (1987) considers that most species rely on inundation of the lowland and floodplain waterbodies in order to spawn. I have assumed that species which spawn in the early to mid-wet season are probably flow-cued, and those spawning at other times are relatively independent of flow increase as a cue (Table 29a). On this basis, spawning in 48% of species is flow-cued, in 43% it is independent of flow increase as a cue (although possibly anticipating it), and in 9% it is probably sometimes flow-cued, sometimes independent. This result is similar to that obtained for the Cooper Creek assemblage. However, it does not appear that either assemblage responds primarily to season as a spawning cue.

In a situation where flow increases are important determinants of reproductive success, but the timing of suitable flows is uncertain, the strategies available to river fish might be described as "double or nothing" - i.e. *spawn at a suitable temperature, and hope a flow event coincides*, or "sure thing"- i.e. *don't spawn until a flow increase is in progress*, or "two bob each way" - i.e. *spawn when the temperature is right, but retain sufficient resources to spawn again if a suitable flow occurs later* (Lloyd *et al.* 1991a).

In systems as hydrologically unpredictable as the Cooper, a strategy of conserving reproductive effort until flow conditions are suitable - a "sure thing" approach, or at least a bet-hedging strategy like "two bob each way" would seem adaptive. In fact, 50% of the native species appear to follow the "sure thing" strategy, and a further 17% the "two bob each way" strategy (Table 28). The "double or nothing" strategy appears to be

followed by 33% of the native species. Sixty-seven percent of the assemblage use a strategy which reduces risk.

In the more predictable Magela Creek system, a "double or nothing" strategy - spawning in anticipation of an increased flow - would presumably be less risky than in the Cooper Creek system. In fact, only 19% of the species in Magela Creek follow a "double or nothing" strategy, 38% follow the "sure thing strategy", and 43% the bet-hedging strategy "two bob each way" (Table 29b). In contradiction of expectation, 81% of the Magela Creek species use a strategy which reduces risk. However, although the Cooper Creek assemblage seems slightly less risk-averse than the Magela Creek assemblage, the limited data suggest that **hypothesis 4.1 (a),** that *fish spawn primarily in response to seasonal, not hydrological cues (i.e. follow a "double or nothing" spawning strategy, sensu Lloyd et al. 1991a)* is rejected for both rivers.

3.7.3.2 .Migration in response to flow

The adaptive value of downstream and lateral migration in the Cooper Creek system in response to increased flows is problematic. Because hydrological events are so irregular, and all waterbodies downstream of Coongie Lakes are ephemeral, the potential for stranding of downstream and lateral migrants is very high. The fish therefore face difficult tradeoffs. However, at least five of the native species undertake a spawning migration in response to flow increase (Table 28), all species move longitudinally in the system, and at least 40% move laterally from the main channel during increased flows. Many of these data are from work on Cooper Creek itself, and so are more robust than those extrapolated from the Murray-Darling species.

In the Magela Creek system, the greater predictability of flow events reduces risks of migration. Most species migrate longitudinally and laterally in response to increases in flow (Bishop 1987, Table 29 b). These migrations are from deeper refuge waterbodies in the early wet to shallower channel and floodplain waterbodies for both spawning and feeding. There is a reverse migration in the late dry. Thus both the Cooper Creek and Magela assemblages are mobile and responsive to hydrological cues. Whether the greater risk of downstream stranding in the Cooper Creek system has selected for fewer downstream colonists remains to be determined. Since migration in both assemblages

appears to be primarily in response to flow rather than season, **hypothesis 4.1 (b),** that *fish migrate primarily in response to seasonal, not hydrological cues* is rejected.

Table 28 Responses of fish of the Cooper Creek system to hydrological variation.

Taxon	Spawning response (in relation to hydrology)	Movement response (in relation to hydrology)	Spawning strategy (sensu Lloyd *et al.* 1991a)
Neme	independent	longitudinal and lateral	double or nothing
Rets	independent	longitudinal	double or nothing
Neoa	prob. flood-cued	longitudinal and lateral, and prob. upstream spawning migration	sure thing?
Neoh	flood-cued	Longitudinal, upstream spawning migration	sure thing
Neos	??	probably very little	??
Crae	??	colonizes downstream during floods	sure thing?
Mels	both independent and flood-cued?	upstream after flooding	two bob each way
Ambm	prob. independent	unknown	double or nothing?
Macs	flood-cued	longitudinal and lateral, and upstream spawning migration	sure thing
Bidw	flood-cued	prob. upstream spawning migration	sure thing?
Scob	prob. flood-cued	unknown	sure thing?
Leiu	prob. independent	longitudinal and lateral, and upstream spawning migration	double or nothing?
Hypk	both independent and flood-cued?	upstream movement during flow	two bob each way?
Cara	independent	increased movement during floods, not strongly directional	double or nothing
Gamh	independent, but repeated broods	colonizes downstream during floods	two bob each way

Table 29 Responses to hydrological variation in the fish of the Magela Creek

(a). Spawning timing and spawning response to hydrology.

Taxon	Spawning timing	Spawning response
		(in relation to hydrology)
Megalops cyprinoides	?	?
Nematalosa erebi	three times per year, peak in early wet	relatively independent
Scleropages jardini	early wet	probably flow-cued
Arius leptaspis	late dry to mid wet	probably anticipating flooding
Arius graeffei	late dry to early wet	probably anticipating flooding
Anodontiglanis dahli	wet season	maybe both flow-cued and
Neosilurus ater	early wet	probably flow-cued
Neosilurus hyrtlii	early wet	probably flow-cued
Porochilus rendahli	early wet	probably flow-cued
Strongylura kreffti	late dry to early wet	probably anticipating flooding
Melanotaenia splendida inornata	anytime, but peak in early wet	relatively independent
Ambassis macleayi	anytime, but peak in early wet	relatively independent
Ambassis agrammus	early wet	probably flow-cued
Lates calcarifer	early wet, late wet	maybe both flow-cued and
Amniataba percoides	early to mid wet	probably flow-cued
Hephaestus fuliginosus	early to mid wet	probably flow-cued
Leiopotherapon unicolor	early wet	probably flow-cued
Syncomistes butleri	late dry to early wet	probably anticipating flooding
Pingalla midgleyi	early wet	probably flow-cued
Glossamia aprion	anytime, though mostly summer	relatively independent
Toxotes chatareus	early wet	probably flow-cued
Liza alata	?	?
Oxyeleotris lineolatus	early wet to mid dry	relatively independent

(b). Movement response and spawning strategy

Taxon	Movement response	Spawning strategy
		(sensu Lloyd *et al.* 1991a)
Megalops cyprinoides	In Magela Creek, most species migrate longitudinally and laterally	?
Nematalosa erebi	in response to the regular hydrological cycle. These migrations	two bob each way
Scleropages jardini	are from deeper refuge waterbodies in the early wet to	sure thing?
Arius leptaspis	shallower channel and floodplain waterbodies for both	double or nothing
Arius graeffei	spawning and feeding. There is a reverse migration in the	double or nothing
Anodontiglanis dahli	late dry.	two bob each way
Neosilurus ater		sure thing?
Neosilurus hyrtlii		sure thing?
Porochilus rendahli		sure thing?
Strongylura kreffti		double or nothing
Melanotaenia splendida inornata		two bob each way
Ambassis macleayi		two bob each way
Ambassis agrammus		sure thing?
Lates calcarifer		two bob each way
Amniataba percoides		two bob each way
Hephaestus fuliginosus		two bob each way
Leiopotherapon unicolor		sure thing?
Syncomistes butleri		double or nothing
Pingalla midgleyi		sure thing?
Glossamia aprion		two bob each way
Toxotes chatareus		sure thing?
Liza alata		
Oxyeleotris lineolatus		two bob each way

3.8 Summary

The lower Cooper Creek in the Lake Eyre Basin is little impacted by water resource use, is temporally variable, hydrologically unpredictable and has a large and complex floodplain. Its biota (including its fish assemblage) and ecological processes are largely intact. Accordingly it provides an excellent example for testing the applicability of the Flow Pulse Concept, the flow templet and the flow - floodplain model of fish recruitment on large, unpredictably variable floodplain rivers in the arid zone.

On the basis of the incomplete existing data, and in comparison with the assemblage of the more hydrologically predictable Magela Creek, the Cooper Creek fish species show no striking adaptations in reproduction or migration to their extreme hydrological environment, except for a lower frequency of K-selected attributes, and a lower parental investment in offspring. Both assemblages show similar responsiveness to hydrological change, although the Magela Creek assemblage, surprisingly, shows a higher frequency of risk-minimising strategies for synchronizing reproduction with flooding. Finally, given the results for **hypotheses 4.1 (a, b)** - (particularly **4.1 (b),** which is less dependent on the validity of assumptions) it appears that **hypothesis 1.9**, that *the biota of hydrologically unpredictable rivers is not adapted to the flood pulse*, is rejected for the fish of Cooper Creek.

The Cooper Creek assemblage does not show the pronounced opportunism suggested in Chapter 1 as a feature of the biota of unpredictable systems. However, these findings must be considered tentative, since they are based on data largely drawn from the Murray-Darling system (which is less hydrologically variable), and in some cases from congeners, not the Cooper Creek species. Further, the comparison is of only two rivers, and the life-history characters for which data were available differ between the two assemblages. Some of these findings will be tested against the results in Chapters 4 and 5.

4. Fish, macroinvertebrate and zooplankton assemblages - overall structures vs waterbody and river reach flow history in Cooper Creek.

4.1 Introduction

Chapter 1 discussed the Flood Pulse Concept as a model of the ecological role of flow variability in floodplain rivers, and identified a number of limitations, particularly in the application of the FPC to large arid zone rivers. A suite of hypotheses was framed to test these limitations at a range of temporal and spatial scales and on several biological assemblages. Chapter 2 provided evidence, at the flow regime temporal scale and whole river spatial scale, for extending the range of significant flow events in the model beyond the "flood pulse" to the "flow pulse". It also confirmed that the flow regimes of dryland rivers, particularly the Cooper and Diamantina, are exceptionally both variable and unpredictable, that this variability is multi-faceted, and that for all rivers a multivariate approach should be taken to modelling hydrology-biology relations. This chapter laid the foundations for a "Flow Pulse Concept", a Flood Pulse Concept extended in the range of flow amplitudes and the variety of facets of flow events considered significant for river ecology.

Chapter 3 described, at the flow regime temporal scale and river reach spatial scale, the distinctive environmental characteristics of lower Cooper Creek. It characterised the Cooper Creek fish assemblage as more *r*-selected and showing less parental investment in offspring than the assemblage of Magela Creek in the wet-dry tropics. The Cooper Creek fauna also appears to be adapted to the river's hydrological regime, but does not show the marked adaptations to hydrological variation that might be expected in such an extreme system.

In this chapter further hypotheses framed in Chapter 1 are tested at spatial scales of the river reach and individual floodplain water-bodies, at temporal scales of flow regime, flow history and the flow pulse and in floodplain and permanent channel habitats, using data for Cooper Creek (December 1986 to April 1992). Specifically, the analysis:

- Tests for differences in the structures of fish, zooplankton and macroinvertebrate assemblages during different flow pulses and flow pulse phases, and between floodplain lake and channel habitats.
- Tests for correlations between fish, zooplankton and macroinvertebrate assemblage structures and multiple facets of flow history and flow pulse.

The results of these analyses are used to test the following hypotheses from Chapter 1:

2. At the flow history and flow pulse temporal scales and the river reach and waterbody spatial scales in Cooper Creek:

2.1. The overbank phases of the flow pulse are biologically more important than the in-channel phases.

2.2 Variations in fish, zooplankton and macroinvertebrate assemblage structures are independent of flow history.

2.3. The facets of the flood pulse listed in Junk *et al.* (1989) are adequate to describe the influence of hydrology on overall structure of fish, zooplankton and macroinvertebrate assemblages.

2.4. Hydrological events at the magnitude of overbank flows are sufficient to describe biology-hydrology interactions in floodplain rivers.

4.2 Methods

The project began in December 1986 as a one-year survey, continued under a series of grants and was reformulated as a PhD program beginning in June 1989.

4.2.1 Study Area

4.2.1.1 Choice of waterbodies and sites

The sampling sites in the field program were in the Coongie Lakes complex on the Northwest Branch of Cooper Creek, 140 km upstream from Innamincka, at sites immediately upstream and downstream of Innamincka, and from the terminus of Strzelecki Creek in Lake Blanche (Fig. 20). As Chapter 3 indicated, Cooper Creek is unregulated and preserves largely intact its associations between the fauna and patterns of flow.

In December 1986 and throughout 1987, 13 waterbodies and 26 sites were sampled, including replicate sites in five waterbodies (Puckridge & Drewien 1988). This indicated spatial variation and patterns of inundation and served to identify habitats for stratified sampling. Stratification involved a primary division between lakes and channels, with lakes further subdivided as *lake littoral*, *sub-littoral* and *pelagic* (Jónasson 1996) (or *open water*) and channels as *channel shore*, *mid-channel* (or *open water*) and *backwaters* (Boulton & Lloyd 1991, Walker *et al.* 1995). These habitats were defined initially by hydrological and geomorphic criteria, later supported by fish and macroinvertebrate data (Puckridge & Drewien 1988). In this thesis, the term *open water* will be used to denote both the *pelagic* zone of lakes and the *mid-channel* zone of channels.

The Coongie Lakes (Fig. 21) are described in Chapter 3. The principal waterbodies are five lakes and their connecting channels spread over 50 km of the Northwest Branch of Cooper Creek. In 1986-91 there were recurrent flow pulses, with magnitudes progressively increasing until 1990, as indicated by the hydrograph at Cullyamurra gauging station, 150km upstream (Fig 20). Thus, previously dry waterbodies were inundated each year. In 1987 it was decided to sample on a north-south axis through the system, viz. Lakes Coongie, Toontoowaranie and Goolangirie and the channel sites Northwest Branch, Browne Creek, Ellar Creek and the internal delta Tirrawarra Swamp (Fig. 21). This provided a steep gradient in such hydrological facets as the frequency and timing of inundation. Lake Apanburra and the Apanburra Channel were added in 1988 and Lake Maroopootanie in 1990, as they were flooded. East-west extensions of the sampled area, in Lakes Maroocoolcanie, Maroocutchanie, Mundooroonie and Apachirie, were not sampled after 1987.

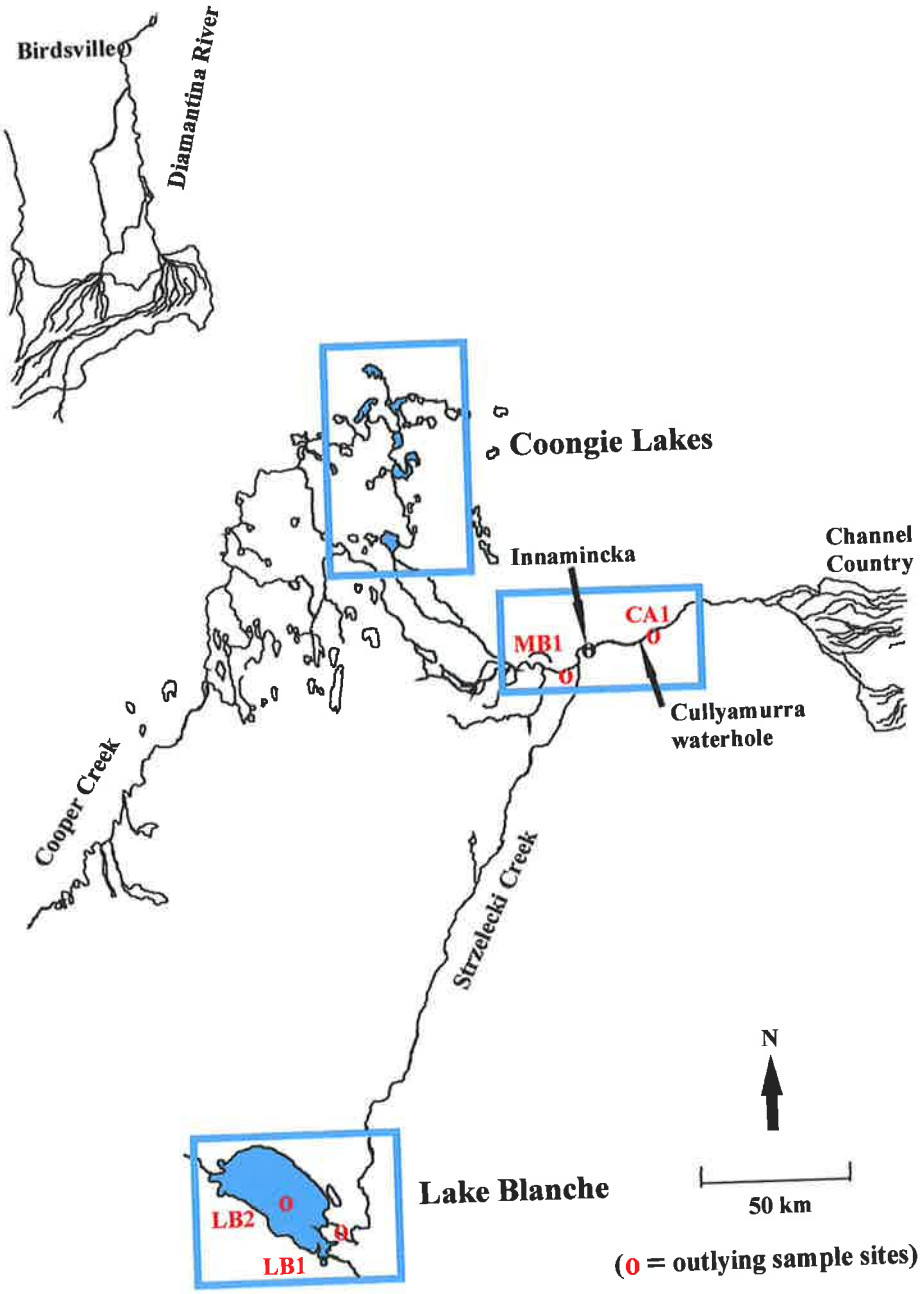


Figure 20. Sample sites on the lower Cooper Creek and lower Strzelecki Creek floodplains.

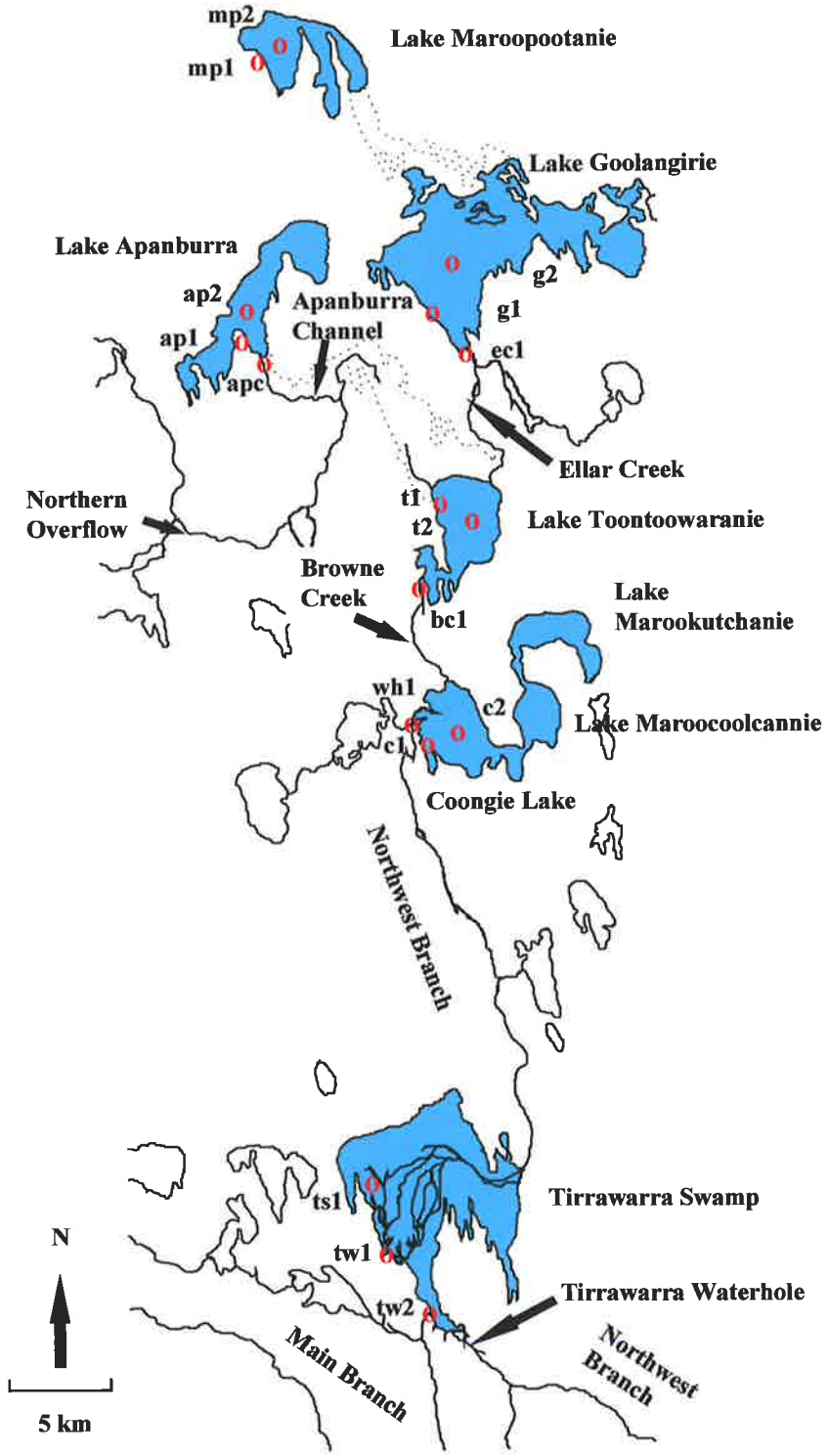


Figure 21. Sample sites in the Coongie Lakes system.

In March 1989, fish movements prompted sampling above and below the Innamincka Causeway (Fig. 20), where it was expected that mobile species (*Neosilurus*, *Macquaria*, *Bidyanus spp.*) might spawn because upstream movements could be impeded by the causeway and the locally high stream gradient. These samples extended the spatial range of the project from 70 to 140 km. The core localities were supplemented by data from outliers such as Lake Blanche (Fig. 20), principally to gauge the mobility of the fauna in large flow pulses.

The locations of sites within waterbodies (Fig. 21) were a compromise between accessibility and other logistic factors. Those sampled often enough to be used in subsequent analyses included six lakes, seven channel reaches and an internal delta (Tables 30, 31).

Table 30. Core waterbodies and sampling sites.

Code	Type	Name
WH1	Northwest Branch Channel	Coongie Crossing Waterhole
C1	Lake	Coongie Lake littoral
C2	Lake	Coongie Lake open water
BC1	Northwest Branch Channel	Browne Creek
T1	Lake	Lake Toontoowaranie littoral
T2	Lake	Lake Toontoowaranie open water
EC1	Northwest Branch Channel	Ellar Creek
G1	Lake	Lake Goolangirie littoral
G2	Lake	Lake Goolangirie open water
APC	Northwest Branch Channel	Apanburra channel
AP1	Lake	Lake Apanburra littoral
AP2	Lake	Lake Apanburra open water
MP1	Lake	Lake Maroopootanie littoral
MP2	Lake	Lake Maroopootanie open water
LB1	Strzelecki Lake	Lake Blanche littoral
LB2	Strzelecki Lake	Lake Blanche open water
CA1	Main Branch Channel	Cullyamurra Waterhole
MB1	Main Branch Channel	Queerbidie Waterhole
TW1	Northwest Branch Channel	Tirrawarra Waterhole north
TW2	Northwest Branch Channel	Tirrawarra Waterhole south
TS1	Internal delta	Tirrawarra Swamp

Table 31. Sampling events for Cooper lakes and channel waterbodies.

Waterbodies	Sampled						
	Dec						Apr
	1986	1987	1988	1989	1990	1991	1992
L.Coongie	y	y	y	y	y	y	y
L.Maroocoolcanie	y	y					
L.Marookutchanie	y	y					
L.Toontoowaranie		y	y	y	y	y	y
L.Goolangirie		y	y	y	y	y	y
L.Apanburra			y	y	y	y	y
L.Maroopootanie					y	y	
L.Blanche					y	y	
Cullyamurra W.				y	y	y	
Queerbidie W.				y	y	y	
Tirrawarra W.				y	y		
Tirrawarra Swamp		y	y	y			
Coongie Crossing W.	y	y	y	y	y	y	
Browne Creek		y	y	y	y	y	
Ellar Creek		y	y	y	y	y	
Apanburra Channel				y	y	y	

4.2.2 Study Design

4.2.2.1 Preamble

In this study scales are large because of the nature of flow variation and the mobility and longevity of fish. Manipulations are impracticable, and an alternative is to study responses to natural variation (cf. MacNally 1996). Accordingly, the sampling program was designed to:

- Record responses in fish, zooplankton and macroinvertebrate assemblages over scales which approximate ecological time for the taxa concerned.
- Match those responses to a variety of flow histories and habitats.

4.2.2.2 Replication

Sampling was extensive in time and space. Replication on a large spatial scale, of course, is problematic. Simultaneous replicates are impossible without duplication of labour and equipment, yet otherwise are pseudoreplicated (Hurlbert 1984). Another constraint is the difficulty of sampling mobile organisms in a relatively inaccessible environment (Benech *et al.* 1983). Most fish sampling gear is selective for species and size-classes (Lyons 1986, Borgstrom & Plahte 1992) and its efficiency varies with habitat (Vigg 1981, Parsley *et al.* 1989). Depending on the effect size sought, sufficient statistical power may be unattainable where there is high variability. For the Cooper, these difficulties are compounded by the remoteness of the region and the variable conditions of access.

4.2.2.3 Between-Site Replication

Replication at the level of systems (e.g. including the Diamantina), or even tracts (e.g. the upper and lower Cooper), was impractical for long-term, regular sampling. Sampling was replicated at the level of river reach (the Cooper Creek Main Branch, the Coongie Lakes system on the Northwest Branch and the lower Strzelecki Creek at Lake Blanche – Fig. 20), stratified between channel and lake sites (Fig. 21) and between littoral and pelagic/mid-channel (or open water) zones (depending on gear type) (Table 32). As the goal was to relate hydrology and assemblages at diverse sites rather than to characterise waterbodies, within-waterbody replication was not crucial.

The study spanned five years, so that there was some chance of including most or all of an ENSO cycle (Allan 1985). In fact the sampling period included a 1 in 30 year flood, two other large events, and a low flow year. Resource limitations meant that sampling was bi-monthly (in February, April, June, August, October, December), and the number and extent of sites was restricted as described above. This regime sampled seasonal and annual temporal replication (diel variation was examined in initial sampling). Bimonthly sampling is coarse to monitor recruitment in zooplankton and macroinvertebrates (Geddes 1984, Maher 1984, Neckles *et al.* 1990), and may miss migration and spawning by some fish (Clifford 1972, Sloane 1984, Gaughan *et al.* 1990). Nevertheless, the first year's data indicated the timing and intensity of most breeding and colonisation events and major

changes in the abundance, disease incidence, age structure and composition of the fish, and gross changes in the abundance and composition of macroinvertebrate populations (Puckridge & Drewien 1988, Geddes & Puckridge 1989, Reid & Puckridge 1990).

4.2.2.4 Within-site Replication

Choice of sampling gear

Choices of sampling gear (for fish) and subsequent evaluations of performance were based on the following requirements.

- The gear would sample size-classes from larvae to adults.
- Catches with some gear could be compared to adjust for selectivity.
- The gear could be used in diverse habitats, from vegetated channels to open lakes.
- The gear would allow for active and passive capture so that corrections could be made for activity related to temperature and other environmental conditions.
- Catches would be sufficient for analyses of relative abundance (absolute efficiency was not tested: cf. Holland-Bartels & Dewey 1996).
- The capture range was from 10m to several kilometres.
- The gear was compact, transportable and operable from a small dinghy.
- The gear minimised injury and mortality to fish and to tortoise, waterbird and water rat populations (the area is a State Government Regional Reserve, a Ramsar site and a National Estate site).
- Costs would be within the project budget.

The routine gear is described in Table 32. A suite of gillnets (5 mesh-sizes), seines (4), trawls (2), drumnets (120mm mesh) and traps (10mm) were used first, but this was refined later where practical. Drumnets and traps were abandoned because catches were low, and 70m and 130m seines likewise were abandoned because they incurred major fish mortalities. Floating gillnets allowed better control of effort and processing, and fykenets

were used to corroborate and supplement gillnet data after December 1988. Electrofishing was discounted for reasons of cost and concerns that low visibility (3-8cm Secchi depth) would limit captures.

Sampling locations

Sampling locations within the two major zones (or habitats) were different for different gears. The zooplankton trawl was used only in the littoral, but could have been used in the pelagic. Seines could be operated only in littoral and sub-littoral areas; gillnets and trawls needed deeper, open water and the fish trawls required transects of several kilometres. Drum and fykenets worked best in channels where fish movement was constrained, and were most effective in littoral areas (Underwood *et al.* 1996). The data therefore variously represent different zones and different subsets of the fish fauna and size-classes of the fish populations. Data from gillnets, 2m and 20m seines and trawl were combined for six major sites, and two databases (open water macroinvertebrates, open water fish larvae and juveniles) were derived from the 500µm trawl. Adult fish were returned alive to the water, but trawled larvae were preserved in 10% formaldehyde.

Table 32. Routine sampling gear.

Gear	Mesh (mm)	Depth (m)	Length (m)	Position
fykenets	30	1.2	15 (wingspan)	Opposite-facing pair in channel sub-littoral
gillnets (mono-mesh)	110, 90, 70, 50, 40, 30	2	40	Cross-channel, lake open water.
Gillnets (multi-mesh)	110, 90, 70, 50, 40, 30	2	36 (3x12m modules, 6x2m single mesh panels per module)	Cross-channel, lake open water.
2m seine	2	1.2	2	Lake, channel sub-littoral
20m seine	13	2	20	Lake, channel sub-littoral
Fish/macroinv. Trawl	500 µm	0.5m diameter	2	Mid-channel, lake open water.
Zooplankton trawl	60 µm	0.3m diameter	1	littoral, lakes and channels

4.2.2.5 Sampling effort per replicate and diel timing

Sampling precision (*sensu* Cyr *et al.* 1992) was not determined because many catch data were not log-normal and parametric statistics were inappropriate. However, effort and timing of replicates were trialled as follows:

Zooplankton Trawl

Relative log 10 abundance per haul of the major zooplankton taxa (Fig.22) shows only a gradual overall increase with trawl haul distance in Lake Goolangirie. A five metre haul length would have been adequate to sample these taxa, but haul length was set at 20m principally to increase the chance of collecting rare taxa. Diel variation in catch was not examined for this gear, but was corrected for by confining samples to mid-morning.

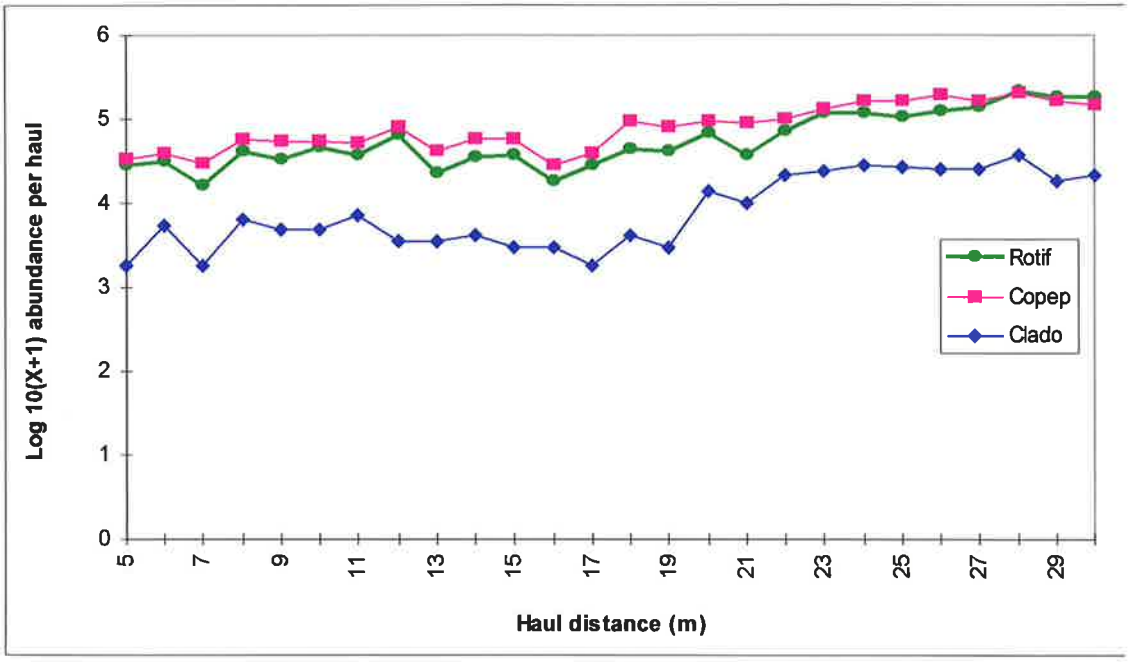


Figure 22. Differences in relative abundance of major zooplankton taxa between trawl hauls of differing lengths in Lake Goolangirie.

Macroinvertebrate trawl

Effort per replicate for trawls was determined from trawl time and from current speed measured with a General Oceanics model 2030 Digital Flowmeter in the trawl mouth. For the common taxa catch increased significantly with increasing time per haul (Fig. 23), and the pattern of increase was similar for increasing flow. To increase opportunity to capture rare taxa, the routine effort was set at 3 min at 4-5 km/hour (cf. Madjenian & Jude 1985), which over the whole program corresponded to a mean 8735 meter revolutions (SE ±48.7). During peak macroinvertebrate blooms, when the trawl could become clogged in 60 seconds, effort was reduced, and catches were corrected by the time ratio to three minutes equivalent. This mode of correction was used in preference to taxon-specific regressions of catch on trawl time (fig. 23) because adequate data for such regressions were not obtainable for many taxa. Corrections for reduced effort were necessary in only 7 of the 144 macroinvertebrate samples and 7 of the 189 fish trawl samples.

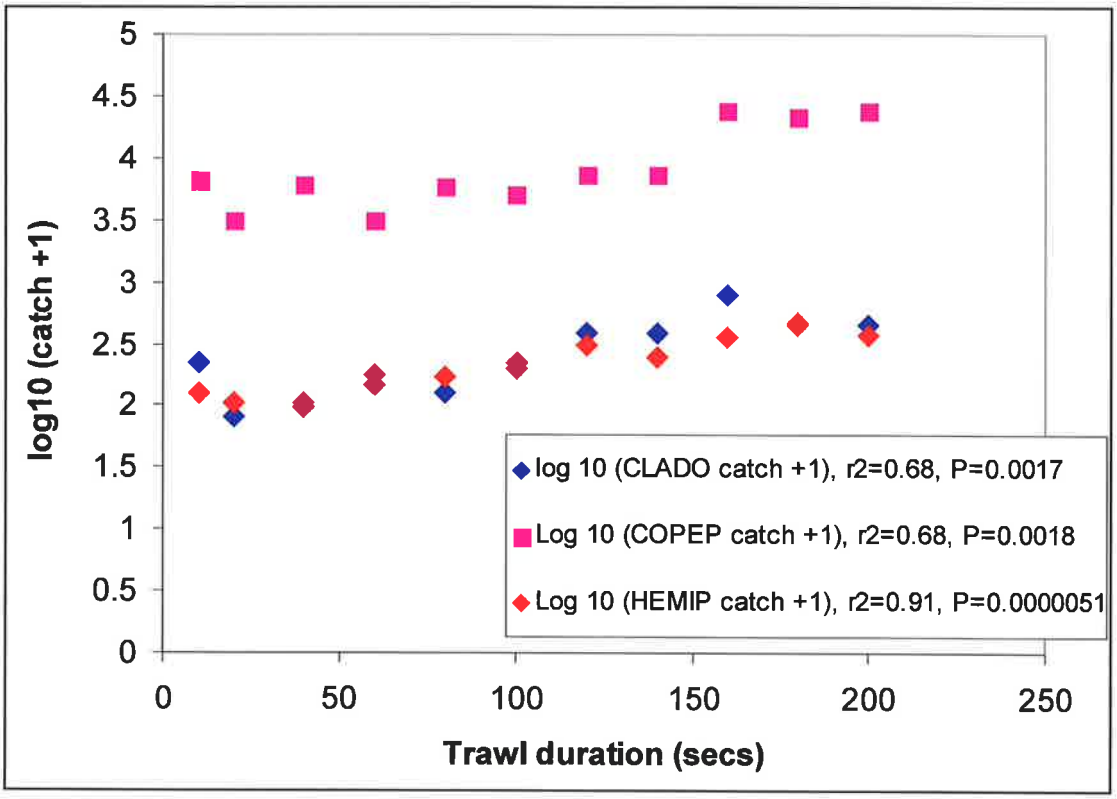


Figure 23. Catches of major macroinvertebrate taxa in trawl hauls of differing durations.

Fish Trawl

Only the three most common fish species were caught in trials of catch per trawl effort. For two of these species catch increased with increasing time per haul (Fig. 24), but catch of *R. semoni* appeared to asymptote, while catches of *N. erebi* continued to increase. Catch of *H. klunzingeri* and total species richness were not significantly related to haul time (Table 33). These patterns were similar for increasing flow. Outside the summer breeding season fish larvae and juveniles were sparse, so as indicated for macroinvertebrate sampling above, sampling time was set at 3 minutes, in the upper portion of the catch curves for *N. erebi* and *R. semoni.*

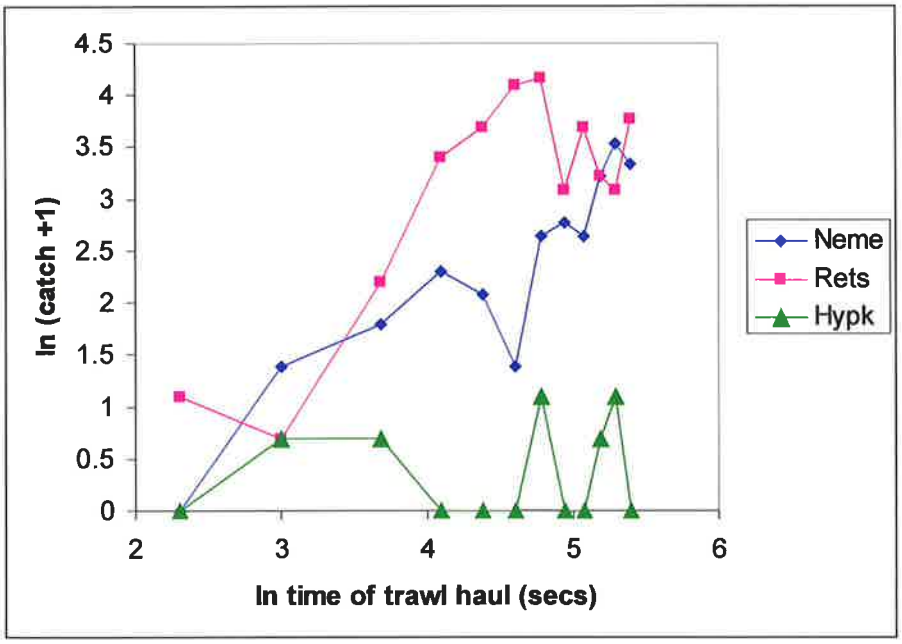


Figure 24. Catch of major fish taxa against time per trawl haul.

Table 33. Regressions of ln (catch per taxon+1) against trawl haul duration and total flow through the trawl per haul.

Taxon	**Trawl parameter**	***n***	**r^2**	***P* (*F*-ratio)**
Nematalosa erebi	duration	12	0.77	0.00018
Nematalosa erebi	flow	11	0.76	0.00048
Retropinna semoni	duration	12	0.41	0.025
Retropinna semoni	flow	11	0.40	0.036
Hypseleotris sp.	duration	12	0.03	0.70
Hypseleotris sp.	flow	11	0.08	0.40
Species richness	duration	12	0.04	0.51
Species richness	flow	11	0.13	0.30

Diel catch differences are commonly reported for fish larvae (Madjenian & Jude 1985). Comparison of replicated night and afternoon trawl haul catches in four sites by two-

way crossed Analysis Of Similarities (ANOSIM: Clarke & Warwick 1994) showed significant differences between night and afternoon catches (P <0.001) and between sites (P <0.001). Although catch/effort of night trawls was higher, routine sampling was practicable only in mid-afternoon (Table 36).

Fykenets

Upstream-downstream paired fykenet sampling was intended to corroborate and supplement gillnet data on fish movement. Species-specific diurnal differences in movement (Harris *et al.* 1992) required the nets to be set over 24 h. Thus diurnal variations in catch and catch per net wet-time were not crucial to sampling design. Seasonal variations in duration between morning, afternoon and night sets were compensated for by correcting all catches to 6 h net wet-time.

Gillnets

Net wet-time was varied for gillnets because variations in catch rate, disease incidence and spawning intensity necessitated longer sampling in winter. In summer, catch rates were often so high that sampling times had to be reduced to allow time to process the catch and to minimise mortalities. To test the catch response to variations in net wet-time, 48 replicate gillnet multimesh module catches (divided between morning and afternoon catches on one day in two sites in Lake Toontoowaranie) were collected over a range of wet-times from 8.5 to 61.8 min. Only the three major species, *Nematalosa erebi*, *Macquaria* sp. and *Bidyanus welchi* were collected in the samples, and the catches of the latter two were low. The relations between species-specific catches and module wet-times were examined by (a) linear regressions of $\log_{10}$(catch + 1) against $\log_{10}$(net wet-time + 1) and (b) exponential regressions of catch against net wet-time.

All regressions except the exponential regression for *Macquaria* sp. were significant and positive (Table 34), confirming the anticipated increase in catch with net wet-time. However, patterns varied markedly between species and there was wide scatter (Fig 25).

Table 34. Regressions of catch per species per gillnet module against net wet-time.

Taxon	*Regression*	*n*	r^2	*P (F-ratio)*
Nematalosa erebi	log-log linear	48	0.23	0.00056
Macquaria sp.	log-log linear	48	0.13	0.011
Bidyanus welchi	log-log linear	48	0.12	0.017

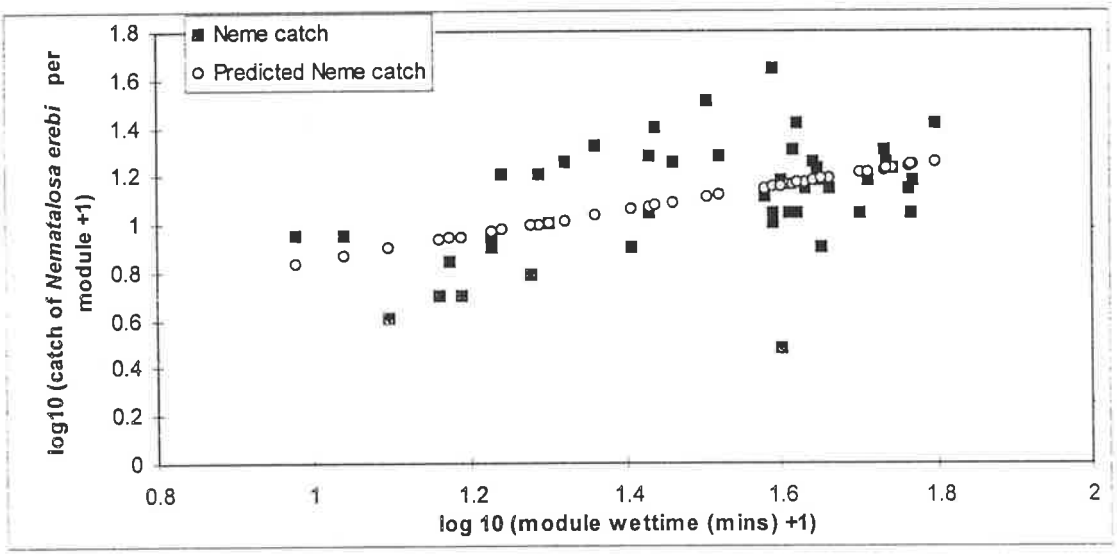


Figure 25. Log-log linear regressions of gillnet module catch against net wet-time.

This relation was also examined between six sites in different waterbodies. Module wet-times here varied from 16–144 minutes, and modules per waterbody varied from 6–14. Most sites showed no relation between module wet-time and catch (Table 35), but G2 showed a highly significant response. It was concluded that that there is a positive but variable relation between net wet-time and catch, and that corrections are advisable.

Table 35. Log-log regressions of catch of *Nematalosa erebi* per gillnet module against module wet-time in six sites at one time.

Site	Waterbody	Mean catch of *N. erebi*	*n* (modules)	r^2	*P*(*F* ratio)
BC1	Browne Creek	9.3	12	0.21	0.13
C2	Coongie L	0.56	9	0.26	0.16
EC1	Ellar Creek	25	6	0.49	0.12
G2	L Goolangirie	10	14	0.76	0.000048
T2	L Toontoowaranie	2.3	14	0.003	0.85
WH1	Coongie Crossing	6.2	14	0.078	0.33

Correction for net wet time effects by species-specific regressions rather than a simple ratio (60/net wet-time (min)) was rejected because it was impractical to obtain adequate data. When catches between sites were compared for raw data and ratio corrected data, there was little change in inter-site pattern (Figs 26-27).

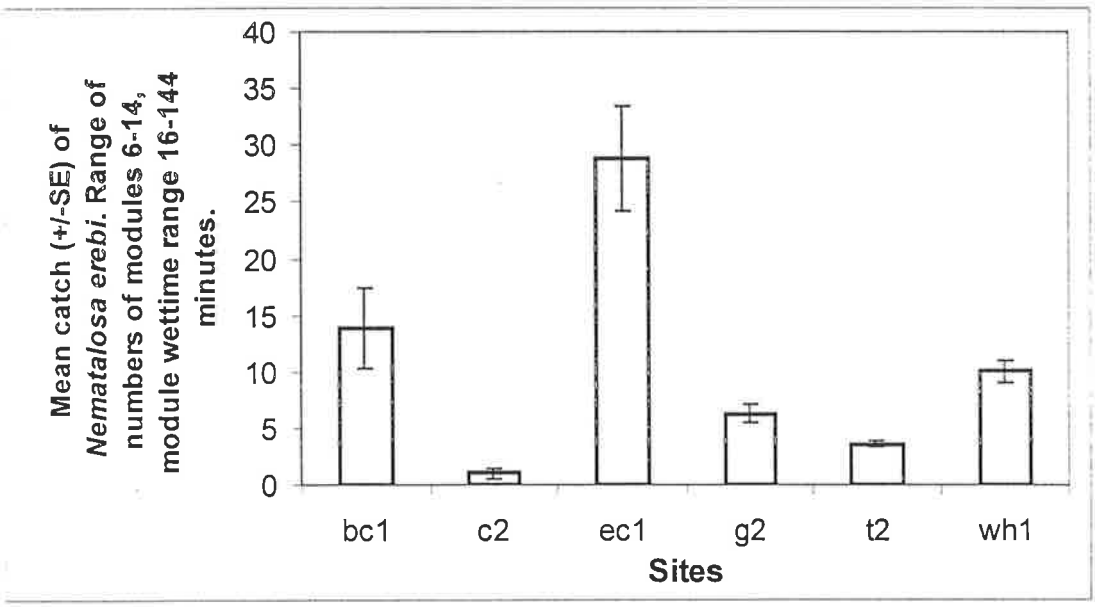


Figure 26. Raw catch per module of *Nematalosa erebi* in six sites at one time.

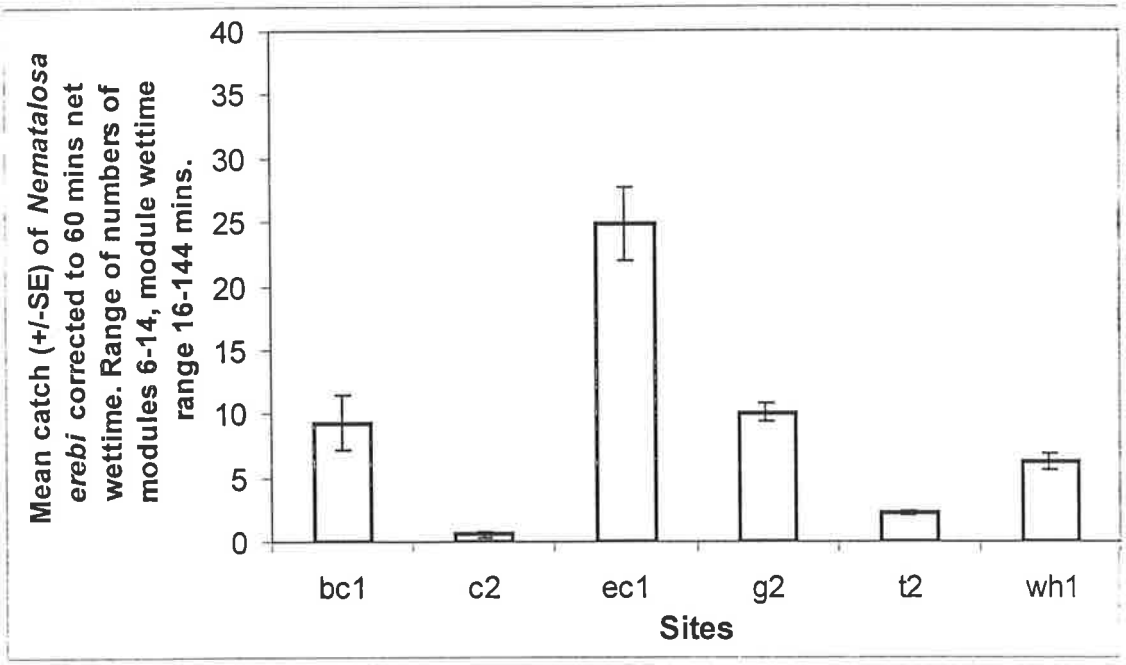


Figure 27. Catch per module of *Nematalosa erebi* corrected for module wet-time at six sites at one time.

For comparisons of gillnet module catches between morning and afternoon and between the two sites, the 48 catches referred to above were corrected by the ratio of actual net wet-time to 30 min (Fig. 28), the average net wet-time in that exercise. The resulting discrepancies were small compared to the fluctuations in catch in subsequent sampling.

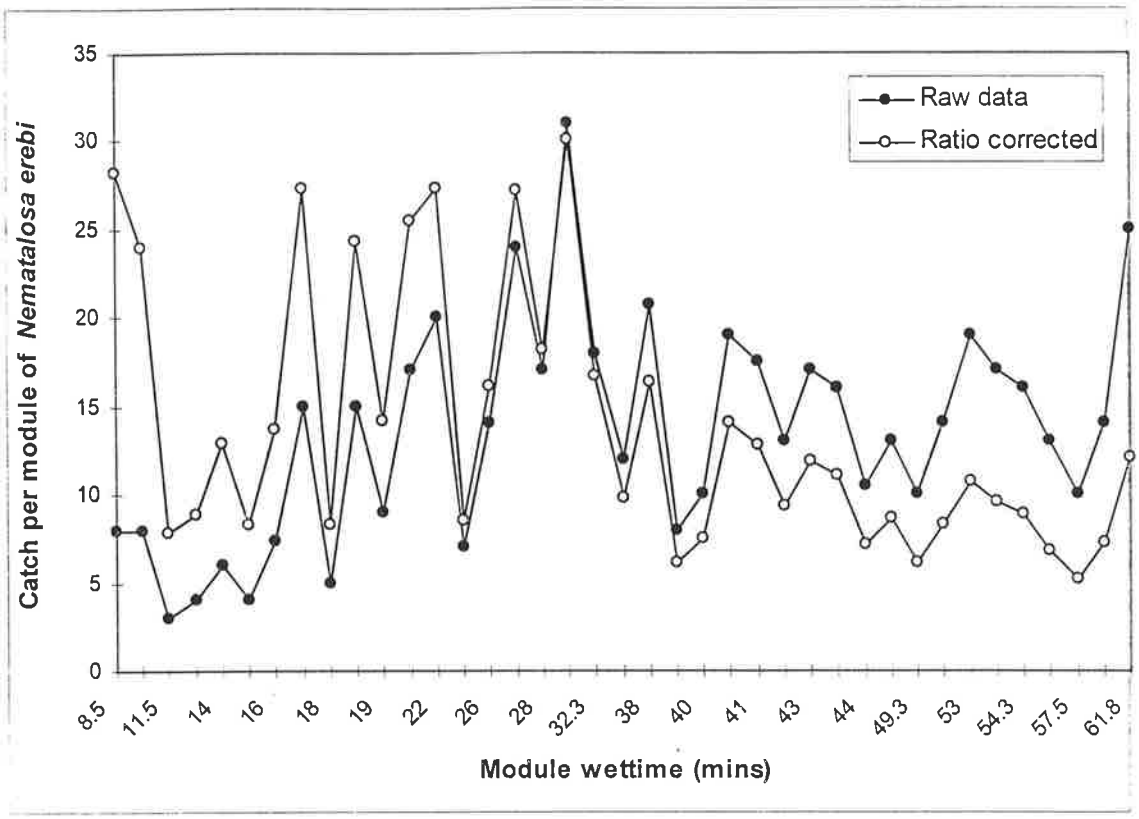


Figure 28. Comparison of actual catch of *Nematalosa erebi* with catch corrected by the ratio 30/module wet-time

The 48 corrected catches per module in morning and afternoon and at the two sites were compared by ANOSIM. Only three species (Neme, Macs, Bidw) were caught in sufficient numbers to make useful comparisons. Results showed a difference between community composition in morning and afternoon catches (P <0.01), principally because morning catches of *Nematalosa erebi* were much greater than afternoon catches. Sites were not significantly different (P >0.05). Diurnal fluctuation in catches was controlled by confining all gillnet sampling to mid-afternoon (Table 36).

20m seine

The relations between haul length of the 20m seine and catch of major species and cumulative species richness were examined using 11 hauls of length increasing in intervals of 3m along the sublittoral of Coongie Lake (Fig. 29). Cumulative species richness appeared to asymptote at 24 m, but $\log_{10}$(catch per haul +1) did not show a response to haul

any species except *Nematalosa erebi*. For the latter species $\log_{10}$ catch peaked at about 24m. Routine haul length was set at 25m.

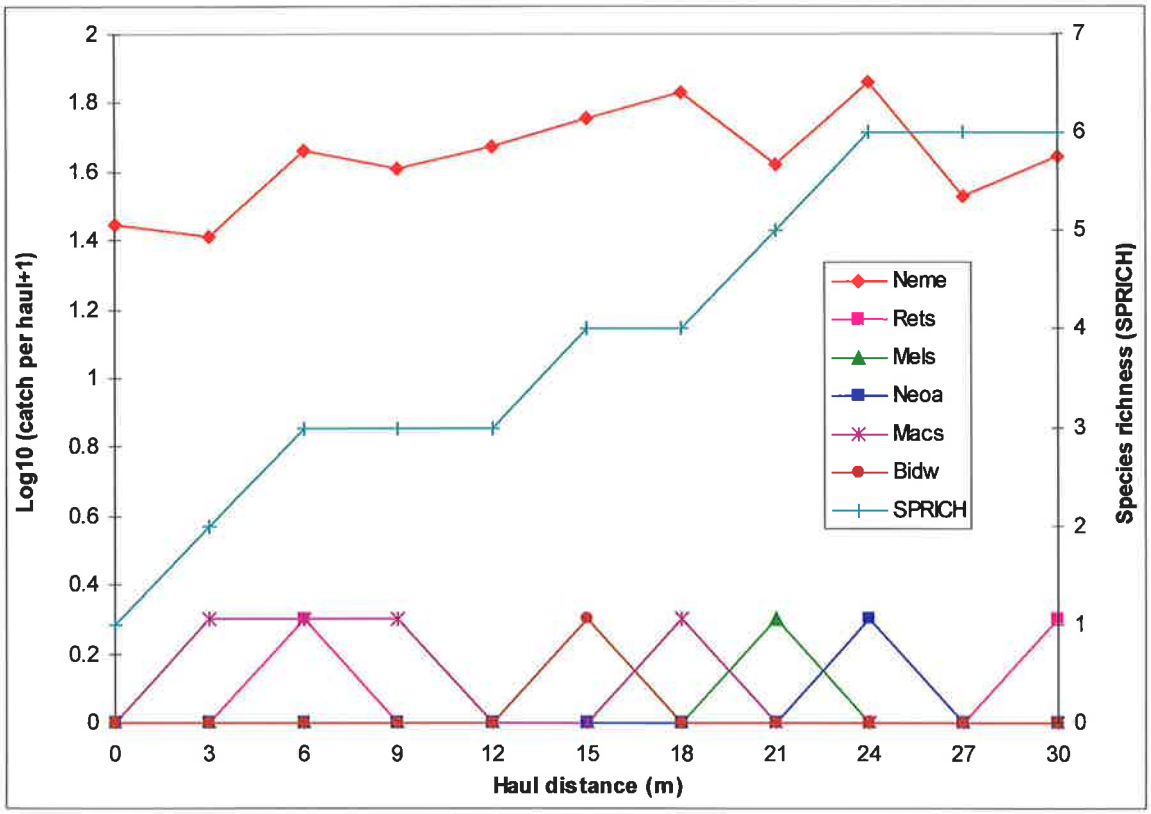


Figure 29 Relation of catch and species richness to haul length of 20m seine. "0" haul distance denotes a stationary encircling haul.

ANOSIM on morning and afternoon 20m seine catches in eight replicated samples from the same site at two-monthly intervals demonstrated differences between morning and afternoon catches (P <0.01) and two-monthly catches (P <0.001). Routine sampling was in mid-morning because the shores then were less subject to wave action (Table 36).

2m seine

The relations between haul length of the 2m seine and both catch of major species and cumulative species richness were examined using 11 hauls of length increasing in intervals of 2m along the sublittoral of Coongie Lake (Fig. 30). Cumulative species richness appeared to asymptote at 4 m., but $\log_{10}$ (catch per haul +1) for the major species peaked at 12 to 16m. Routine haul length was set at 10m.

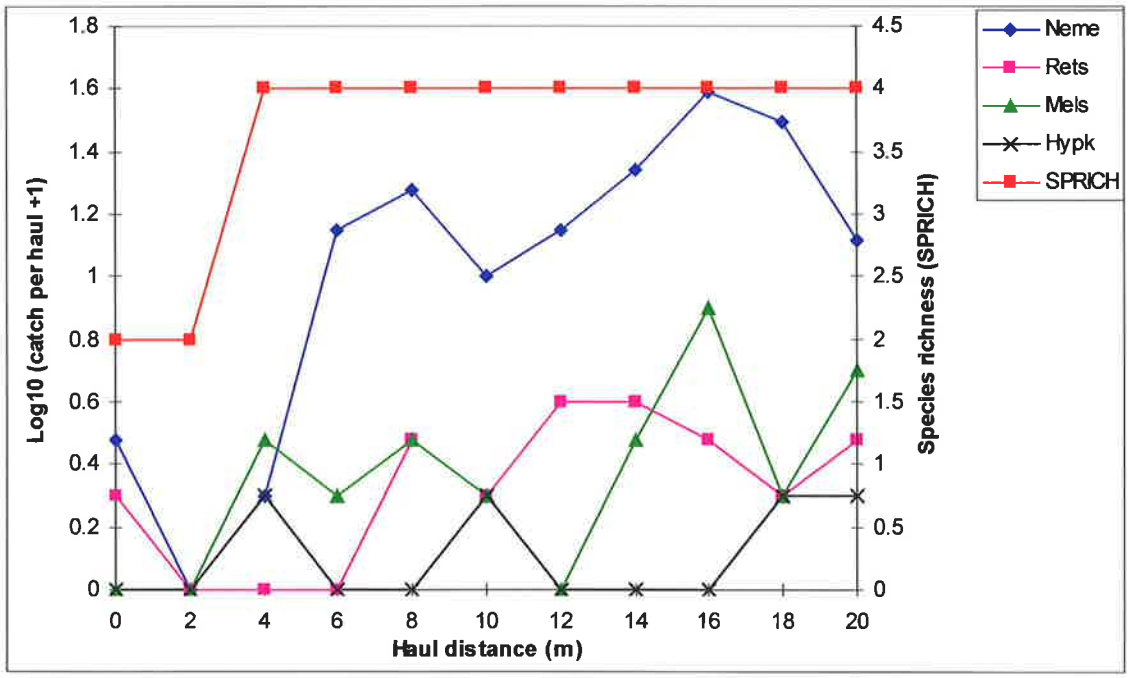


Figure 30. Relation of catch and species richness to haul length of 2m seine. "0" haul distance denotes a stationary encircling haul.

ANOSIM between morning and afternoon 2m seine catches in two replicated samples from the same site at two-monthly intervals did not show significant differences between morning and afternoon catches (P =0.053) but did between two-monthly catches (P <0.001). However, the result for diurnal difference, given the low replication and the result for the 20m seine analysis, was close enough to P =0.05 to warrant consideration. Accordingly, 2m seine sampling also was confined to mid-morning (Table 36).

Table 36. Application of sampling gear.

Gear	Position	Timing
fykenets	opposite-facing pair along channel sub-littoral	24 h cycle
gillnets (mono-mesh)	5 nets cross-channel, lake open water	mid-afternoon
gillnets (multi-mesh)	3-9 modules cross-channel, lake open water	mid-afternoon
2m seine	5-10 by 10m haul (lake, channel sub-littoral)	mid-morning
20m seine	5-10 by 25m haul (lake, channel sub-littoral)	mid-morning
fish/macroinv. trawl	5-10 by 3min tow (mid-channel, lake open water)	mid-afternoon
zooplankton trawl	10 by 20m tows (littoral in lakes and channels)	mid-morning

4.2.2.6 Replication and Stratification per Sampling Gear per Waterbody

Replicates per site

Initially, numbers of replicates taken with each gear were based on prior experience on the Murray-Darling (Puckridge 1988, Puckridge & Walker 1990). However, cumulative catches per species per number of replicates taken were later examined for seine nets, trawls and multimesh modular gillnets, and replicate numbers adjusted. Fykenets and mono-mesh gillnets were too labour-intensive to replicate more than twice at each site.

Zooplankton Trawl

Zooplankton taxon richness appeared to plateau between two and four trawl hauls (Fig. 31). Ten hauls were initially taken per sample, but because of the time required for sorting and counting, only five (chosen at random) were processed and included in analysis.

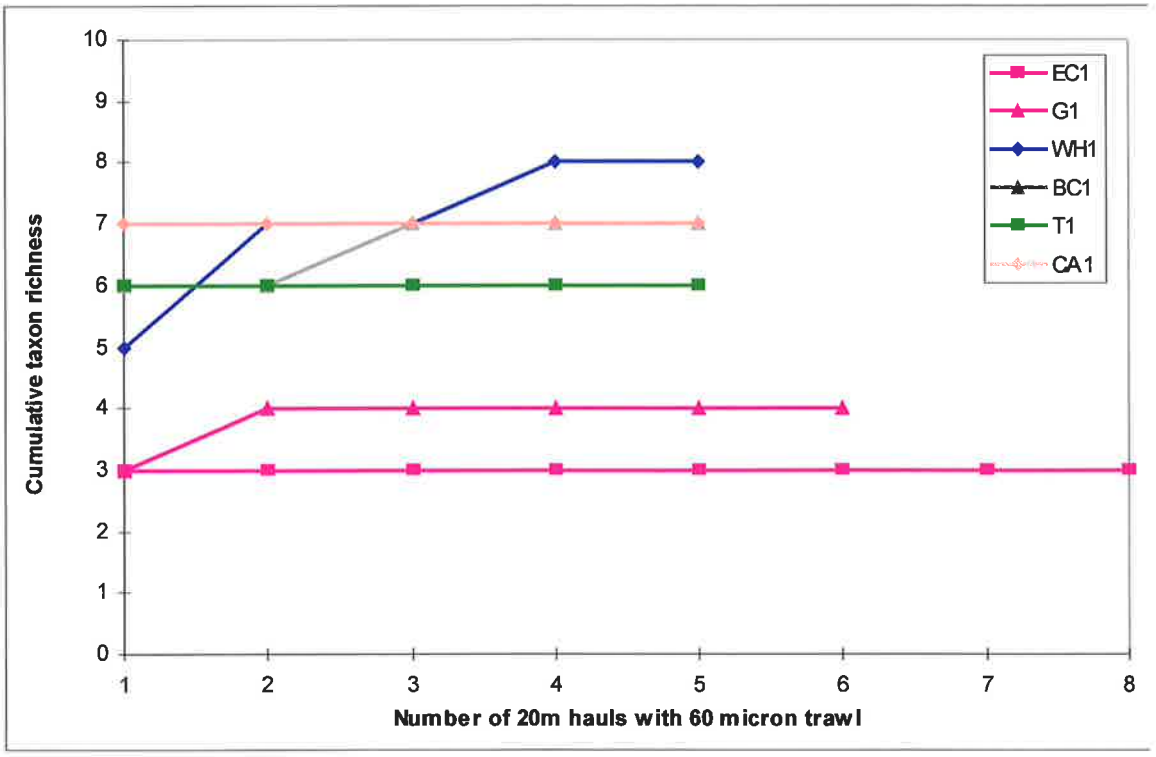


Figure 31. Changes in cumulative zooplankton taxon richness with haul number in four channel and two lake sites.

Macroinvertebrate Trawl

Curves of ln(X+1) cumulative catch per macroinvertebrate taxon per number of hauls (Figs 32-33) showed taxon richness increased up to eight hauls in Lake Apanburra and up to four hauls in Coongie Lake. In the first two years of the program 10 hauls were taken per site, but sorting this many samples was too time-consuming, so subsequently six hauls were taken per site, from which five were randomly selected for sorting.

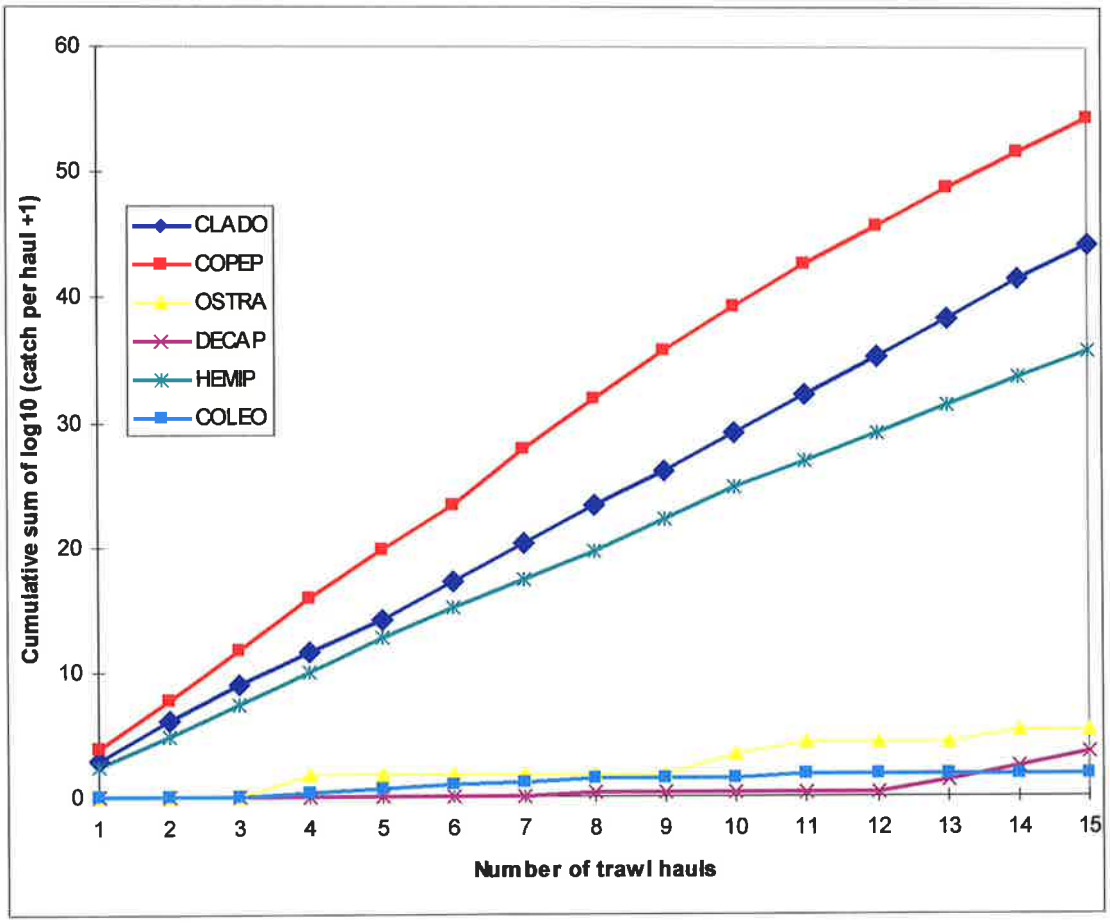


Figure 32. Cumulative catch of major macroinvertebrate taxa for number of trawl hauls in Lake Apanburra

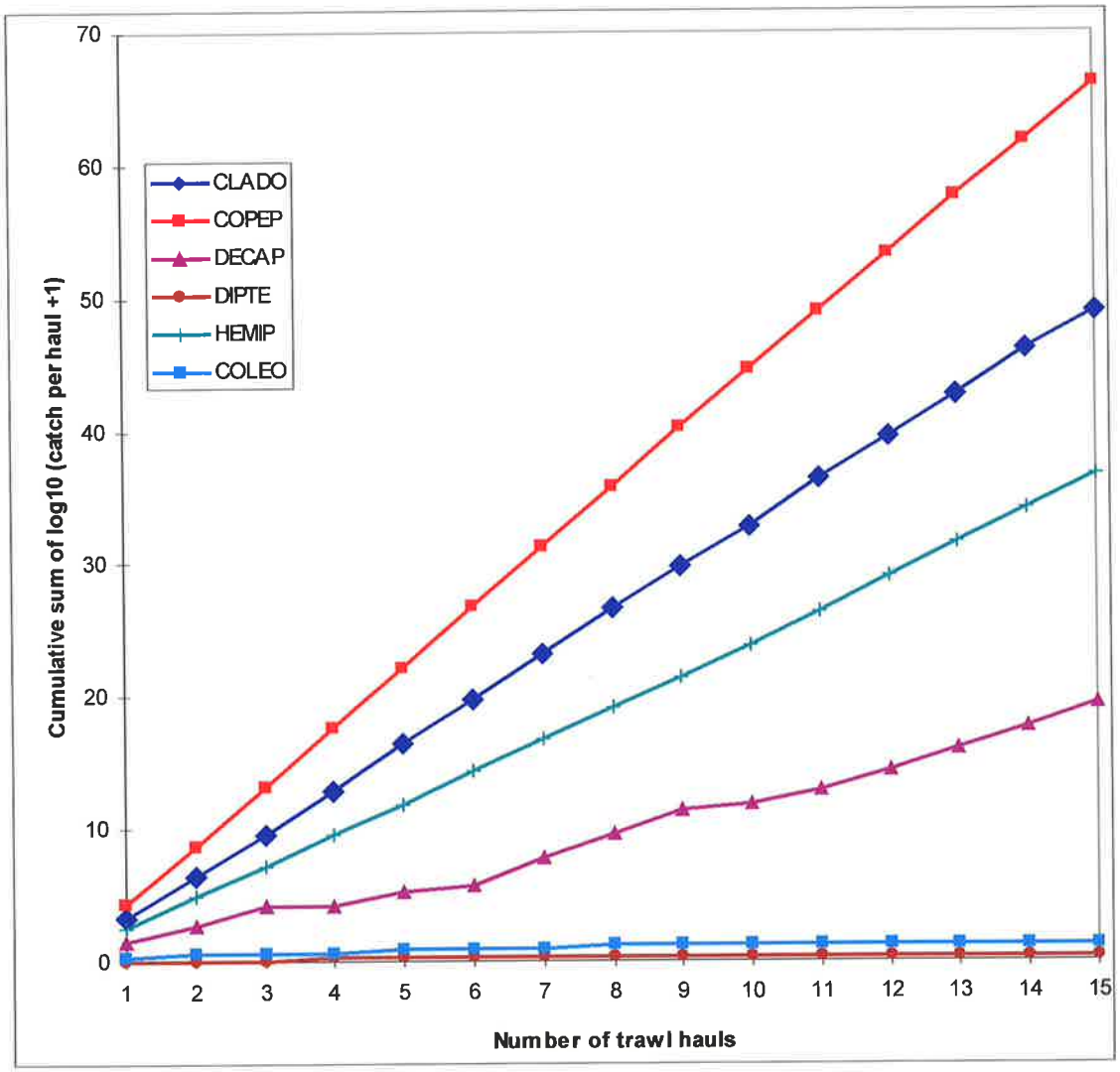


Figure 33. Cumulative catch of major macroinvertebrate taxa for number of trawl hauls in Coongie Lake.

Fish Trawl

Curves of ln(X+1) cumulative catch per fish species per number of hauls (Figs 34-35) showed species richness did not change with haul number in Lake Apanburra, but increased in Coongie Lake after six hauls. As indicated for the macroinvertebrate trawls above, although ten hauls were taken initially in the project, six hauls were subsequently taken per site, from which five were randomly selected for sorting.

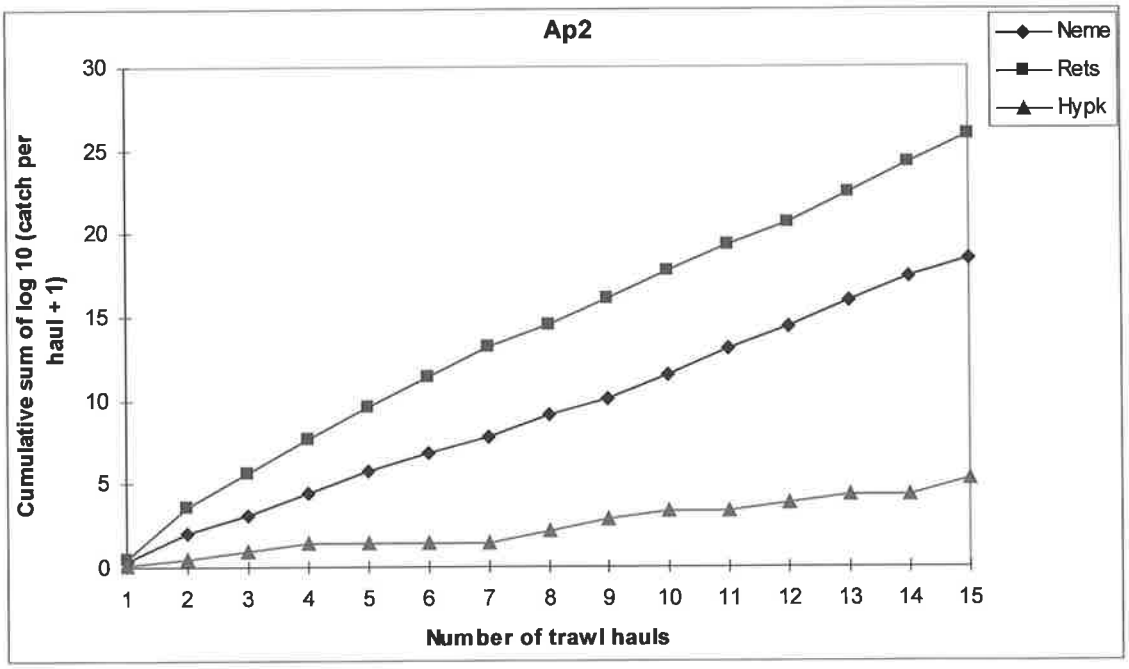


Figure 34. Cumulative catch of major fish species for number of trawl hauls in Lake Apanburra (AP2)

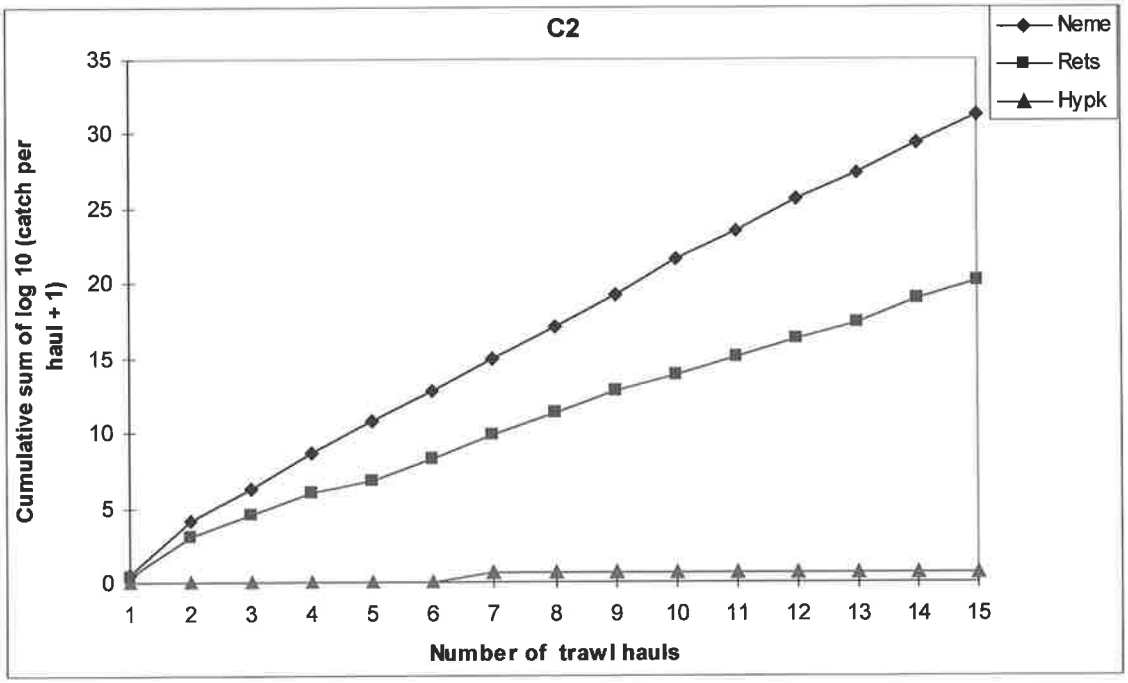


Figure 35. Cumulative catch of major fish species for number of trawl hauls in Coongie Lake (C2).

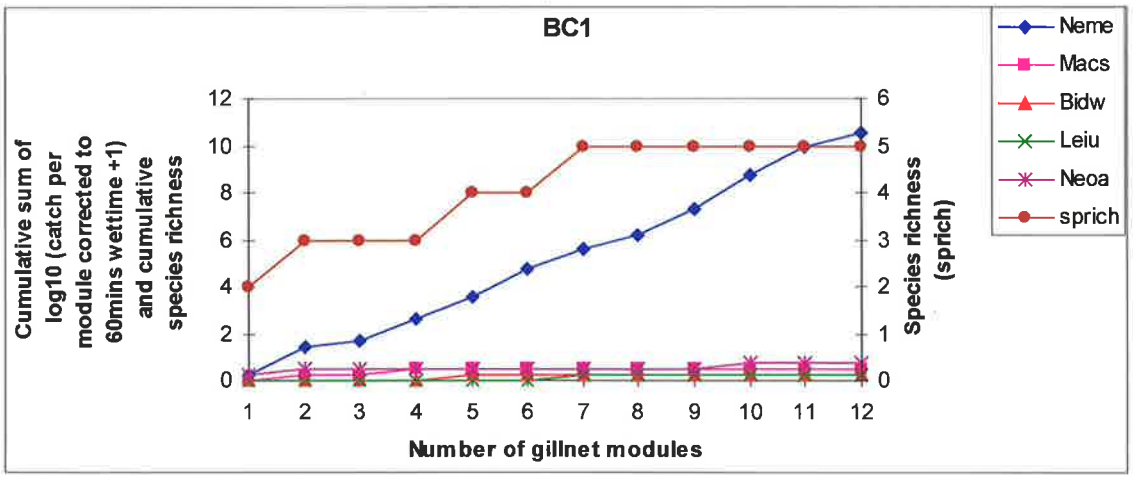
Fykenets

Fykenets were paired at each site, oriented in opposite directions in relation to the channel. It was not practicable to routinely replicate paired fykenets within sites.

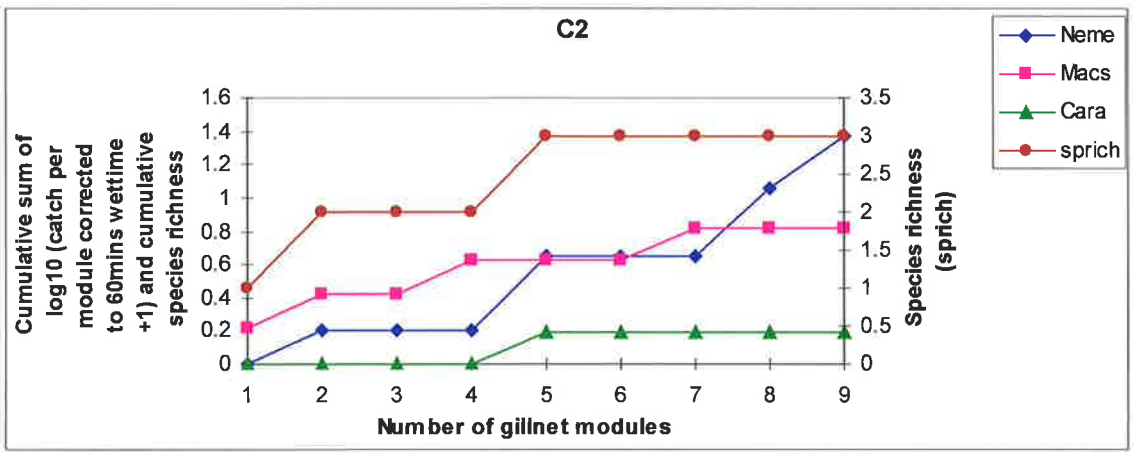
Gillnets

The relation between cumulative catch of major species and the number of gillnet modules used was examined in the catch of 9-14 modules in the open water of four waterbodies (Fig. 36(a-d)). Cumulative species richness peaked at 5-9 modules, depending on site. Routine sampling used six modules.

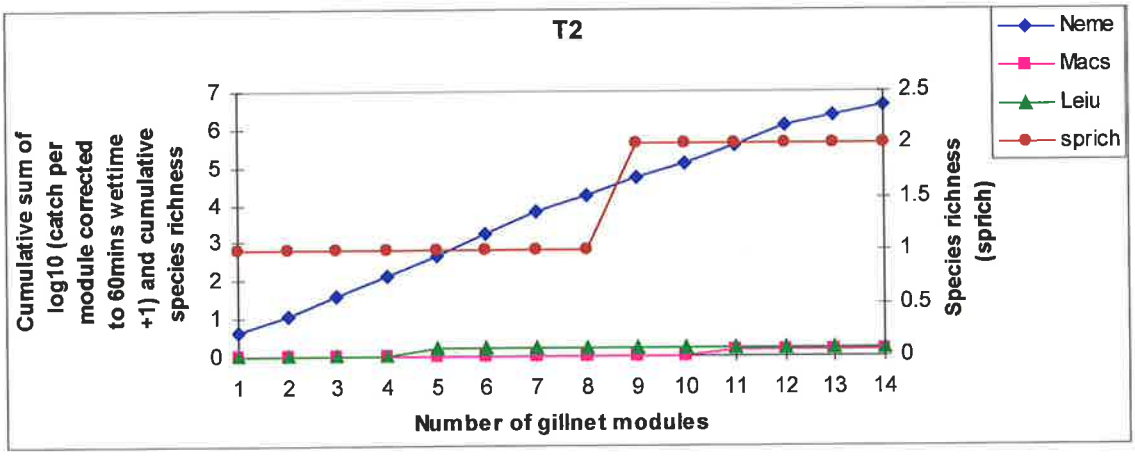
(a)



(b)



(c)



(d)

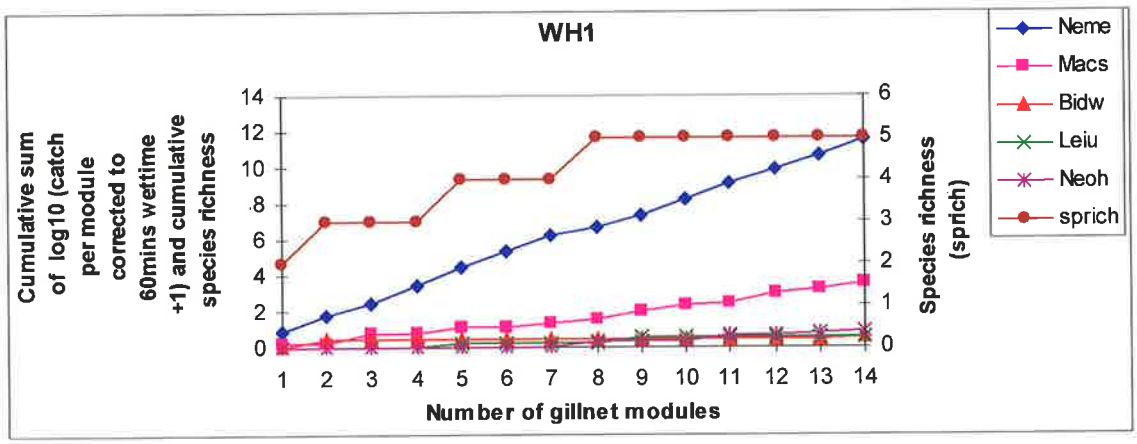


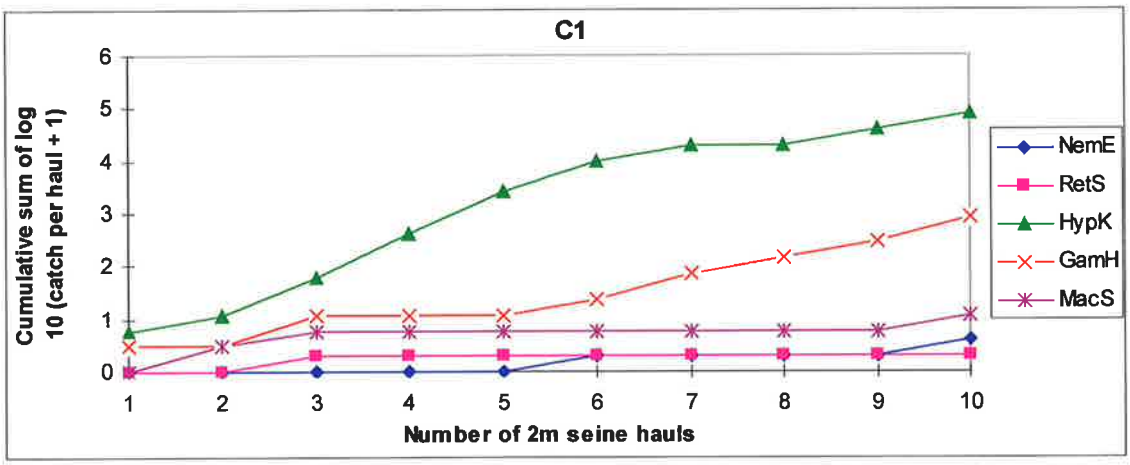
Figure 36(a-d). Relations (in four waterbodies) of cumulative catch and cumulative species richness to number of gillnet modules used.

2m seine

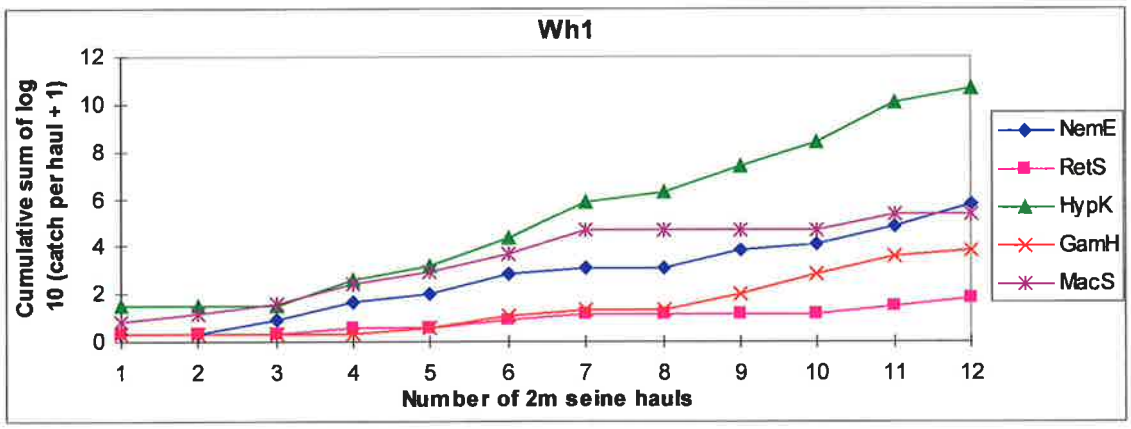
The relation between cumulative catch of major species and number of hauls of the 2m seine was examined with 10 hauls in the littoral of four waterbodies (Fig. 37 (a-d)). Species richness peaked at 1-10 hauls depending on site. Routine sampling in 1986-88 used 10 hauls. Five hauls usually were enough in warmer months to collect adequate numbers of individuals of the common species (i.e. with sufficient non-zero catches to support meaningful analyses

of, for example, recruitment patterns), and the small increase gained to cold-month catch size and to representation of rarer species by taking 10 hauls was considered not justified by the resources required. Accordingly, five hauls were taken per site in 1989-92.

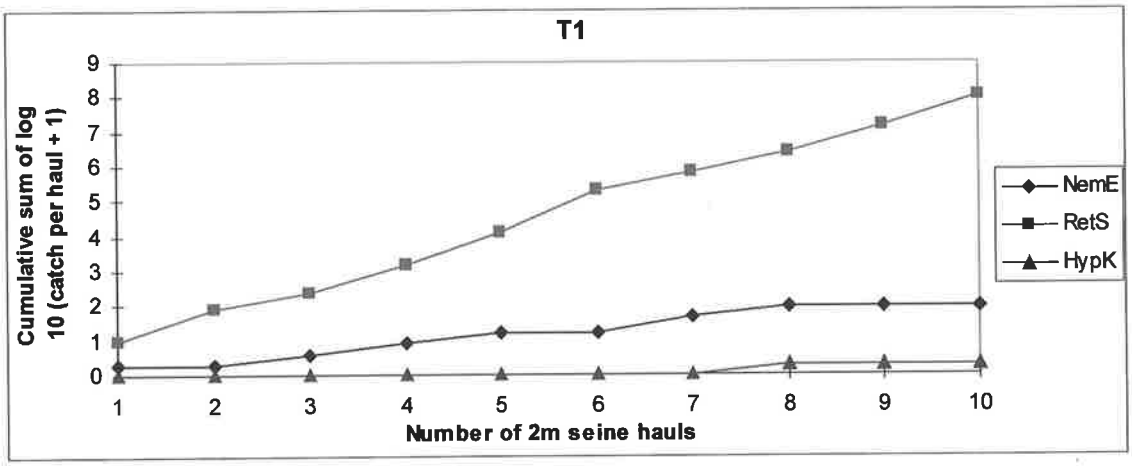
(a)



(b)



(c)



(d)

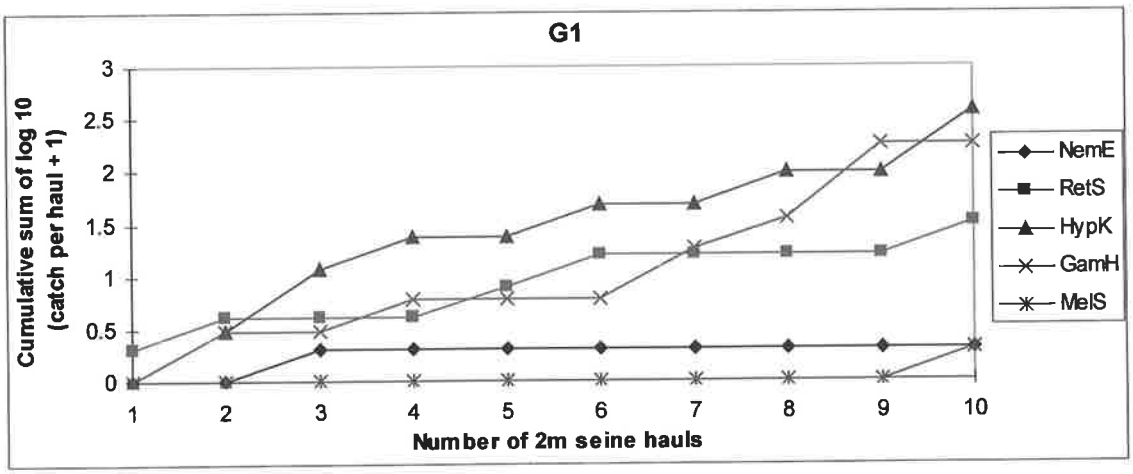


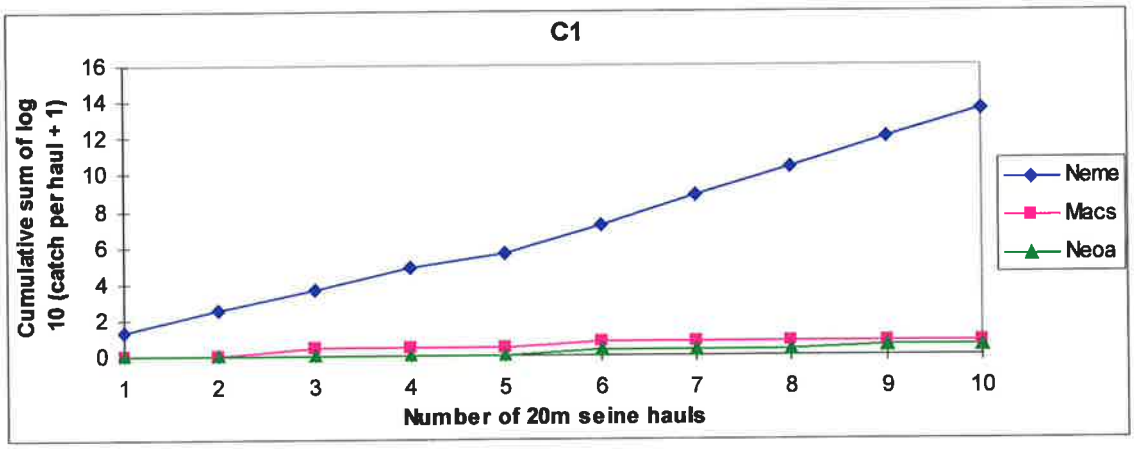
Figure 37 (a-d) Relation (in four waterbodies) between catch and number of 2m seine hauls.

20m seine

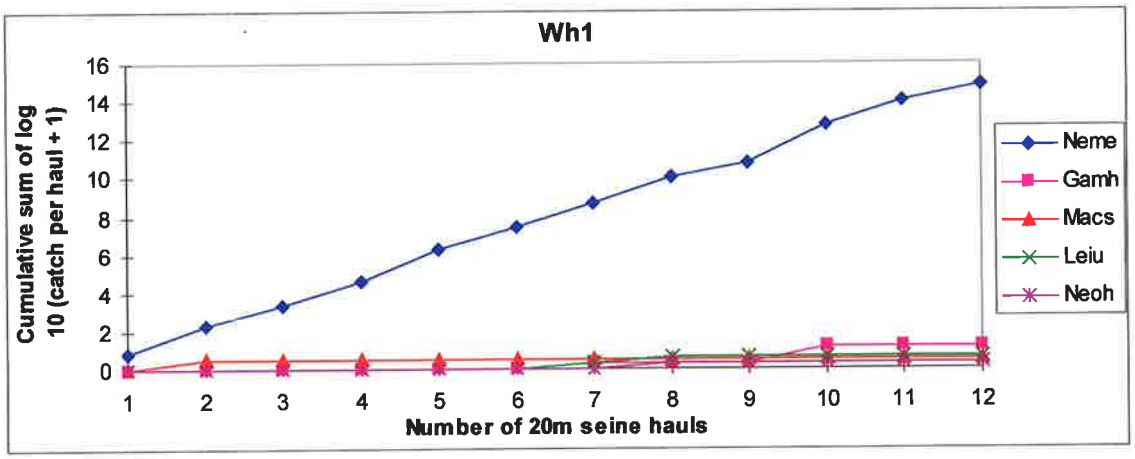
The relation between cumulative catch of major species and number of hauls of the 20m seine was examined with 10 hauls along a transect in the littoral zone of four waterbodies (Fig 38 (a-d)). Maximum species richness was at 6-9 hauls depending on site.

Routine sampling in 1986-88 used 10 hauls, but five 20m seine hauls were taken per site in 1989-92.

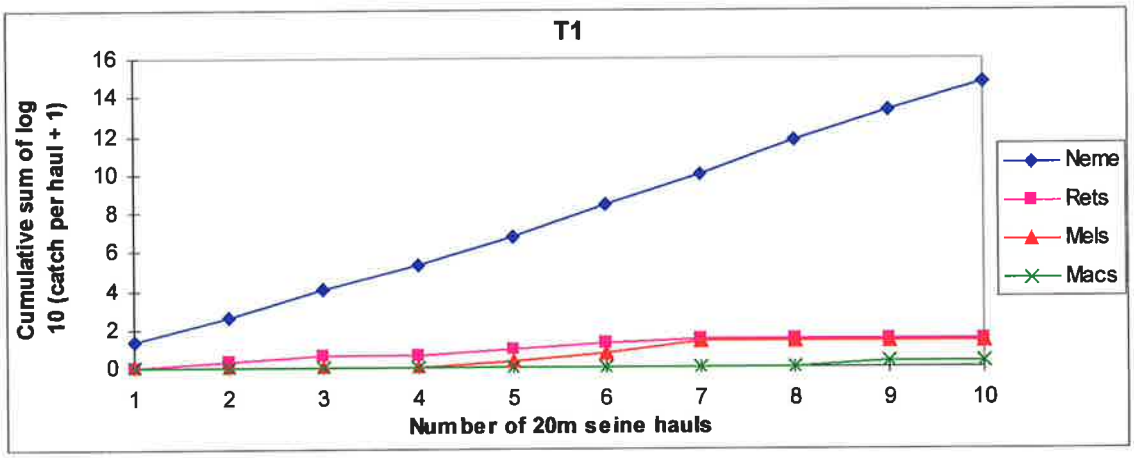
(a)



(b)



(c)



(d)

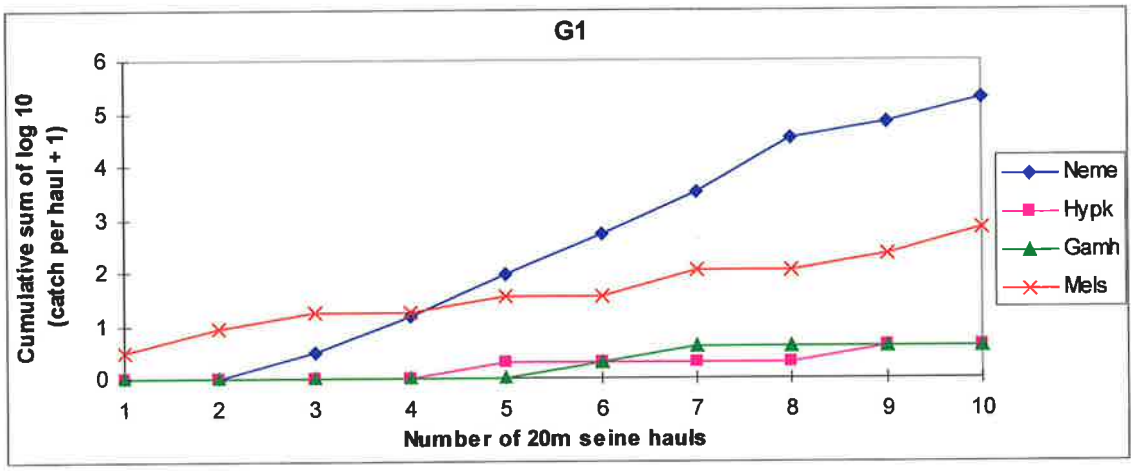


Figure 38 (a-d). Relation (in four waterbodies) between cumulative catch and number of 20m seine hauls.

Within-waterbody stratification

The significance of stratification of replicates by spatial scale within waterbodies was assessed for each gear type.

Between-site differences for the seines, zooplankton trawl and larval fish/macroinvertebrate trawl were tested in the lakes, and for the gillnets in both lakes and channels. Three or four sites (or for seines and trawls, transects) were chosen at random

around each lake within the habitat zone appropriate for the different gears. In the channels, three gillnet sites were chosen at least 0.5 km apart. Using three teams when necessary, 3-5 sample replicates were taken on one day at each site, at approximately the same time. The major lakes and channel waterbodies thus were sampled on succeeding days. A test of between-site differences in fykenet samples within a waterbody was conducted in the Coongie Crossing channel waterbody at two sites on three dates (23 replicates in all). Catch-effort data were transformed ($\log_{10}(X+1)$ or fourth root), Bray-Curtis distance matrices derived (Bray & Curtis 1957), and significance of differences between sites groups, between lakes groups and between channel waterbody groups were determined by one–way ANOSIM. For the fykenet samples, differences between sites and between dates were tested by two-way crossed ANOSIM.

Analysis of lakes multimesh gillnet samples showed a difference between lakes (P <0.01), but not between sites (P >0.05), and analysis of channel multimesh gillnet samples showed a difference between channel waterbodies (P <0.001), but not between sites (P >0.05). However, analysis of lakes 2m seine samples gave differences between lakes (P <0.001) and also between sites (P <0.01), as did the analysis of 20m seine samples (P <0.01, P <0.001), the combined 2m seine and 20 seine data (P <0.01, P <0.001), the zooplankton trawl data (P <0.001, *P<0.001*) the macroinvertebrate trawl data (*P<0.001, P<0.001*) and the fish trawl data (P<0.001, P<0.05). Two-way crossed ANOSIM showed significant differences between dates (P <0.001) for the fykenet samples, but not between sites (P >0.05).

Quantifying these within-waterbody differences in routine sampling presented practical difficulties. Only one team was routinely available, and attempting to replicate sampling at even three sites in each lake would have created discrepancies in diurnal timing of samples. Thus only one site or transect was sampled per waterbody, and results from analysis of one dataset alone were not assumed to characterise the assemblage of a waterbody.

Application of individual gears (Table 37)

Zooplankton trawl

Surface 20m trawl hauls were replicated randomly along a single 300-m transect parallel to the western shore of each lake, and approximately within the 1m depth contour. As water levels changed over time, the position of this transect shifted over a maximum distance of 1 km. Sampling in channel habitats had to be opportunistic, because locations of open shallow littoral and sub-littoral areas varied over flow cycles.

Fish/Macroinvertebrate Trawls

In the lakes ichthyoplankton/nekton trawls were along open water transects. Half the hauls was taken upwind and half downwind, so that wind and wave effects were compensated. Over the project period a subsample of five hauls was randomly selected for processing from 6-15 collected. This provided randomness in positioning hauls along the transects.

No trawls were taken in Browne Creek (BC1), Ellar Creek (EC1) and the Apanburra Channel (APC) because these channels had narrow sections and snags which made use of the trawl hazardous. However, samples were taken consistently along mid-channel transects at Coongie Crossing (WH1-2), Queerbidie Waterhole (MB1) and Cullamurra Waterhole (CA1), and occasionally at Tirawarra Waterhole (TW2) (Fig. 21). Again, equal numbers of hauls were taken upstream and down to correct for effects of current.

Fykenets

Fykenets were set in the channels in the vicinity of gillnet sets, but far enough away (0.5 km) to avoid interference. Nets were set in pairs along the channel margin, one net facing upstream the other downstream, in depths of 0.8-1.2 m. Fykenets were not set in the lakes, owing to time constraints. For the same reason no within-waterbody replication of fykenet pairs was attempted.

Gillnets

Gillnet sites were within the deeper open water of the lakes, at least 500m from the nearest shore and from topographic features such as islands. Since diurnal variation in gillnet catches was significant (see above), gillnetting was confined to mid-afternoon.

Gillnet sampling in the channels was conducted in 1986-88 using five nets of different mesh sizes. Because one purpose of the sampling was to monitor fish movement (although this function was later performed by fykenets), nets were set across the channel, at 2-5 standard stations (depending on the length of suitable channel available) 0.5km apart. Nets of the five different mesh sizes were allocated between these sites in a random temporal sequence. From December 1988, the use of multimesh nets meant that all mesh sizes could be fished simultaneously at different sites. Comparison and standardisation of mono- and multi-mesh net catches are discussed under *Data Structure* below.

Seine nets

Seine hauls were replicated randomly along a single 300-m transect parallel to the western shore of each lake, and within approximate depth contours for each seine type. As water levels changed over time, the position of this transect shifted over a maximum distance of 1 km. The completion of one transect typically took 2-3h. Sampling in channel habitats had to be opportunistic, because locations of open shallow littoral and sub-littoral areas varied over the flow cycles and hauls could not be confined to a transect.

Table 37. Temporal and spatial replication per sampling gear.

Gear	Temporal replication	Spatial replication
Fykenet	regular 2-monthly, am/pm/night	paired at channel mouths
Gillnet (mono)	regular 2-monthly, pm	single in channels and lakes
Gillnet (multi)	regular 2-monthly, pm	1-5 in channels and lakes
2m seine	regular 2-monthly, am	5-15 in channels, 5-15 randomly on 300m transect in lakes littoral
20m seine	regular 2-monthly, am	5-15 in channels, 5-10 randomly on 300m transect in lakes littoral
Fish/macroinv. trawl	regular 2-monthly, pm	5-10 on 2km lake or channel transects
zooplankton trawl	regular 2-monthly, am	5-10 on 300m lake or channel transects

Two of the sampling gears (zooplankton trawl and fykenets) were used only in the later years of the program (Table 38), and sampling with all gears missed dates in 1987, 1988 and 1991.

Table 38 Years sampled per gear

Gear	Dec. 86	87	88	89	90	91	Apr. 92
zooplankton trawl					y	y	y
Fish/macroinvertebrate trawl	y	y	y	y	y	y	y
2m seine	y	y	y	y	y	y	y
20m seine	y	y	y	y	y	y	y
fykenets				y	y	y	y
gillnets	y	y	y	y	y	y	y

Sorting and subsampling

Zooplankton (60μ trawl)

The raw sample was poured into a 2L measuring cylinder, the volume made up to 2L, the contents poured into a large jar, and mixed carefully with a perforated plunger. A 10mL sample was quickly withdrawn by a wide-mouth pipette, transferred to a maze tray, and counted under a binocular microscope. Counts were corrected by the ratio: total volume made up/sample volume. The total volume made up was varied between 1 and 4L to keep the count of animals to approximately 100-500.

Macroinvertebrates, larval and juvenile fish (500 μ trawl)

The sample was washed through a set of sieves (250 μm, 2mm, 4mm). All animals in the 4mm sieve were counted. Animals in the smaller sieves were subsampled as follows. The sieve contents were poured into a Folsom splitter, a plastic cylindrical subsampler with a radial part-closed partition. The volume in the subsampler was made up to 250mL of water, the sample mixed with a glass rod and quickly split by tilting the subsampler. The half of the sample in the open section was tipped into a beaker. The process was repeated with the sample remaining in the subsampler until the number left in the subsampler was about 200 animals. The counts of the subsampled taxa were multiplied by the ratio *sample volume/subsample volume*. Chi-squared comparison of subsample estimates with total counts showed no significant differences for common taxa (i.e. those for which a majority catches were non-zero), although not surprisingly rare species were not accurately estimated.

Other gears

Animals in all other gears were counted in full.

4.2.3 Data Structure

4.2.3.1 Taxonomy

Fishes were identified to species, with the caveat that some juvenile and larval specimens identified in the field as *Hypseleotris klunzingeri* could be *Hypseleotris* "sp. 4"

(Midgley's carp gudgeon) or *Hypseleotris* "sp. 5" (Lake's carp gudgeon). Through 1986-87, macroinvertebrates were collected by a variety of techniques, and were identified principally to family (Appendix 1). However, macroinvertebrates collected throughout the project from open water in the 500μm trawl, were identified only to order. Patterns of assemblage structure at this level may not differ greatly from that at the level of genus, particularly for quantitative data (Bowman & Bailey 1997).

4.2.3.2 Hydrology

Following Chapter 2, a *facet* of the hydrograph is a feature of biological significance, and a *measure* is the quantification of that facet at a given scale. The term *attribute* is used here in statistical analysis as a collective term, denoting hydrological measures, biological characters (e.g. abundance, biomass), or non-hydrological environmental parameters. Hydrological measures were chosen in accord with Chapter 2, qualified by considerations of the shorter temporal scale and smaller spatial scale of the study, the two-monthly temporal resolution and practical constraints. In particular, with the exception of "relative drying frequency" (which could be estimated from the Landsat record), the time-scale of waterbody records did not allow for statistically generalised measures appropriate to the *flow regime* temporal scale. Instead, hydrological measures (with the exception of waterbody permanence) relate only to the period 1986-92 and therefore to the *flow history* temporal scale.

Waterbody spatial scale, flow history temporal scale

Several facets of hydrology have been proposed as important for the ecology of rivers, but there is general agreement that timing, frequency, duration, rate of change, magnitude, predictability and variability should be included (Chapter 2, Richter 1996, 1997, Young 1999). The only long-term data available at the waterbody scale was waterbody frequency of drying – a measure of permanence. However, at the waterbody scale, another facet, connectivity, is recognized as important (Amoros & Roux 1988, Heiler *et al.* 1995, Schumaker 1996, Statzner *et al.* 1997). The waterbody scale data also were inadequate to reliably determine rates of depth change throughout the study period. "Pulse shape" was included as a facet separate to pulse duration because of the special implications of

differences in rising and falling limb duration for fish ecology (Welcomme 1989, Mallen-Cooper & Brand 1991). "Amplitude" was used instead of "magnitude", to distinguish between other components of "magnitude" such as duration and (at the river reach scale) "volume" (Young 1999). The 30 measures selected at the waterbody scale (Table 39) hence characterise six facets of flow history (viz. amplitude, duration, pulse shape, connectivity, frequency, and timing) and one of flow regime (viz. permanence). A "pulse" was delimited between the beginning of the rising limb and the end of the falling limb of waterbody depth, at the two-monthly scale.

Values for these measures were derived from Landsat records, hydrological data from Cullyamurra gauging station, onsite measurements during the study and local knowledge. Some measures could not be spatially replicated within waterbodies. "Relative frequency of drying" was used (measure 30) rather than the quantitative data provided by the Landsat record because the inundation status of the channel waterbodies could not be resolved directly from the Landsat imagery. The relative permanence of the channel reaches in relation to larger waterbodies, however, could be deduced from extrapolation of the relations established during the study period between inundation of particular swamps or lakes and associated channel flows.

Values for measures of hydrological events more than two events past were not included because for sites inundated late in the study period these measures had too many missing values to be informative. Variation in flow pulse timing was measured as the temporal deviation in months of a given pulse in a given waterbody from the long-term average timing of pulses. The long-term average was derived from the timing of peaks and troughs of monthly flows in the gauging record at Cullyamurra Waterhole. The lags between the peak and minimum stage heights at the gauging station and peak and minimum depths in the waterbodies downstream were determined from on-site depth readings throughout the project. Such extrapolations from a single gauge station are admittedly crude, but were the best that could be achieved in this poorly gauged system.

Table 39: Flow history measures for each waterbody (except no. 30 which is a flow regime measure).
"Connection" defined as a fish-negotiable passage to a large waterbody - either a lake or a channel reach of at least 5km. "Flow" in relation to lakes defined as current speed in inflow channel immediately upstream

Code	Facet	Measure
1 MXTIM	Timing	Departure of peak waterbody depth from long-term average timing
2 MNTIM	Timing	Departure of minimum waterbody depth from long-term average
3 DPFLO	Flow	Duration of present flow (if any)
4 DLFLO	Flow	Duration of flow at one remove from present (last flow)
5 DLFL1	Flow	Duration of flow at two removes
6 DPNFL	Flow	Duration of present cessation of flow (if any)
7 DLNFL	Flow	Duration of cessation of flow at one remove from present
8 DLNF1	Flow	Duration of cessation of flow at two removes
9 PSDEP	Amplitude	Present standard depth
10 LMADE	Amplitude	Last maximum depth
11 LMAD1	Amplitude	Maximum depth at one remove from last
12 LMIDE	Amplitude	Last minimum depth
13 LMID1	Amplitude	Minimum depth at one remove from last
14 DPRLM	Pulse shape	Duration of present rising limb (if any)
15 DLRLM	Pulse shape	Duration of rising limb at one remove from present
16 DLRL1	Pulse shape	Duration of rising limb at two removes
17 DPFAL	Pulse shape	Duration of present falling limb (if any)
18 DLFAL	Pulse shape	Duration of falling limb at one remove from present
19 DLFA1	Pulse shape	Duration of falling limb at two removes
20 DPINU	Duration	Duration of present inundation (if any)
21 DLINU	Duration	Duration of inundation at one remove from present
22 DLDRY	Duration	Duration of dry at one remove from present
23 DLDR1	Duration	Duration of dry at two removes
24 DPUCO	Connection	Duration of present upstream connection (if any).
25 DLUCO	Connection	Duration of upstream connection at one remove from present
26 DLUC1	Connection	Duration of upstream connection at two removes
27 DPDCO	Connection	Duration of present downstream connection (if any)
28 DLDCO	Connection	Duration of downstream connection at one remove from present
29 DLDC1	Connection	Duration of downstream connection at two removes
30 RPINU	Permanence	Relative frequency of drying

River reach spatial scale, flow history temporal scale

At the river reach scale, the Cullyamurra gauge station record provided complete data coverage of the sampling period and the immediately preceding years. This allowed preparation of a more comprehensive range of hydrological measures than was possible at the waterbody scale. Flow pulse volume and rates of change (rise and fall of the pulse) could be added to the range of facets, connectivity and permanence were deleted. As at the waterbody scale, the period of biological sampling and of site-specific records of hydrology (i.e. 5 years) was too short to usefully compare biological responses to long-term statistical measures of flow regime, so the measures chosen characterize only flow history.

The river reach hydrological measures (Table 40) were calculated from the discharge record (mean monthly discharge, ML) at the Cullyamurra gauging station. A "flow pulse" was delimited between the beginning of the rising limb and the end of the falling of Cullyamurra discharge, at the monthly scale. Means per month were used because medians gave misleadingly high numbers of zero flow months. Data were lagged according to the median delays (in months) over 1986-92 between pulse peaks at Cullyamurra and pulse peak arrivals at key Coongie Lakes waterbodies. These median delays were determined from onsite measurements during 1986-92, and from the longer record of the remote sensing data. This tailored the Cullyamurra record approximately to the timing of events at each sampling site.

Per event timing of pulse maxima and minima were calculated as the number of months earlier in the year (-ve) or later (+ve) than the long-term average at Cullyamurra, adjusted for the lag between Cullyamurra and each waterbody. Three measures of strictly seasonal (as distinct from hydrological) conditions were included for comparison with the hydrological measures. These seasonal measures were mean monthly maximum and minimum air temperatures and mean monthly daylength, all measured at Moomba, 50km southwest of Cullyamurra gauge station (Bureau of Meteorology, Adelaide).

Table 40 Seasonal measures and hydrological measures from the Cullyamurra discharge record, lagged to fit the Coongie Lakes wetlands flow history 1986-92

	CODE	FACET	Description
1	MXTEM	season	maximum air temperature (C)
2	MNTEM	season	minimum air temperature (C)
3	DLENG	season	daylength (mins)
4	MTOTL	Flow volume	monthly total discharge (ML)
5	PTOTL	Flow volume	total discharge to date of present pulse (ML)
6	LTOTL	Flow volume	total discharge to date of past pulse (ML)
7	LTOT1	Flow volume	total discharge to date of pulse before last (ML)
8	LTOT2	Flow volume	total discharge to date of pulse two before last (ML)
29	PDISC	Amplitude (current discharge)	present monthly discharge (ML)
30	LMADS	Amplitude (maximum per pulse)	last maximum discharge (ML)
31	LMAD1	Amplitude (maximum per pulse)	maximum discharge before last (ML)
32	LMAD2	Amplitude (maximum per pulse)	maximum discharge two before last (ML)
33	LMIDS	Amplitude (minimum per pulse)	last minimum discharge (ML)
34	LMID1	Amplitude (minimum per pulse)	minimum discharge before last (ML)
35	LMID2	Amplitude (minimum per pulse)	minimum discharge two before last (ML)
9	LRLAM	Amplitude (of rising limb)	amplitude of last rising limb (ML)
10	LRLA1	Amplitude (of rising limb)	amplitude of rising limb before last (ML)
11	LRLA2	Amplitude (of rising limb)	amplitude of rising limb two before last (ML)
12	LFLAM	Amplitude (of falling limb)	amplitude of last falling limb (ML)
13	LFLA1	Amplitude (of falling limb)	amplitude of falling limb before last (ML)
14	LFLA2	Amplitude (of falling limb)	amplitude of falling limb two before last (ML)
15	RLRSL	Rate of change (rise of flow pulse)	rate of last rise (ML/month)
16	RLRS1	Rate of change (rise of flow pulse)	rate of rise before last (ML/month)
17	RLRS2	Rate of change (rise of flow pulse)	rate of rise two before last (ML/month)
18	RLFLL	Rate of change (fall of flow pulse)	rate of last fall (Ml/month)
19	RLFL1	Rate of change (fall of flow pulse)	rate of fall before last (ML/Month)
20	RLFL2	Rate of change (fall of flow pulse)	rate of fall two before last (Ml/Month)
21	DPFLO	Duration of flow	duration of present flow (months)
22	DLFLO	Duration of flow	duration of last flow (months)
23	DLFL1	Duration of flow	duration of flow before last (months)
24	DLFL2	Duration of flow	duration of flow two before last (months)
25	DPNFL	Duration of no flow	duration of present no flow (months)
26	DLNFL	Duration of no flow	duration of last no flow (months)
27	DLNF1	Duration of no flow	duration of no flow before last (months)
28	DLNF2	Duration of no flow	duration of no flow before last (months)
36	DPRLM	Pulse shape (duration of rising limb)	duration of present rising limb (months)
37	DLRLM	Pulse shape (duration of rising limb)	duration of last rising limb (months)
38	DLRL1	Pulse shape (duration of rising limb)	duration of rising limb before last (months)
39	DLRL2	Pulse shape (duration of rising limb)	duration of rising limb two before last (months)
40	DPFAL	Pulse shape (duration of falling limb)	duration of present falling limb (months)
41	DLFAL	Pulse shape (duration of falling limb)	duration of last falling limb (months)
42	DLFA1	Pulse shape (duration of falling limb)	duration of falling limb before last (months)
43	DLFA2	Pulse shape (duration of falling limb)	duration of falling limb two before last (months)
44	LMXTM	Timing of pulse maximum	Timing of last maximum discharge (months +/- average)
45	LMXT1	Timing of pulse maximum	Timing of maximum discharge before last (months +/- average)
46	LMXT2	Timing of pulse maximum	Timing of maximum discharge two before last (months +/-average)
47	LMNTM	Timing of pulse minimum	Timing of last minimum discharge (months +/- average)
48	LMNT1	Timing of pulse minimum	Timing of minimum discharge before last (months +/- average)
49	LMNT2	Timing of pulse minimum	Timing of minimum discharge two before last (months +/- average)

4.2.3.3 Biological data collected per gear type

Not all gear types were used at all sites. Further, the different intervals for which the waterbodies were inundated meant different lengths of sampling record for different waterbodies. Finally, some sites were sampled opportunistically, or were used for initial determinations of within-waterbody variance.

Biological information from each sampling gear also varied (Table 41). Fykenets provided most information, partly because the catches were easily processed with minimal mortality. For example, seine nets were often used in shallow wetlands where access and sample processing were difficult.

Fish length was measured in total length (TL), although sufficient measures of fork length (FL) were made to establish a TL-FL relation to be used when the caudal fin of a specimen was damaged. Live weight was measured to the nearest gram on a field electronic balance (Salter model 323, capacity 5000 gm, accurate to 0.1gm). Incidence of spawning was assessed by running finger and thumb along the fish's abdomen to test for release of genital products. Direction of fish movement was assessed by direction of orientation at capture in cross-channel gillnets, and (more reliably) by capture in upstream/downstream facing paired fykenets. Fin-clipping of large-growing species was also trialled, but recaptures were too few to be informative.

Incidence of fungal disease was determined by recording the presence of ulcerated skin lesions containing obvious mycelia. In the field, samples of fungal mycelium were transferred with flamed forceps to vials of sterile river water. Some mycelial samples were transferred in the laboratory to Chloramphenicol–cornmeal agar plates for culture. Mycelia kept in sterilized river water were examined before sub-culturing to check the selectivity of the agar medium (Willoughby 1978). Hyphal tips from the agar colonies were repeatedly subsampled until bacteria-free. Following Puckridge *et al.* (1989) some isolates were transferred to sterile distilled water to observe zoospore release, others were maintained in the dark at 7 °C on sterilized hemp seed in filtered and autoclaved river water to allow observations of sexual structures. Samples of infected tissue were excised with a flamed

scalpel, preserved in 10% formalin and sent to Dr. J.S. Langdon of the Australian Fish Health Reference Laboratory for histopathological examination.

Table 41. Faunal attributes measured per gear type.

Gear	*Selected fauna*	*Attributes measured*
Fykenets	Large fish (juveniles, adults) in the littoral	Species, relative abundance, length, weight, disease incidence, breeding condition, direction of movement
Gillnets (mono, multi mesh)	Large fish (juveniles, adults) in open water	Species, relative abundance, length, disease incidence, breeding condition, direction of movement
2m seine	Larval, juvenile fish in the littoral	Species, relative abundance
20m seine	Juvenile and adult small fish in the littoral	Species, relative abundance
500µm trawl	Larval, juvenile fish: nektonic macro-invertebrates, large zooplankters in open water	*Fish*: species, relative abundance, length, disease incidence; *Macroinvertebrates and zooplankton*: Taxa, relative abundance.
60µm trawl	Littoral zooplankton	Taxa, relative abundance

The data in Table 41 enabled assemblage structures to be determined for macroinvertebrates, zooplankton and fish, and for some of the fish datasets, relative densities and biomass, population structures, and patterns in spawning, growth, recruitment, migration, colonisation, condition and health were also determined.

4.2.3.4 Non-hydrological habitat data

Physico-chemical and vegetation habitat data were collected for each site (Table 42) and sample (Table 43). The site measurements were at standard locations determined by triangulation in the lakes (later by GPS, using a Garmin 100) and by cross-channel

measurements in the channels. Density of vegetation was ranked along seine transects, adjacent to fykenet and gillnet sites. In 1986-87 maximum current speed was measured by timing a floating orange over 100 m (Gordon *et al.*, 1992). From February 1988, current speed was measured in channels with an Ott Mk5 current meter, "Arkansas" 18039. Although mean current speed is advisedly measured at 0.6 depth from the surface (Gordon *et al.* 1992) to maintain comparability with the earlier records current meter measurements were made at 0.2 m depth (the minimum advised operating depth). Temperature and dissolved oxygen were measured throughout the water column with a YSI meter 51B meter and also at 0.2m with an alcohol-in-glass thermometer. pH was measured with a Selby 800 meter, conductivity with a Kent Electronic Instruments bridge, correcting to 25°C, both at 0.2m. All meters were calibrated between field trips.

Waterbody width and length were estimated from Department of Lands topographic maps 7042, 6943 and 6944, and lake area was determined by the Department of Housing and Urban Development using ARC/info software and 1:40,000 aerial photo (1986) boundaries transferred to 1: 100,000 map sheets and digitized. Depth data for lake bathymetry were obtained by boating along transects set up with GPS and sampling depths with a weighted tape.

Depending on habitat type, subsets of the data in Table 43 were measured. Physico-chemical data and substratum composition were recorded per sample for all gears. For trawls and gillnets in open water, vegetation usually was absent. For seines and fykenets in the littoral and sublittoral, vegetation and substratum composition were scored by presence/absence in five grabs per replicate along the transects. For channel sites where seines were not used, substratum types and submerged vegetation were determined from five randomly-placed benthic grabs. For lake sites and channels where seines were used, these data were averaged from the results of per sample benthic grabs.

Table 42. Non-hydrological environment data recorded per site.

Site data	Measure
waterbody type	text (channel, lake)
wind	rank 1-4 (calm, light, moderate, strong)
sun	rank 1-3 (dense overcast, cloudy, fine)
density of terrestrial adjacent vegetation	rank (1-5)
density of terrestrial submerged vegetation	rank (1-5)
density of aquatic emergent vegetation	rank (1-5)
density of aquatic submergent vegetation	rank (1-5)
density of aquatic floating vegetation	rank (1-5)
density of aquatic floating vegetation	rank (1-5)
wave action	rank (1-5)
current speed	integer (m/s)
fetch	integer (km)
relative area of rock substratum	rank (0,1)
relative area of gravel substratum	rank (0,1)
relative area of sand substratum	rank (0,1)
relative area of mud substratum	rank (0,1)
relative area of clay substratum	rank (0,1)
relative area of vegetation litter	rank (0,1)
bank slope	rank 1-5 (undercut, vertical, acute, shallow flat)
waterbody width	integer (m/km)
relative waterbody length	integer (km)
relative waterbody area	integer (km^2)
depth at standard site	integer (m)
conductivity @ 25C	integer (µS/cm)
Secchi depth	integer (cm)
pH	integer
mean surface water temperature C	integer (°C)
mean concentration of oxygen at 0.2m	integer (ppm)
Oxygen and temperature at 0.2m intervals	ppm, (°C)
Temperature stratification	integer (surface – bottom)
Dissolved oxygen stratification	integer (surface - bottom)

Table 43. Non-hydrological environment data recorded per sample.

Data recorded per replicate	Measure
mean depth	integer (m)
concentration of dissolved oxygen at 0.2m	integer (ppm)
surface water temperature C	integer (°C)
SURFACE VEGETATION DENSITY	
Muehlenbeckia florulenta	rank (1-5)
Eucalyptus coolabah	rank (1-5)
Acacia stenophylla, Acacia salicina	rank (1-5)
Sesbania cannabina, Aeschynomene indica	rank (1-5)
snags	rank (1-5)
Cyperus sp.	rank (1-5)
Polygonum lapathifolium	rank (1-5)
Marsilea drummondii	rank (1-5)
Ludwigia peploides	rank (1-5)
Pseudoraphis spinescens	rank (1-5)
Sporobolus sp.	rank (1-5)
filamentous algae	rank (1-5)
Azolla filiculoides	rank (1-5)
Lemnadisperma	rank (1-5)
BENTHIC VEGETATION DENSITY	
Marsilea drummondii	rank (1-5)
filamentous algae	rank (1-5)
other algae	rank (1-5)
Snags	rank (1-5)
Cyperus sp.	rank (1-5)
Myriophyllum verrucosum	rank (1-5)
Ludwigia peploides	rank (1-5)
Pseudoraphis spinescens	rank (1-5)
Marsilea hirsuta	rank (1-5)
Sporobolus sp.	rank (1-5)
Muehlenbeckia florentula	rank (1-5)
Sesbania cannabina, Aeschynomene indica	rank (1-5)
Polygonum sp.	rank (1-5)
SUBSTRATUM COMPOSITION	
benthic leaf litter	rank (1-5)
benthic stick litter	rank (1-5)
benthic roots	rank (1-5)
mud	rank (1-5)
clay	rank (1-5)
sand	rank (1-5)
rock	rank (1-5)

4.2.4 Data Preparation

4.2.4.1 Weighting of gillnet multimesh data to consistency with monomesh data

From 1986-88 six monomesh gillnets of 40m length, each of a different mesh size, were used. From December 1988 these were replaced with modular multimesh nets, each module comprising six 2m panels of different mesh sizes. Catches per unit effort of the six mesh sizes of monomesh and multimesh nets were compared for thirty-six concurrent sets over three days in Lake Toontoowaranie. The patterns of relative catch for the major species were similar for the two sets of gear (Figs. 39-40).

Ratios of mean catch per 40-m monomesh panel against concurrent mean catch per 2m multimesh panel were calculated from the above data (Table 44). Only catches for bony herring in meshes 40, 50, 70, 90 occurred with sufficient frequency in both mono- and multi-mesh nets to allow for reliable comparisons. However, since the patterns of relative catch between species were similar for the two gear types, it seemed justifiable to use the mean of the ratios for bony herring (16.0) to approximate the ratios for other species and for mesh sizes 30 and 110. This mean differed sufficiently from the 20:1 ratio of monomesh net length to multimesh panel length (Table 32) to justify using it to weight the multimesh catches of 1989-92 to make them comparable with the monomesh catches of 1986-88.

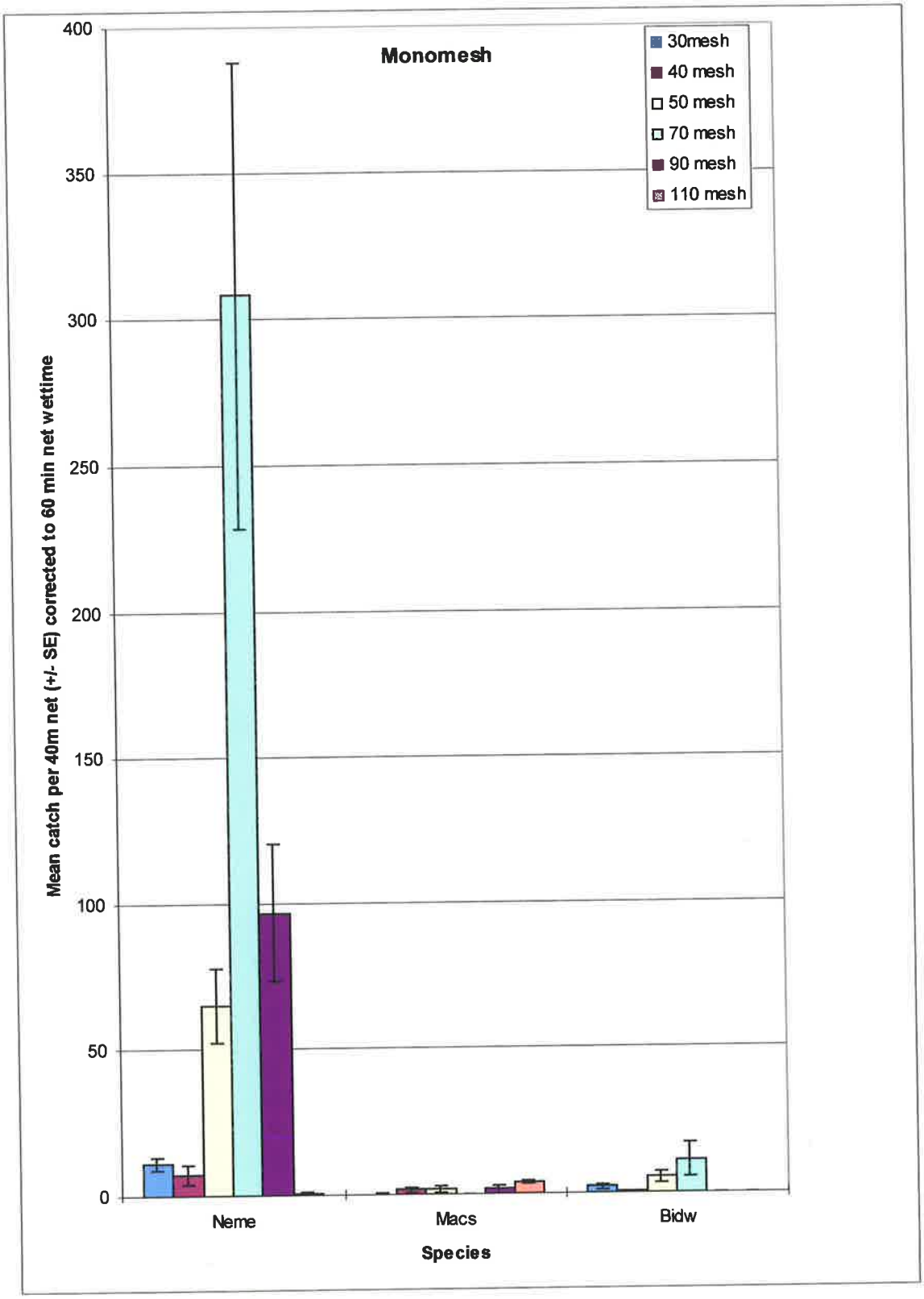


Figure 39. Mean catch per unit effort per taxon in 40m monomesh gillnets.

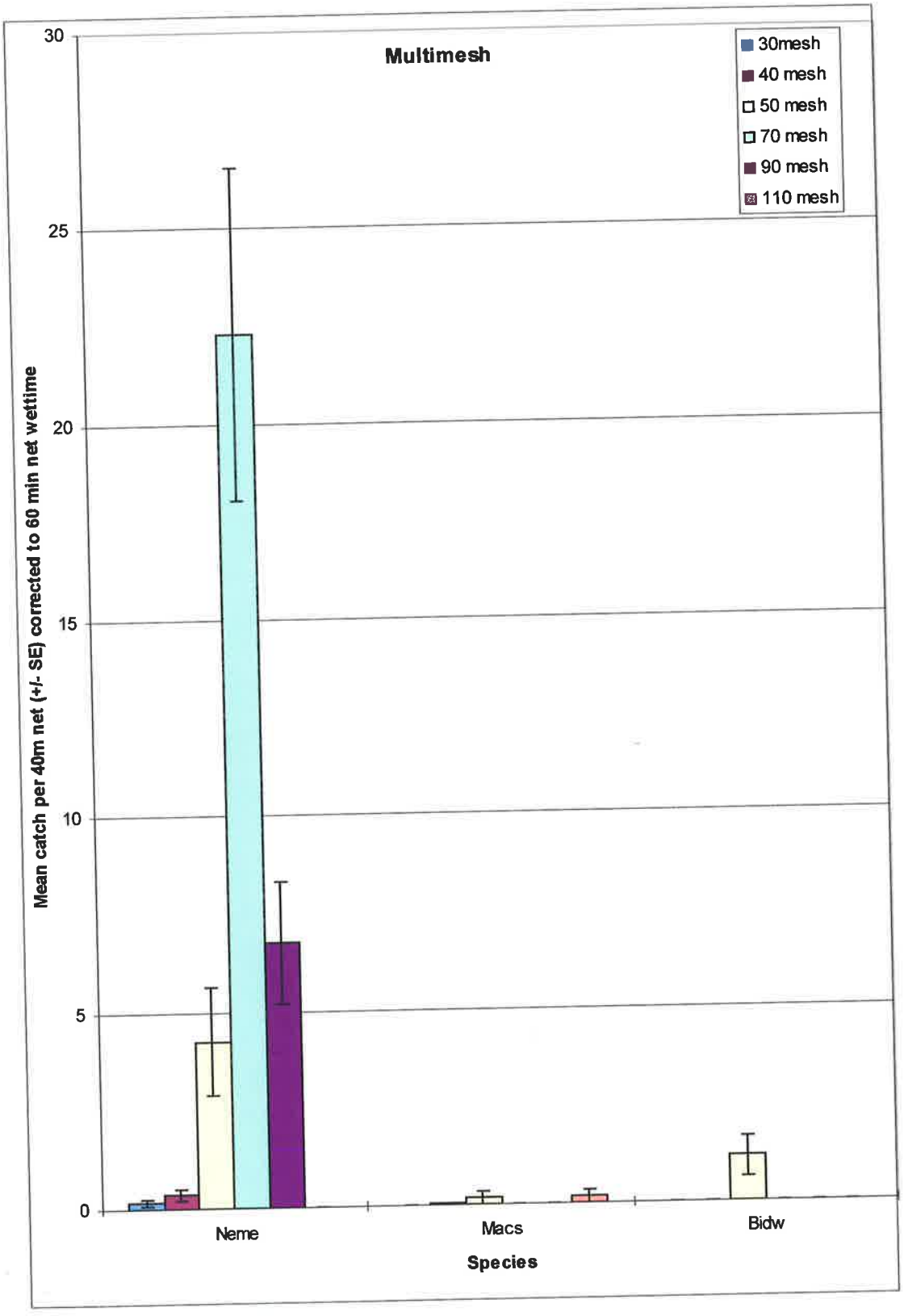


Figure 40. Mean catch per unit effort per taxon in 2m multimesh gillnet panels.

Table 44. Ratios per mesh of bony herring catch in 40m multimesh nets / 2m monomesh panels.

Mesh (mm)	30	40	50	70	90	110
Ratio	Zero catch	20.5	15.2	13.8	14.3	Zero catch

4.2.4.2 Adjustments for replicate number and non-normality of data

To overcome biases in estimates of assemblage structure from unequal replication in all databases which were unequally replicated per site, replicates for analysis were chosen by randomly re-sampling for the minimum replicate number.

Departures from normality of the replicated data varied between species, sites and dates, even when $\log_{10}$-transformed. Use of means in these circumstances was not justified, and the median is misleading for samples with more than 50% zero replicates. Also, because spatial replication of biotic data within samples was not matched by corresponding spatial replication of all site-specific hydrological data, within-site replicates of biological data were not necessary for exploration of the biology-hydrology relations. Replicates were therefore summed within each waterbody for each sampling occasion. This meant that each summed sample corresponded to a single sampling occasion with a given gear in an individual waterbody.

In summary, each of the seven raw datasets (zooplankton, gillnets, 2m seines, 20m seines, fish trawls, macroinvertebrate trawls, fykenets) was prepared as follows. The raw abundance data were corrected for effort and $\log_{10}(X+1)$ transformed. The number of replicates was equalised for each sample by randomly selecting the minimum number of replicates, and these were summed per sample. These summed data were matched with the

hydrological data for the same site and time. Although this approach discards information about variance, it was used because many hydrological data could not be replicated per site, so biological values had to be summarized per sample (either by central tendency or by sum) in the hydrology-biology analyses. With data having many zeroes, both median and mean can be misleading.

For four of the fish databases (2m seine, 20m seine, fish trawl and gillnets), sample sums from sampling events at the same time in the same waterbody were added to give a combined gears fish database. However analysis of this database was not pursued through all of the procedures below because it became clear that the different subsets of the fish fauna captured by the different gears responded differently to hydrological events, so they represented different assemblages and should be analysed separately.

4.2.5 Data Analysis

The following analysis was performed on data from individual gears with corresponding hydrological data. The analysis protocol (Tables 45-47) followed Faith (1991), Belbin (1991b) and Clarke and Warwick (1994). The protocol and statistical packages used are as in Chapter 2, with some differences of detail.

All *ratio* data (*sensu* Belbin 1993) (i.e. all biological and most hydrological attributes analysed here) were $\log_{10}(X+1)$ transformed, range standardized by attribute (measure or taxon) and used to calculate Bray-Curtis distances. This procedure is recommended by Clarke & Warwick (1994) to balance the influence of rare and common species. Range standardisation is also recommended by Belbin (1993) prior to derivation of the Bray-Curtis coefficient, which is robust (Faith *et al.* 1987) and recommended for ratio data (Belbin 1993). The seven biological data matrices and the corresponding hydrological matrices were submitted to analysis using PATN (Belbin 1993) and Primer (Clarke & Warwick 1994).

As in Chapter 2, clustering was by Flexible Agglomerative Hierarchical Fusion (UPGMA: Sneath & Sokal 1973, Belbin *et al.* 1992). The ordination technique used was Semi-Strong Hybrid Multidimensional Scaling (SSH MDS: Kenkel & Orloci 1986, Faith *et al.* 1987, Belbin 1991a) in PATN. SSH MDS copes with unimodal responses of taxa to the

underlying ordination space. Flexible UPGMA and SSH MDS were used to detect groupings in the hydrological and biological data.

Differences in hydrological patterns between waterbodies, seasons and years, and in biological assemblage structures between waterbodies, seasons, years, months, flow pulses and flow pulse phases, were tested by ANOSIM (Clarke & Green 1988) as in PATN and PRIMER. Both packages were used for ANOSIM because only PRIMER provides for two-way analyses of similarities, but it is limited to datasets of less than 125 objects. PATN is not limited by matrix size, but provides only for one-way designs. Contributions of attributes, measures or species to inter-group similarities and dissimilarities were determined using the SIMPER algorithm of PRIMER (Clarke & Warwick 1994). In relation to testing of differences between flow pulse phases, only four phases (low water, rising limb, peak depth, falling limb) rather than 10 given in Chapter 1 could be distinguished from the data. This was partly because of the two-monthly resolution, partly because bankfull level varied between waterbodies and between sites within waterbodies, and partly because no hyporheic zone was detectable.

Ordination was used to investigate the grouping of samples of taxon abundance and the corresponding hydrological values in multidimensional space, according to their similarity. The ordinal/ratio cut values for SSH MDS ordination were determined from histograms of dissimilarity values. The number of dimensions for ordination was determined by the change in stress with change in dimension number, and by interpretability. The distributions of samples in the ordination spaces were examined in ordination plots for groupings of samples labelled by waterbody, season, month, year, flow phase and flow. Temporal change in biological assemblages was explored by ordinating the biological samples in each major site separately, then plotting temporal connections between samples in the biological ordination spaces, using SYGRAPH (Wilkinson 1990).

The fit of the biology ordinations to the corresponding hydrology ordinations was determined by Procrustean rotation in PATN. This procedure was employed only with the five assemblages for which the full five years' data were available, viz. macroinvertebrates in open water (trawl), juvenile and larval fish in the shallow littoral (2m seine) and in open

water (trawl), juvenile and adult small fish in the deep littoral (20m seine), and juvenile and adult large fish in open water (gillnets).

The transformed and standardised hydrological data were fitted to the biological ordinations by multiple regression (Faith & Norris 1989), to estimate the correlation between ordinations and individual attributes or measures. These correlations potentially show the relative importance of hydrological measures in structuring the biota. The significance of these correlations was assessed using Monte Carlo simulations of the multiple regression, based on 1000 random permutations of each hydrological measure. The vectors of those hydrological measures which were significantly correlated with the ordination were mapped into the ordination space, to indicate their relative independence of orientation and potentially of their biological influence.

Table 45. Analysis protocol for biological-hydrological associations, 1: Patterns in biological and hydrological data.

Data preparation	
Hypothesize significant groups	
$Log_{10}(x+1)$ transform all non-ranked data	
Range standardize attributes/measures	
Derive Bray-Curtis association matrix	
Plot a histogram of associations	
Classification	**Ordination**
Flexible Agglomerative Hierarchical scaling	Semi-strong hybrid multi-dimensional scaling
	(ratio/ordinal cut-points from histogram of associations)
Derive dendrogram	
Create group definition file	Plot and label groups
Test significance of groups using ANOSIM	Link data in biological ordination spaces to indicate changes over time

Table 46. Testing hypotheses about intergroup differences, and determining contributions by attributes to these differences between groups.

Grouping of biological transformed and standardized data by flow pulse, flow phase, year, season, month, site and mesohabitat

Derivation of Bray-Curtis association matrix

Analysis of similarities between groups

Simper analysis of percentage contribution of attributes to intergroup differences

Table 47. Analysis protocol for testing biological-hydrological associations.

1. Matching biological and hydrological ordinations by Procrustean rotation.

2 Multiple regression of transformed and standardized hydrological attributes on the ordinations

3. Testing the significance of regression results by Monte Carlo randomisation

4.3 Results

4.3.1 Hydrological Environment

The sampling period December 1986 - April 1992 encompassed a major La Niña event, in which peak discharges in Cooper Creek increased annually from 1987 to a 1 in 30 year flood in 1990 (Fig. 41). This was reflected in the depths of the major lakes and channels of the Coongie Lakes system (Figs 42, 43). The annual advance of floodwaters enabled sampling to extend progressively to more infrequently flooded waterbodies: to Lakes Toontoowaranie and Goolangirie in February 1987, to Lake Apanburra in April 1988, and in 1990 to Lakes Maroopootanie and Blanche. It also provided highly variable hydrological conditions in each of the more permanently inundated waterbodies sampled, and extensive opportunity for exchange of aquatic fauna between waterbodies.

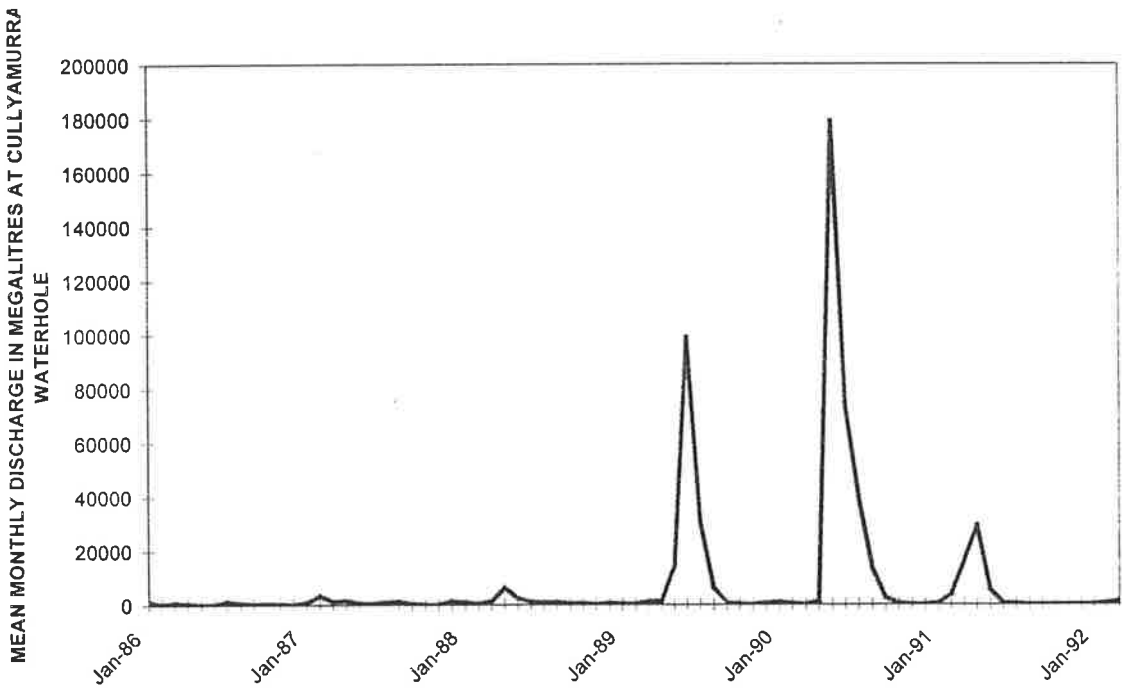


Figure 41 Mean monthly discharge (ML) at Cullyamurra gauge station, 1986-92

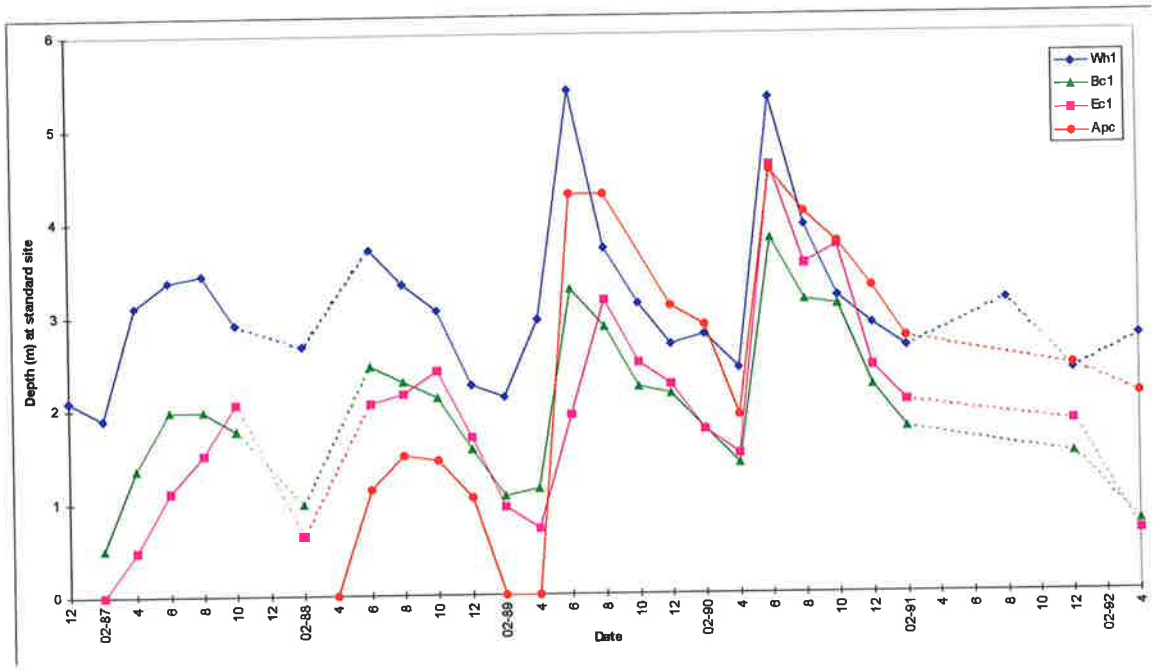


Figure 42 Depth at major channel sites over the sampling period

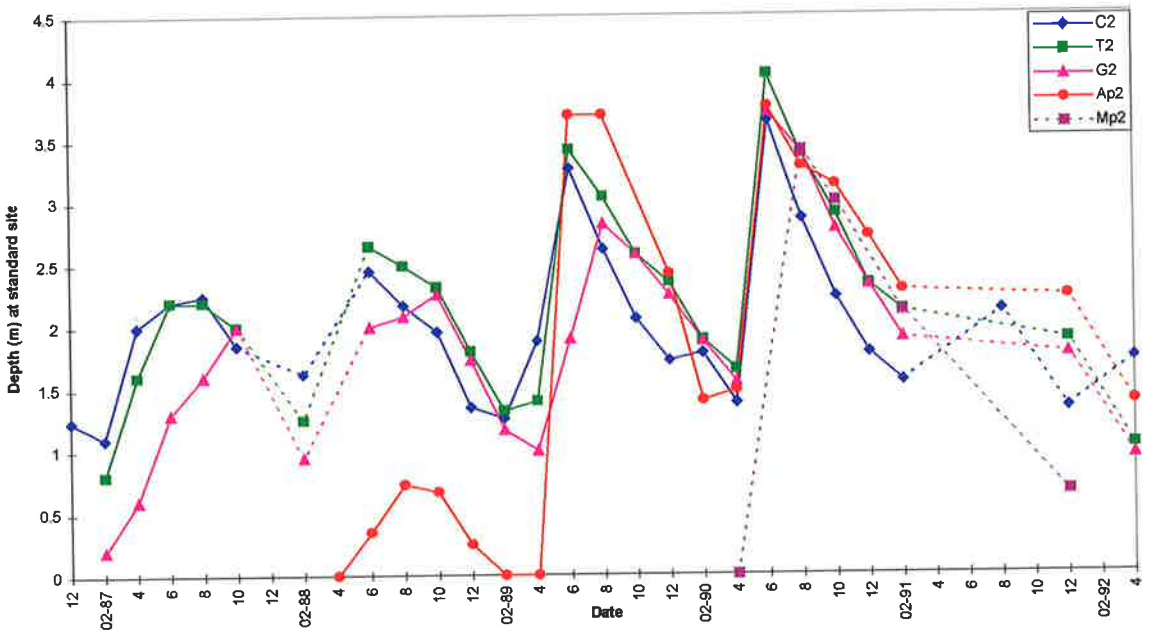


Figure 43 Depth at major lake sites during sampling period

4.3.2 Non-hydrological environment

(see also Puckridge *et al.* in press)

4.3.2.1 Physicochemistry

Since the hydrological environment is the focus of this thesis, vegetation and substratum data will not be presented here. However, the physicochemical changes likely to be associated with hydrological variation are illustrated below (Figs. 44 -59). For brevity, only the lake and channel waterbodies most consistently sampled are included. All physicochemical data shown are from measurements in open water rather than in the littoral zone. Some sample dates were missed (dotted lines) for various reasons, including difficulties of access under flood conditions.

Conductivity at all sites peaked around February-April each year (Figs 44-46) - the main period of low water for flow pulses during this project. The exception to this pattern was 1987, when flows began in December-January, and consequently conductivities fell in Wh1 from January-April. The lake sites (Fig. 45) showed overall higher conductivities than the channel sites (Figs. 44, 46: Note that to maximize the clarity of intersite distinctions the Y-axis scales differ for the lakes and channel sites). Within both lake and channel sites, conductivity increased with drying frequency. Mp2, the Maroopootanie site, in the most rarely flooded lake, and Ec1, in the second most frequently drying channel, showed the highest peak conductivity in lakes and channels respectively. The upstream channels, Mb1 and Ca1 (Fig. 46) showed the lowest conductivity overall.

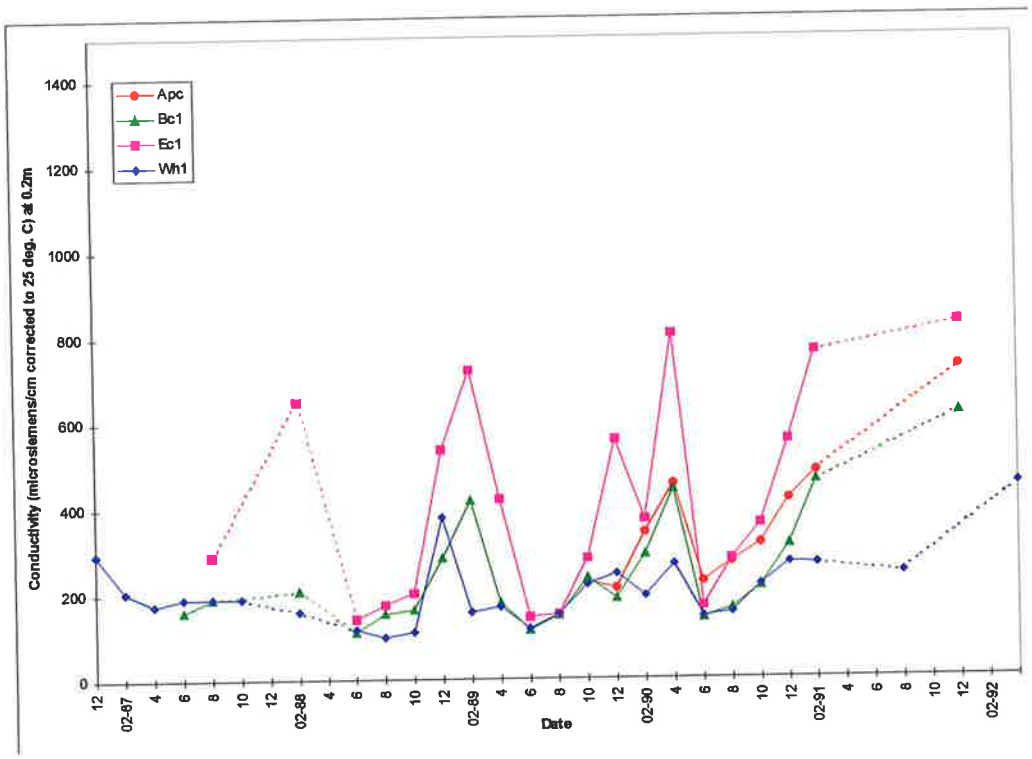


Figure 44 Conductivity at downstream channel sites over the sampling period

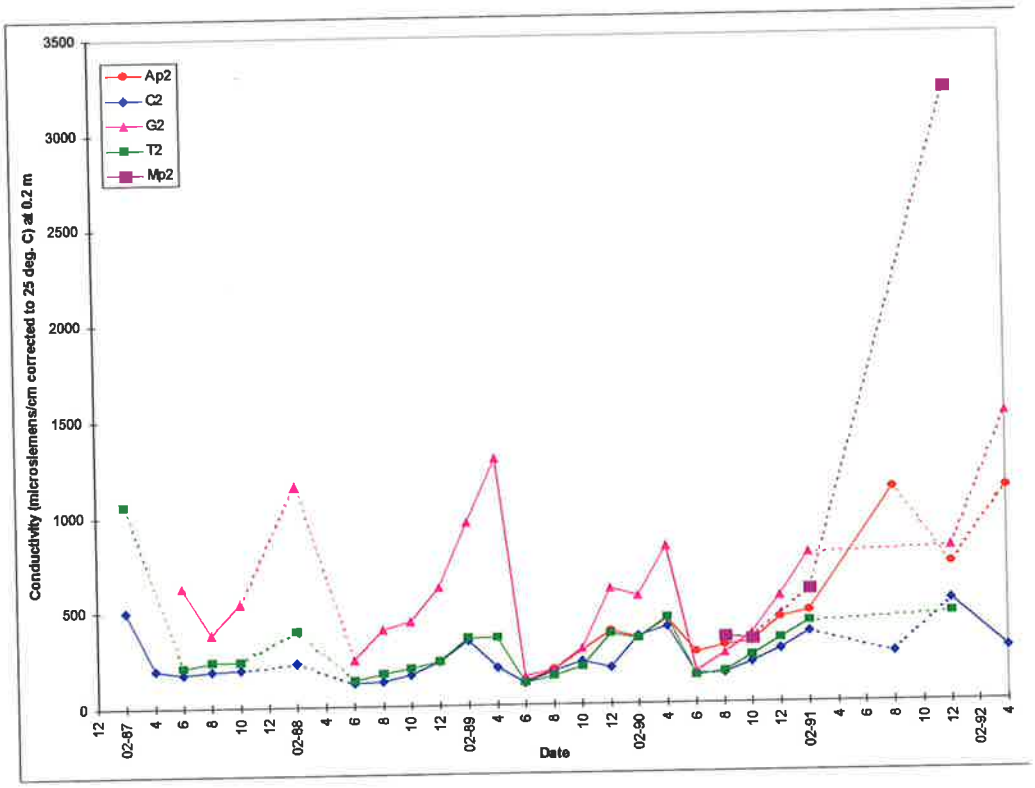


Figure 45 Conductivity at lake sites over the sampling period

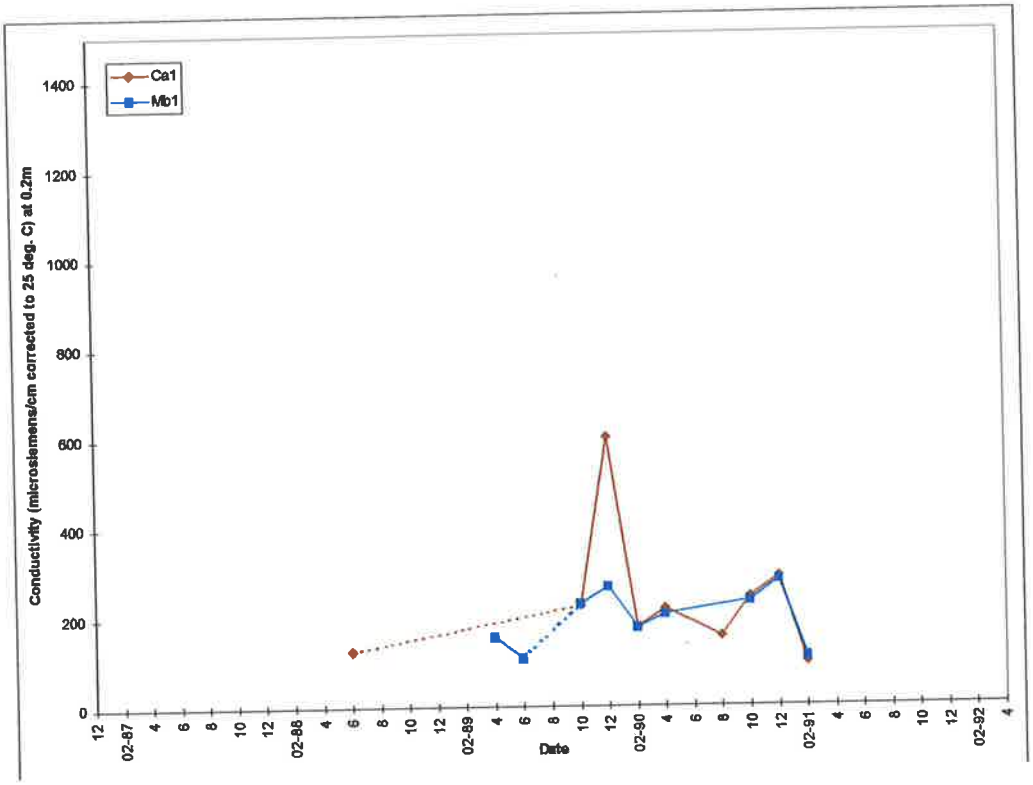


Figure 46 Conductivity at upstream river channel sites over the sampling period

pH at all sites fell during strong inflows and peaked in February - March (Figs 47-48). The lake sites (Fig. 48) showed this pattern most clearly.

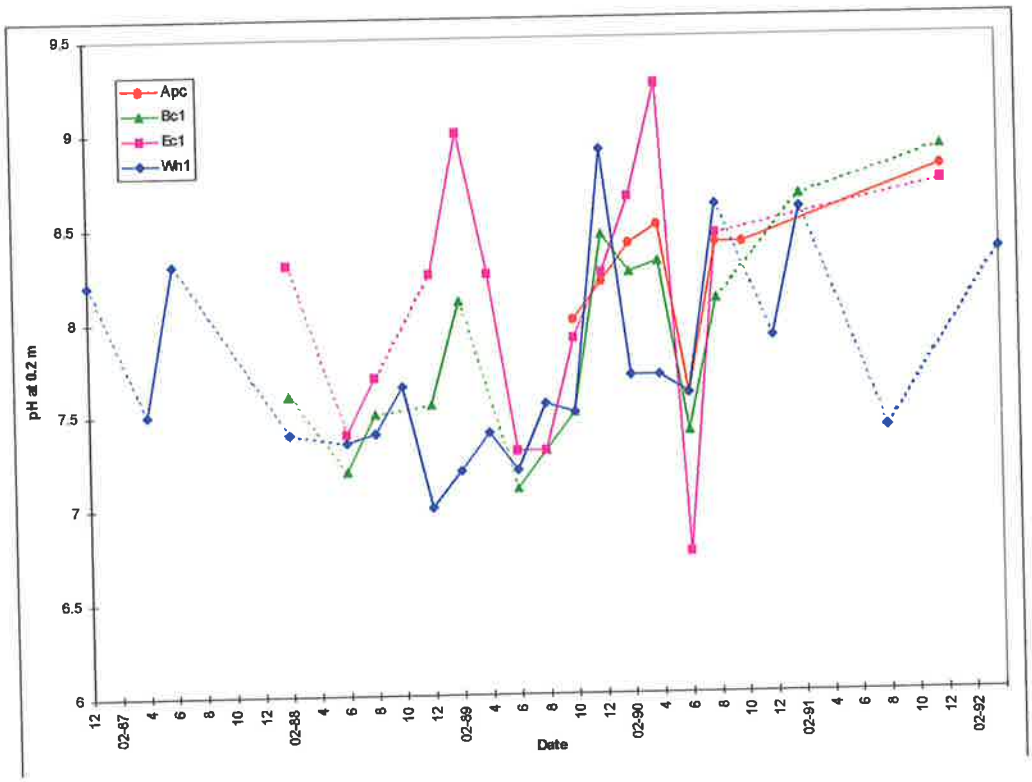


Figure 47 pH at channel sites over the sampling period

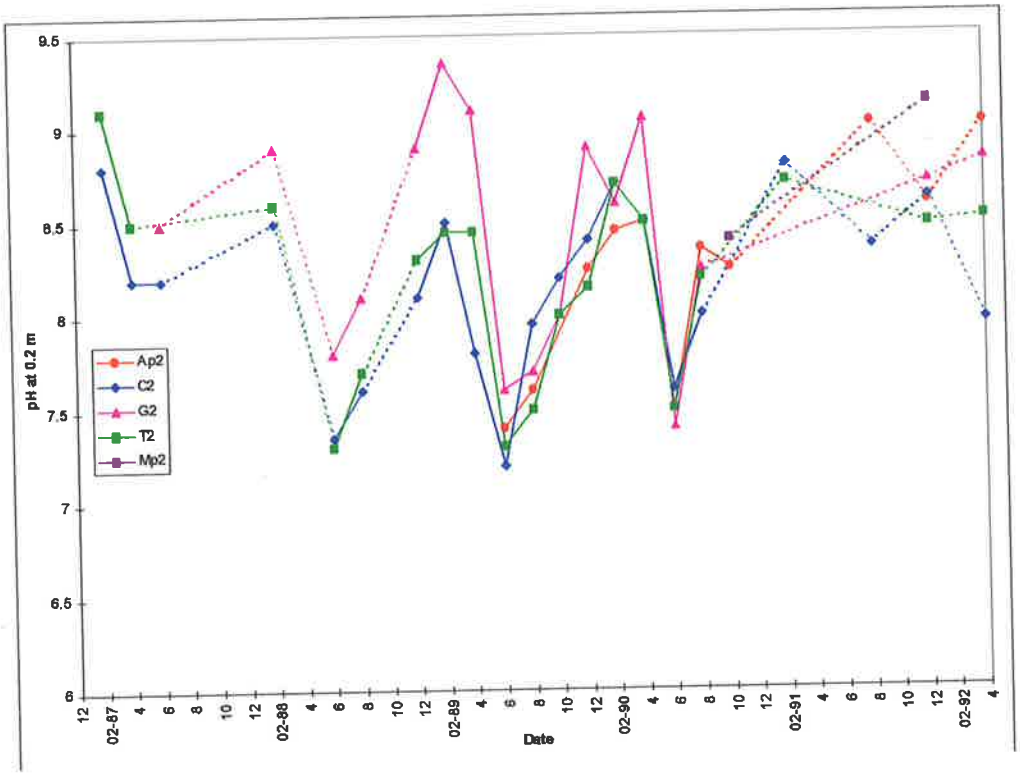


Figure 48 pH at lake sites over the sampling period

Water transparency at all sites peaked during periods of high flow (Figs 49-50). There was also an overall increase in water transparency over the flow pulse series 1988-91. The channel sites (Fig. 49) showed a clearer pattern of response to flows, and reached higher transparencies, than the lake sites. Transparencies peaked lower in the more frequently drying channel sites.

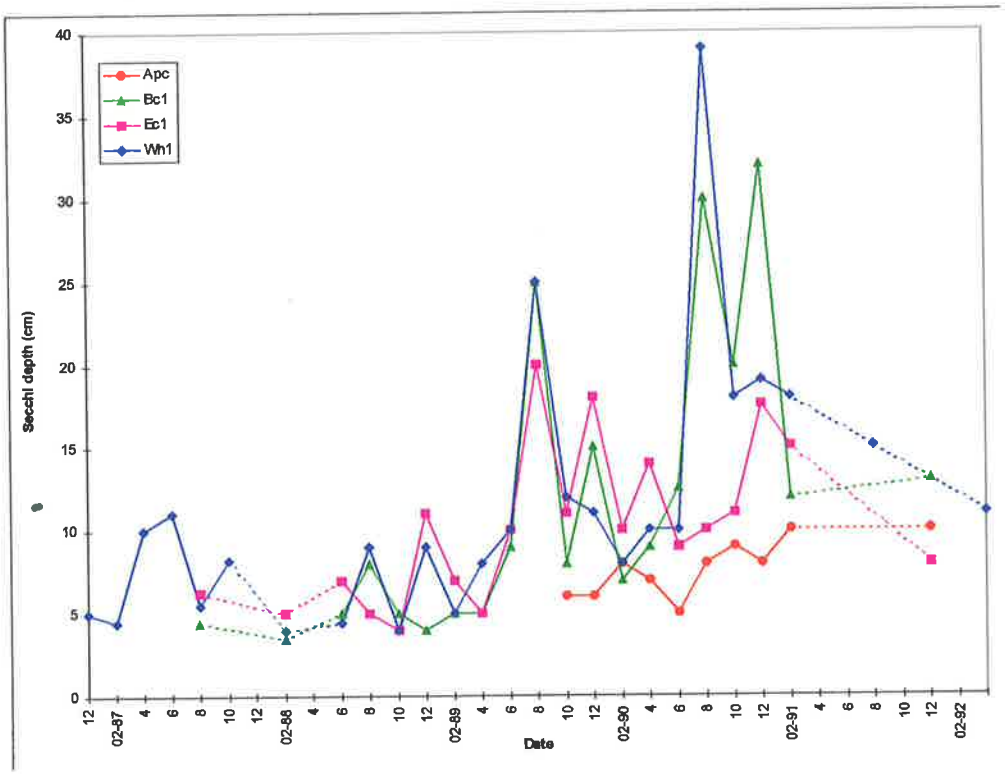


Figure 49 Water transparency (Secchi depth) at channel sites over the sampling period

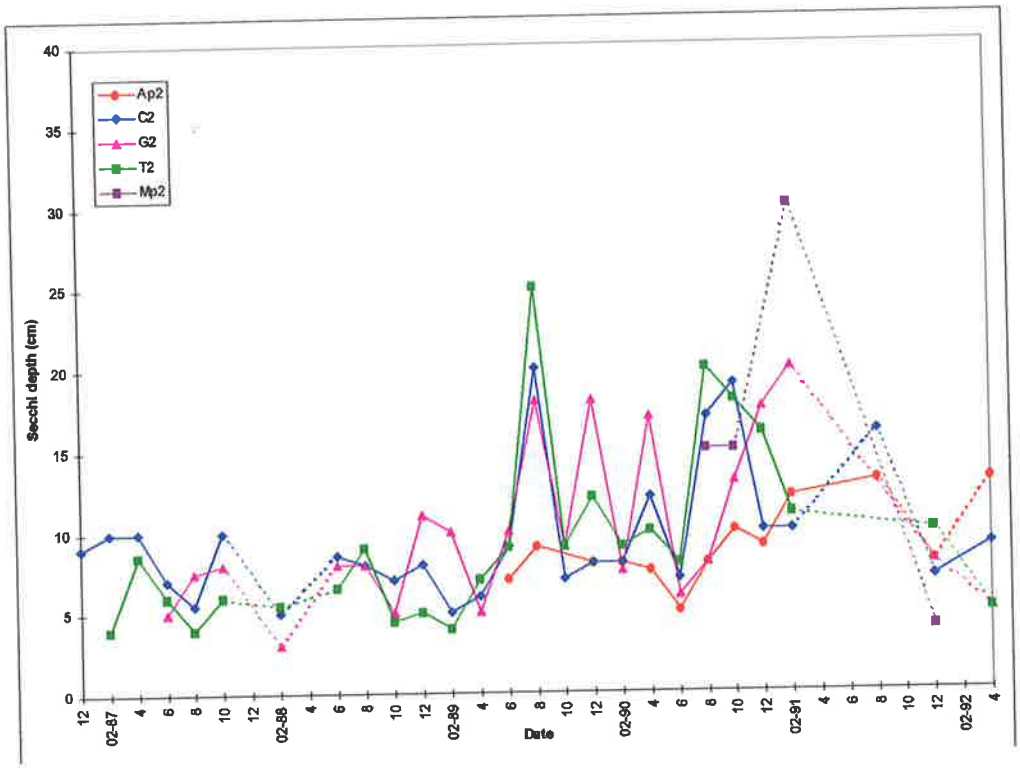


Figure 50 Water transparency (Secchi depth) at lake sites over the sampling period

Water temperature at all sites had maxima in January and minima in June-August (Figs 51, 52), approximately in synchrony with air temperatures (Fig. 53). However, in contrast to air temperatures, both maximum and water temperatures at both lake and channel sites increase markedly and progressively at most sites over the sampling period, in parallel with increases in waterbody depth (Figs. 51, 52).

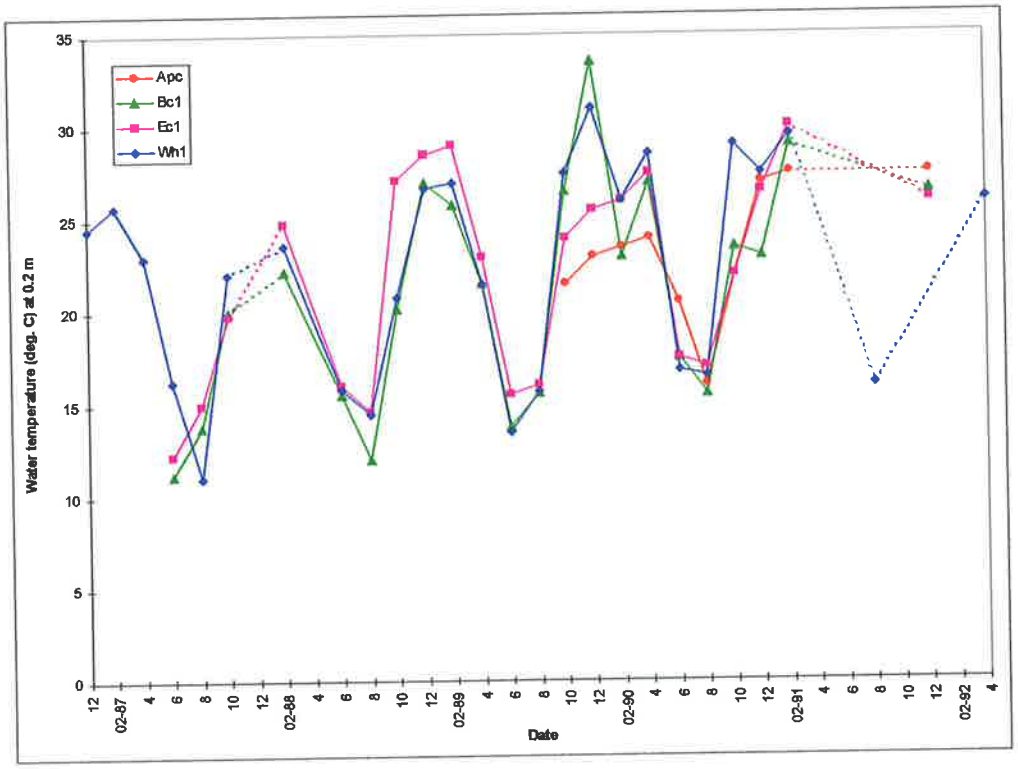


Figure 51 Water temperature at channel sites over the sampling period

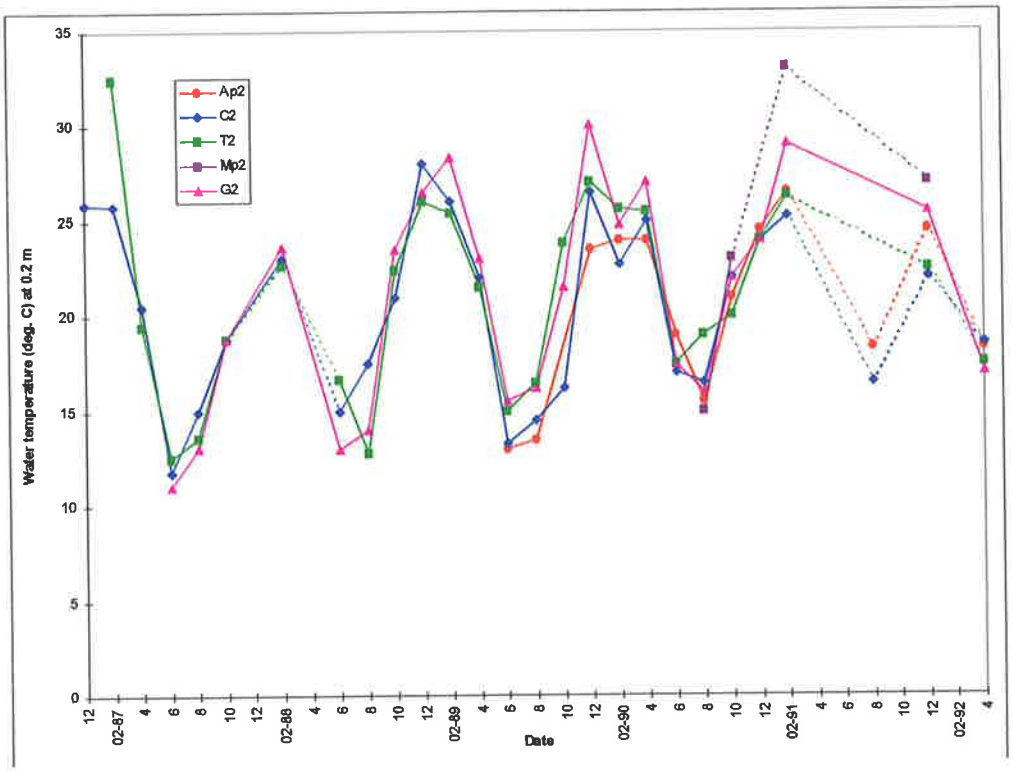


Figure 52 Water temperature at lake sites over the sampling period

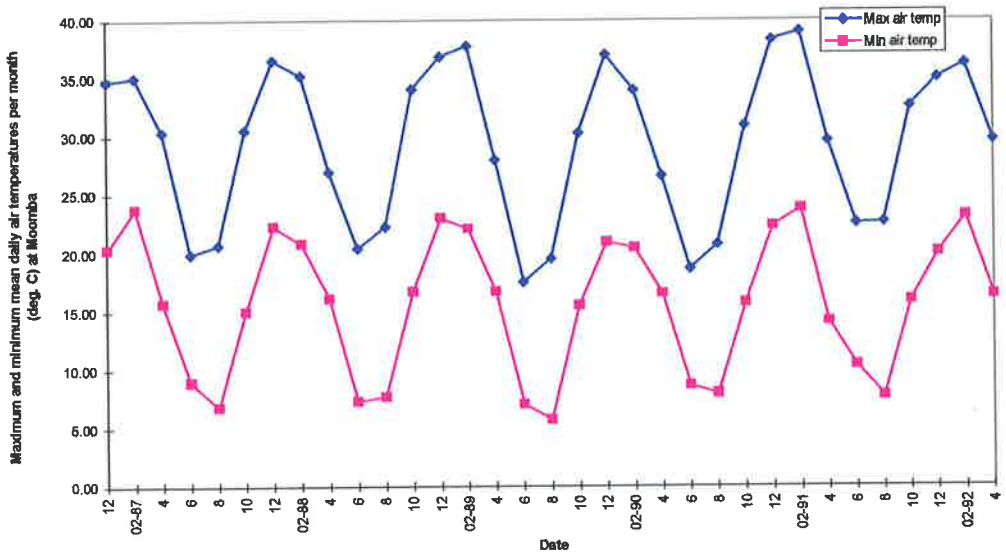


Figure 53 Air temperature at Moomba over the sampling period

Dissolved oxygen concentration varied erratically between sites at this temporal scale (Figs 54, 55). However the period of low flows (1987) appeared to show a wider range of DO, particularly in the channel sites.

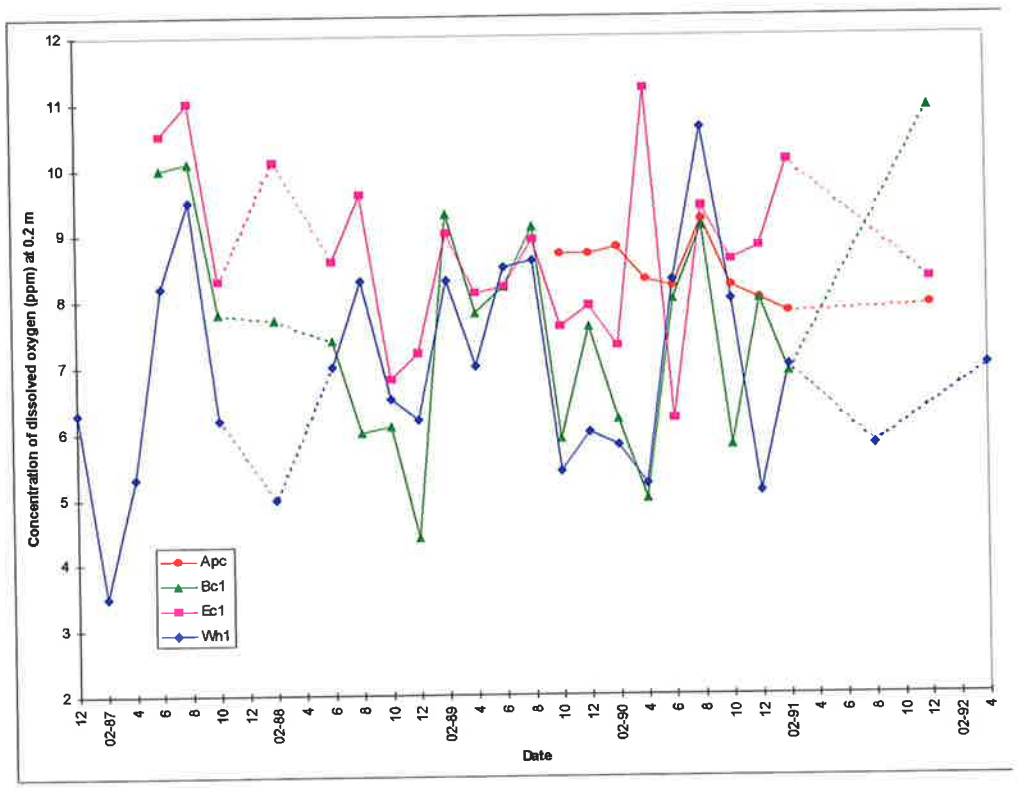


Figure 54 Concentration of dissolved oxygen at channel sites over sampling period

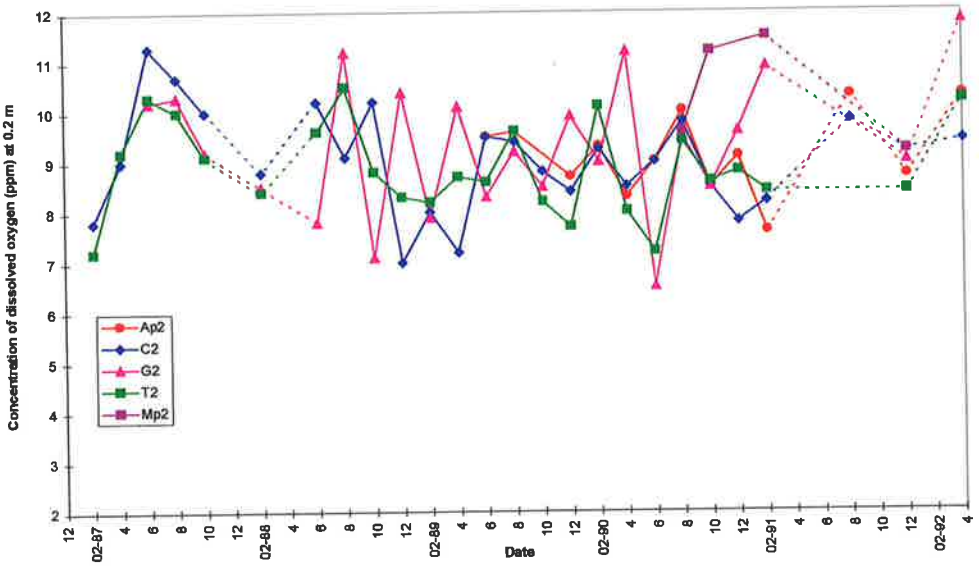


Figure 55 Dissolved oxygen concentration at lake sites over sampling period

Water temperature stratification at channel sites had maxima in spring-summer and minima in autumn-winter (Figs 56, 57). In the lake sites, stratification occurred more erratically.

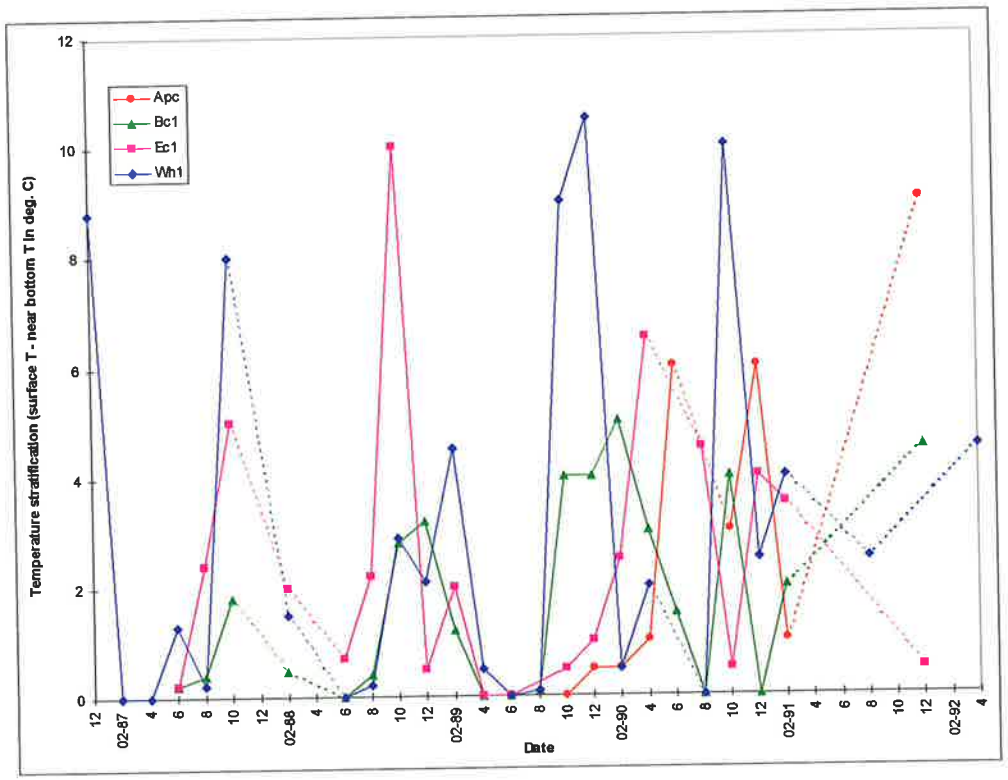


Figure 56 Temperature stratification at channel sites over the sampling period

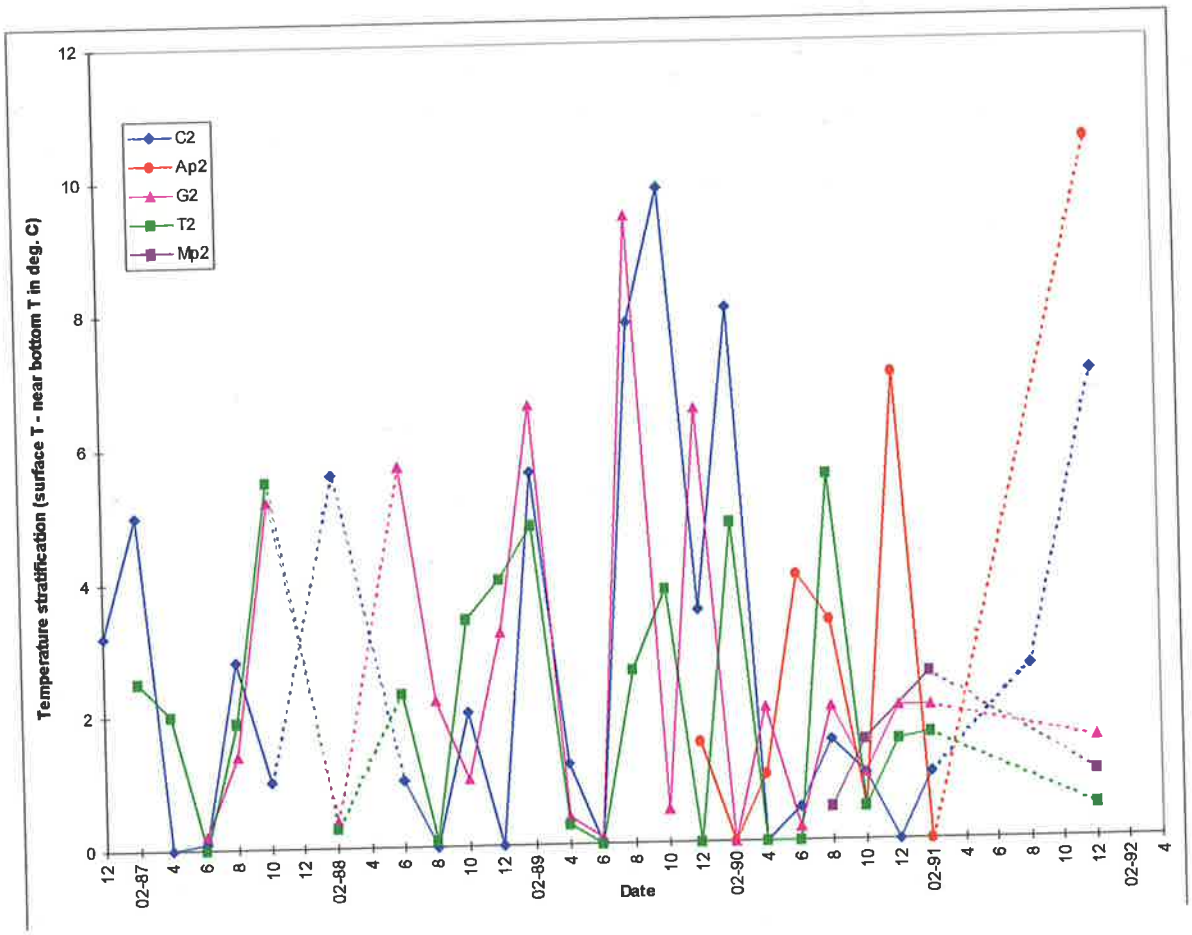


Figure 57 Temperature stratification at lake sites over the sampling period

Despite considerable variation between sites, overall dissolved oxygen stratification had maxima in spring-summer and minima in late winter (Figs 58, 59). In the lake sites, stratification occurred more erratically.

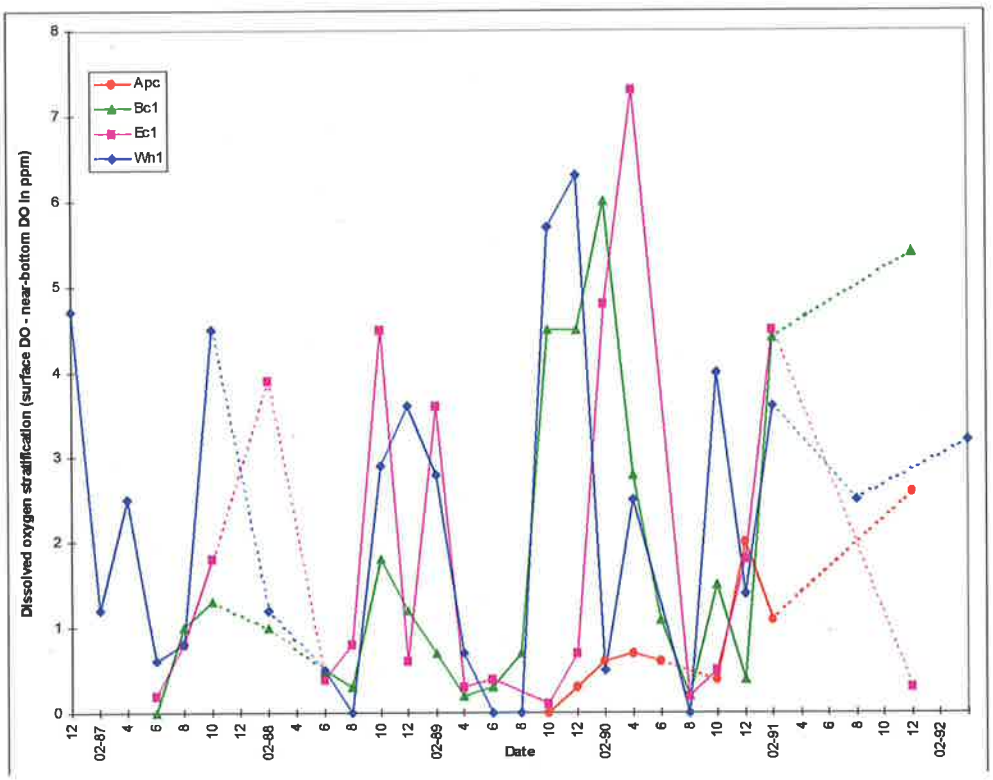


Figure 58 Dissolved oxygen stratification at channel sites over the sampling period

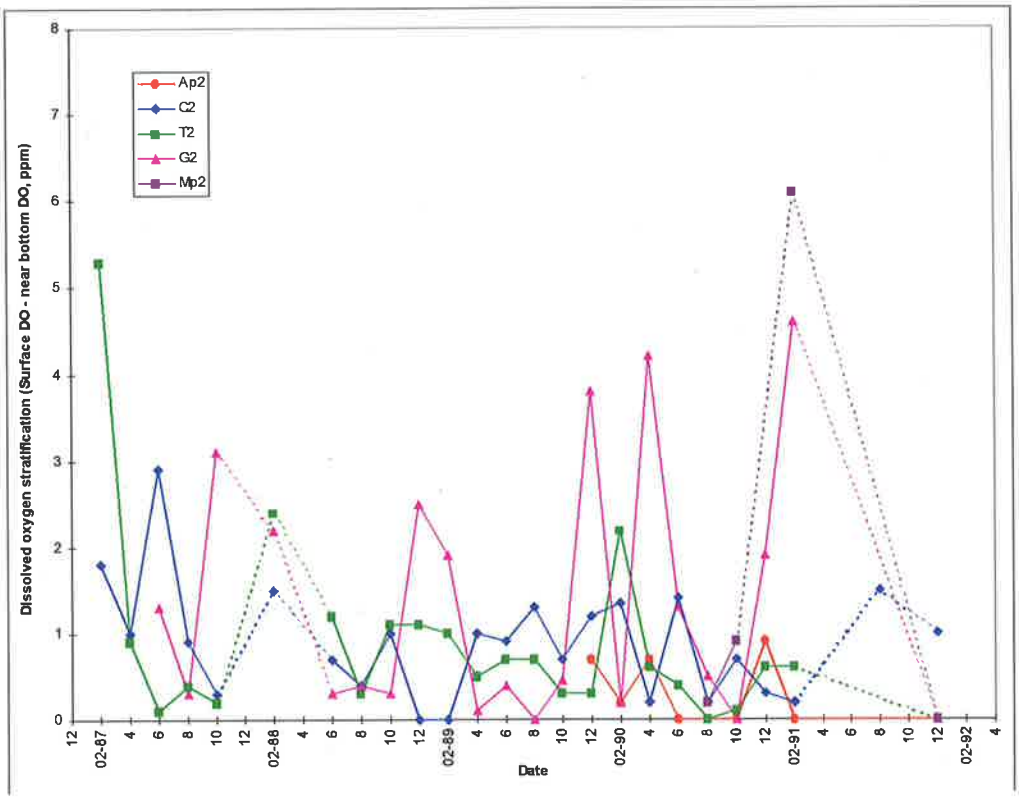


Figure 59 Dissolved oxygen stratification at lake sites over the sampling period

4.3.2.2 Physicochemistry – Summary.

The most substantial changes were in water temperature and transparency. Although the temporal resolution of the data is coarse, mean minimum daytime water temperatures rose progressively over 1987-90 by 3.8°C (or 30% of the mean minimum for 1987). Similar trends occurred in June or August temperatures alone. There was no such clear trend in air temperatures at nearby Moomba, South Australia. Nor was there a clear trend for mean maximum water temperatures. Mean maximum transparency (Secchi depth) peaked in August 1989 at 97% above the 1987 maximum, and was still 62% above the 1987 value in October 1990. Between January 1988 and June 1990 mean minimum Secchi depth rose 44% above the January 1988 minimum. Mean conductivity declined or changed little over 1989-91, then rose as the flow pulse amplitude fell. There were similar trends in the means for channel and lake sites separately.

4.3.3 Aquatic taxa collected

Twenty-three zooplankton taxa (16 identified to order, seven to class or phylum), seventeen macroinvertebrate taxa (15 identified to Order, two to Class) and fourteen fish taxa (12 native, two exotic, 13 identified to species, one to genus) were collected during sampling (Tables 48-50).

Table 48 Zooplankton taxa collected

PHYLUM	*CLASS*	*ORDER/ SUBORDER*	*CODE*
Protozoa	Mastigophora		Volvo
Cnidaria		Hydrozoa	Hydrz
Platyhelminthes	Turbellaria		Turbe
Rotifera			Rotif
Nematoda			Nemat
Tardigrada			Tardi
Annelida	Oligochaeta		Oligo
Arthropoda	Crustacea	Copepoda	Copep
		Cladocera	Clado
		Ostracoda	Ostra
		Conchostraca	Conch
	Insecta	Diptera	Dipte
		Odonata	Odona
		Collembola	Colle
Arthropoda	Arachnida	Hydracarina	Hydra

Table 49 Macroinvertebrate taxa collected

CLASS	*ORDER/SUBORDER*	*CODE*
Gastropoda		Gastr
Oligochaeta		Oligo
Crustacea	Cladocera	Clado
	Copepoda	Copep
	Ostracoda	Ostra
	Conchostraca	Conch
	Notostraca	Notos
	Anostraca	Anost
	Decapoda	Decap
Insecta	Diptera	Dipte
	Ephemeroptera	Ephem
	Odonata	Odona
	Hemiptera	Hemip
	Coleoptera	Coleo
	Trichoptera	Trich
	Plecoptera	Pleco
Arachnida	Hydracarina	Hydra

Table 50 Fish taxa collected

FAMILY	*GENUS & SPECIES*	*CODE*
Native species		
Clupeidae	*Nematalosa erebi*	Neme
Retropinnidae	*Retropinna semoni*	Rets
Plotosidae	*Neosilurus argenteus*	Neoa
Plotosidae	*Neosilurus hyrtlii*	Neoh
Plotosidae	*Neosilurus sp.*	Neos
Melanotaeniidae	*Melanotaenia splendida tatei*	Mels
Chandidae	*Ambassis mulleri*	Ambm
Percichthyidae	*Macquaria ambigua*	Macs
Terapontidae	*Bidyanus welchi*	Bidw
Terapontidae	*Scortum barcoo*	Scob
Terapontidae	*Leiopotherapon unicolor*	Leiu
Gobiidae	*Hypseleotris klunzingeri*	Hypk
Exotic species		
Cyprinidae	*Carassius auratus*	Cara
Poeciliidae	*Gambusia holbrooki*	Gamh

4.3.4 Analysis of similarities of biological data (waterbody and flow history scales)

The term "database" below refers to the seven assemblages defined in Table 41. For brevity, they are referred to by the gear type in which they were collected. Where replication within a group was inadequate for a meaningful test, this is indicated by "one site" or "too few reps". Where the number of samples in a database was too large for PRIMER's ANOSIM algorithm, the global comparison was performed in the ASIM module of PATN. Since the latter does not perform individual comparisons, such comparisons are not available (n.a.) for such databases. Site codes are further abbreviated (Table 52) to fit into ANOSIM, UPGMA and SSH MDS tables and figures.

4.3.4.1 Differences between samples grouped by site and by hydrological attributes.

Global comparisons

Comparisons between results from the different databases should be qualified by the fact that zooplankton and fykenet databases included only the years 1989-92 and 1988-92 respectively. In all but the 20m seine database (Table 51), there were significant global differences between lake and channel sites. In all but the zooplankton and fykenet databases, there were significant differences between lake sites, but fykenet data was only collected in one lake site. In four of the databases the channel sites were significantly different, but the 20m seine data were collected from only one channel site. When data from lake and channel sites were combined, the differences between sites were significant in all databases.

In only the 2m seine database were there significant global differences between samples grouped by flow pulses in lake sites. However when only flow pulses sampled over the full duration of the pulse (complete pulses) were included, four databases showed significant differences between pulses. Of the three databases showing no such differences, the fykenet data had too few replicates for an adequate test. For the channel sites, only the fykenet database showed significant global differences between flow pulses, but for complete pulses only, three more databases (zooplankton, macroinvertebrates and gillnets) showed significant differences. When lake and channel samples were combined, three databases showed significant differences between flow pulses, and when only complete flow pulses were included, four databases showed significant differences. The database for the 20m seine showed no globally significant differences between flow pulses.

Only two databases, those from gillnets and fykenets, did not show significant differences between lake samples grouped by flow phase, and of these the fykenet data did not provide adequate samples for this test. For the channel sites, all the databases showed significant differences between flow phases. When lake and channel sites were combined, all databases again showed significant global differences between flow phases.

Overall, the most pronounced differences were between sites and between phases of the flow pulse. For littoral zooplankton, open water macroinvertebrates, larval fish in the open water trawl and in the littoral 2m seine, the strongest differences were between phases of the flow pulse, although the macroinvertebrate and 2m seine data also showed strong differences between sites. Lake sites differed more strongly in the fish trawl data and channel sites differed more in the 2m seine data. The 20m seine data showed differences between lakes sites, and between flow phases in lakes. The gillnet data showed differences between sites, flow pulses and flow phases, at moderate probabilities. The fykenet data were not adequate for comparisons between samples in lakes, but showed strong differences for all other comparisons, notably for differences between flow pulses.

Table 51 Analysis of Similarities. Global differences for each biological database between groups defined by site and by hydrological attributes.

P-values for global differences between:	zoo-plankton in littoral trawl	Macro-inverts in open water trawl	Larval & juvenile fish in open water trawl	Larval & juvenile fish in littoral 2m seine	Juvenile & adult small fish in sublittoral 20m seine	Juvenile & adult large fish in open water gillnets	Juvenile & adult large fish in sublittoral fykenets
lakes & channels:	<0.01	<0.001	<0.05	<0.001	>0.05	<0.001	<0.01
lake sites:	>0.05	<0.05	<0.001	<0.05	<0.001	<0.05	one site
channel sites:	>0.05	<0.05	>0.05	<0.001	one site	<0.05	<0.01
sites in lakes + channels	<0.05	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
flow pulses in lakes	>0.05	>0.05	>0.05	<0.01	>0.05	>0.05	too few reps
flow pulses in lakes (complete pulses only)	<0.001	>0.05	<0.05	<0.01	>0.05	<0.05	too few reps
flow pulses in channels	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	<0.001
flow pulses in channels (complete pulses only)	<0.05	<0.05	>0.05	>0.05	>0.05	<0.05	<0.01
flow pulses in lakes + channels	<0.05	>0.05	>0.05	>0.05	>0.05	<0.05	<0.001
flow pulses in lakes + channels (complete pulses only)	<0.01	>0.05	>0.05	<0.01	>0.05	<0.01	<0.001
flow phases in lakes:	<0.01	<0.001	<0.001	<0.001	<0.05	>0.05	too few reps
flow phases in channels:	<0.01	<0.001	<0.01	<0.01	<0.05	<0.01	<0.01
flow phases in lakes + channels:	<0.001	<0.001	<0.001	<0.001	<0.01	<0.01	<0.01

Individual differences

Table 52 Abbreviated site codes for multivariate results.

Lake/Delta Site	Code	Channel Site	Code
Coongie	co	Cullyamurra	ca
Toontoowaranie	to	Queerbidie	mb
Goolangirie	go	Tirrawarra	tw
Apanburra	ap	Coongie Crossing	wh
Maroopootanie	mp	Browne Creek	bc
Tirrawarra Swamp	ts	Ellar Creek	ec
		Apanburra Channel	ac

Of the significant lake site comparisons in all databases (Table 53), Coongie Lake vs Lake Goolangirie (co-go) occurred most frequently. Lake Maroopootanie (mp) also differed from several other lakes. In the significant channel site differences in all databases, Tirrawarra swamp (ts), Tirrawarra channel (tw), Ellar Creek (ec), Apanburra Channel (ac), Coongie Crossing waterhole (wh) and Queerbiddie Waterhole (mb) occurred equally frequently. Of the lakes and channels sites comparisons, Coongie Crossing waterhole channel site (wh) differed most frequently from lakes sites, principally because *wh* was the only site represented in the 20m seine database.

In comparing frequencies of contrasts between different flow pulses, the results for the zooplankton and fykenet databases are considered separately. For the remaining five databases, of the significant flow pulse contrasts in lakes sites only, six flow pulse contrasts were significant, and all occurred only once. The 1990 and 1987 pulses occurred most frequently in these contrasts. In the channel sites, only three flow pulse

contrasts were significant and all occurred only once. Again the 1990 and 1987 pulses occurred most frequently in contrasts. Of the databases with lake and channel sites combined, four were too large for analysis by ANOSIM, and the 20m seine database showed no significant result. For the zooplankton and fykenet databases in the lakes sites, the fykenets had too few replicates in lakes and the zooplankton showed one significant contrast. In the channel sites, the zooplankton contrast was the same and the fykenets showed three significant contrasts. In the channel and lakes sites combined, the pattern was the same as for the channel sites alone. Not surprisingly (given the time-spans of these two databases) the 1989 and 1990 pulses occurred most often in these contrasts.

Of all the flow pulse contrasts, only 87-90, 88-90, 89-90 and 88-89 involved pulses which were sampled in their entirety, and so represented comparisons which did not confound differences attributable to flow pulses and those attributable to differences in the phases of the pulses sampled. Overall the peak flood of 1990 was the most frequently different from the flow pulses of other years, even excluding the zooplankton and fykenet database results.

Of the nine significant flow phase comparisons (in all databases, lakes sites only), their frequency of occurrence was in the order low water – peak depth (*lw-pd*), low water –falling limb (*lw-fl*), and falling limb – peak depth (*fl-pd*) equal with rising limb – falling limb (*rl-fl*). Low water was the most frequently contrasted phase. The corresponding result for channel sites gave 16 significant contrasts, in a similar order of frequency: *lw-pd*, *lw-fl*, *fl-pd* equal with *rl-pd*, and *rl-fl* equal with *lw-rl*. Again low water was the most frequently contrasted phase. Results for the lakes and channel sites combined are incomplete, because four of the databases were too large for ANOSIM analysis. For the zooplankton, 20m seine and fykenet databases, there were seven significant contrasts in the order of frequency *lw–fl*, *lw–pd*, with *rl-fl* and *lw-rl* equal. Again *lw* was the most frequently contrasted phase. In summary, the low water – peak depth contrast is most commonly significant, the low water phase is most commonly distinguished from other phases, and the rising limb phase is least frequently distinguished.

Table 53. Analysis of similarities. Particular differences for each biological database between groups defined by site and by hydrological attributes.

Significant differences (at *P*-values <0.01 to allow for multiple comparisons) between:	zoo-plankton in littoral trawl	Macro-inverts in open water trawl	Larval & juvenile fish in open water trawl	Larval & juvenile fish in littoral 2m seine	Juvenile & adult small fish in sublittoral 20m seine	Juvenile & adult large fish in open water gillnets	Juvenile & adult large fish in sublittoral fykenets
lake sites	none	co-go	ap-mp, co-go, co-mp, go-mp, to-mp	co-go, go-to	co-go, co-ap, co-to	co -go	*n.a.*
channel sites	none	none	none	ts-tw, ts-wh		ca-ec, ec-wh	ac-mb, ac-tw, bc-mb
lake and channel sites	ap-bc, go-mb, ap-mb	*n.a.*	*n.a.*	*n.a.*	wh-go, co-go, co-ap, co-to wh-co, wh-to wh-ap	*n.a.*	ac-mp, ac-mb ac-tw, mp-bc mp-ca,mp-wh
flow pulses in lakes	89-90	86-89	87-91, 88-90	86-90, 87-89, 87-90	none	none	too few reps
flow pulses in channels	89-90	87-90, 88-90	87-91	none	none	none	88-89, 88-90, 89-90
flow pulses in lakes + channels	89-90	*n.a.*	*n.a.*	*n.a.*	none	*n.a.*	88-89, 88-90, 89-90
flow phases in lakes	lw-fl, lw-pd	lw-pd, pd-fl	lw-pd	fl-lw, fl-rl	lw-pd	lw-pd	*n.a.*
flow phases in channels	lw-fl, lw-pd lw-rl	rl-pd, rl-fl lw-pd, fl-pd	fl-pd, lw-pd rl-pd	fl-lw, lw-pd	lw-pd	fl-lw, lw-pd	lw-fl
flow phases in lakes + channels	lw-fl, lw-pd lw-rl, fl-rl	*n.a.*	*n.a.*	*n.a.*	fl-lw, lw-pd	*n.a.*	lw-fl

4.3.4.2 Differences between samples grouped by temporal intervals - year, month and season

Global comparisons

Years 1986 and 1992 were omitted from the years comparisons, since only one sample was taken in each of these years. Global differences were more frequent and at higher levels of significance in all site types for samples grouped by month and by season than by year (Table 54). Significant differences were less frequent and at lower levels of significance for the fykenet and 20m seine data than for other datasets. The frequency and levels of significance of group differences were both higher for this temporal interval data than for the data on site and hydrological attributes (Table 53).

Table 54. Analysis of Similarities. Global differences for each biological database between groups of samples defined by temporal intervals.

P-values for global differences between:	zoo-plankton in littoral trawl	Macro-inverts in open water trawl	Larval & juvenile fish in open water trawl	Larval & juvenile fish in littoral 2m seine	Juvenile & adult small fish in sublittoral 20m seine	Juvenile & adult large fish in open water gillnets	Juvenile & adult large fish in sublittoral fykenets
years in lakes	<0.01	>0.05	<0.001	<0.001	<0.01	>0.05	too few reps
years in channels	<0.001	>0.05	>0.05	>0.05	>0.05	<0.01	>0.05
years in lakes + channels	<0.001	>0.05	>0.05	<0.01	<0.05	<0.01	>0.05
months in lakes	<0.01	<0.001	<0.001	<0.001	<0.05	<0.01	too few reps
months in channels	<0.001	<0.001	<0.001	>0.05	>0.05	<0.001	<0.01
months in lakes + channels	<0.001	<0.001	<0.001	<0.001	<0.01	<0.001	<0.01
seasons in lakes	>0.05	<0.001	<0.001	<0.001	>0.05	>0.05	too few reps
seasons in channels	<0.01	<0.001	<0.001	<0.05	>0.05	<0.001	>0.05
seasons in lakes + channels	<0.001	<0.001	<0.001	<0.001	<0.05	<0.001	>0.05

Individual differences

Years 1986 and 1992 were omitted from the years comparisons, since only one sample was taken in each of these years (Table 55). 1991 is included, but sampling frequency was lower for this year than for others. Comparisons between results from the different databases should be qualified by the fact that zooplankton and fykenet databases included only the years 1989-92 and 1988-92 respectively. For all the databases except zooplankton and fykenets, of the eight significant differences between samples grouped by year in lakes sites, the 89-90 contrast is most frequent. For channels sites, there were only three significant contrasts. For lake and channel sites combined only the 20m database could be analysed using ANOSIM, and from this database there was only one significant contrast. Overall, the 89-90 contrast was most frequent. For the fykenet and zooplankton databases, fykenet data were unavailable for lakes sites, and there were no significant years contrasts for channel sites. In both channel and lake sites for the zooplankton database, the two contrasts were the same, viz. 89-90, 89-91. For all databases and site types, and discounting comparisons with 1991 because sampling was not complete in this year, by far the most common difference was between 1989 and 1990.

Of the significant differences between samples grouped by month, the three most common differences were between April and June, April and August, and February and August. Of the significant differences between samples grouped by season, the three most common differences were between Summer and Spring, Autumn and Winter, and Summer and Winter.

Table 55. Analysis of similarities. Particular differences for each biological database between groups of samples defined by temporal intervals.

Significant differences (at P-values <0.01 to allow for multiple comparisons) between:	zoo-plankton in littoral trawl	Macro-inverts in open water trawl	Larval & juvenile fish in open water trawl	Larval & juvenile fish in littoral 2m seine	Juvenile & adult small fish in sublittoral 20m seine	Juvenile & adult large fish in open water gillnets	Juvenile & adult large fish in sublittoral fykenets
years in lakes	89-90 89-91	none	87-91 88-90 88-91 89-90 89-91	87-90 89-90	89-90	n.a.	n.a.
years in channels	89-90 89-91	none	87-91	none	none	87-91 88-91	none
years in lakes and channels	89-90 89-91	n.a.	n.a.	n.a.	89-90	n.a.	none
months in lakes	apr-jun apr-aug apr-oct	feb-jun feb-aug apr-jun apr-aug jun-oct jun-dec aug-oct aug-dec	feb-jun feb-aug jun-dec aug-dec oct-dec	feb-aug feb-oct apr-aug apr-oct jun-oct jun-dec aug-dec oct-dec	apr-jun	feb-jun feb-aug	n.a.
months in channels	feb-aug apr-jun apr-aug aug-dec	feb-jun feb-aug apr-jun apr-aug apr-jun jun-dec aug-oct aug-dec	feb-jun feb-aug apr-jun apr-aug jun-oct jun-dec aug-oct aug-dec	feb-aug	none	feb-jun feb-aug feb-oct apr-jun apr-aug jun-oct jun-dec aug-oct aug-dec	feb-aug apr-aug aug-oct
months in lakes + channels	feb-jun feb-aug feb-oct apr-jun apr-aug apr-oct aug-dec	n.a.	n.a.	n.a.	feb-jun apr-jun apr-aug aug-dec	n.a.	feb-aug apr-aug aug-oct
seasons in lakes	aut-win	sum-win sum-spr aut-win win-spr	spr-sum sum-win	sum-spr aut-spr win-spr	aut-win	none	n.a.
seasons in channels	sum-spr aut-win aut-spr	sum-win sum-spr aut-win aut-spr	aut-win spr-sum sum-win	sum-win sum-spr	sum-win	sum-win sum-spr aut-win	aut-spr
seasons in lakes + channels	sum-win sum-spr aut-win aut-spr	n.a.	n.a.	n.a.	aut-win	n.a.	none

4.3.5 Classification of biological and hydrological data (waterbody and flow history scales)

A classification of the hydrological data corresponding to the 20m seine samples and a classification of the 20m seine biological data are provided (Figs 60-61) as examples of the results for all databases. The major features of the 20m seine classifications were shared by the classifications of the other hydrological and biological datasets (Puckridge & Walker 1996).

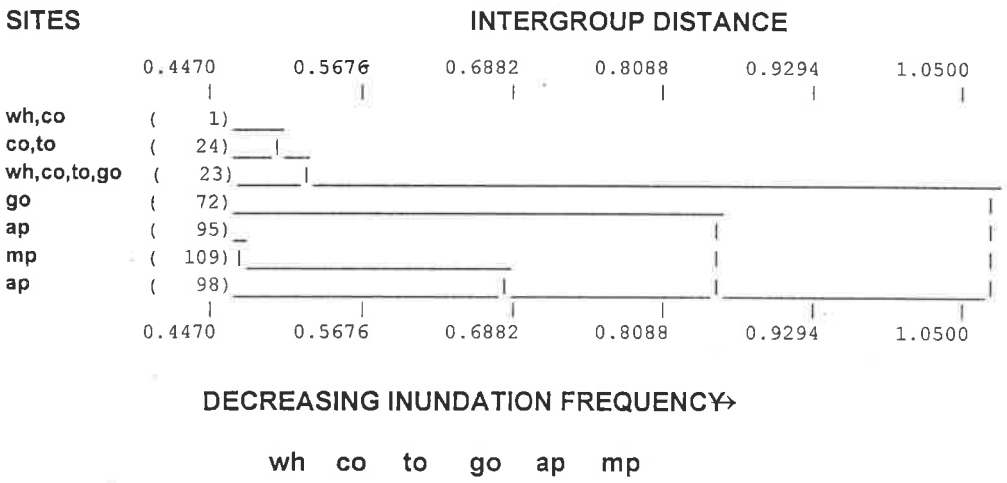


Figure 60. UPGMA classification of site hydrology data for samples of juvenile and adult small fish species in the deep littoral (110 samples, groups labelled by site, defined by 30 hydrological attributes, ANOSIM P = 0.000).

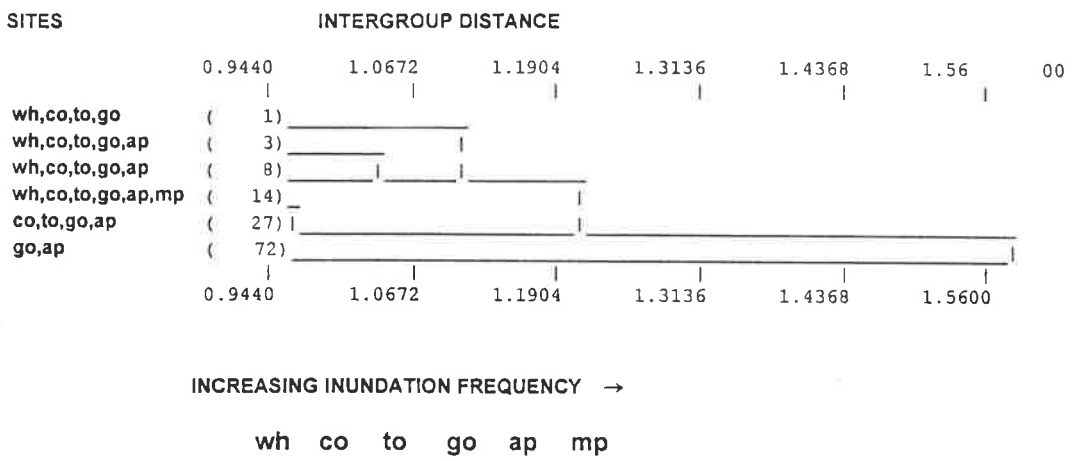


Figure 61 UPGMA classification of CPUE for samples of juvenile and adult small fish species in the deep littoral (groups labelled by site, defined by abundance of 10 species in 110 samples, ANOSIM P = 0.000)

Classification of the hydrological data produced some significant separation of waterbodies for all six datasets (e.g. Fig 60). In particular, the least frequently flooded waterbodies (Lakes Goolangirie *go*, Apanburra *ap* and Maroopootanie *mp*) tended to be separated from the more frequently flooded waterbodies (Coongie Crossing channel *wh*, Coongie Lake *co*, Lake Toontoowaranie *to*). The trawl and gillnet hydrology datasets (classifications not shown) included in addition the main branch channel waterbodies (Queerbidie waterhole *mb*, Cullyamurra waterhole *ca*), and these permanent waterbodies were also separated from others.

Classification of the biological data (e.g. Fig. 61) showed little distinct, consistent and significant separation of waterbodies, although occasional separations of rarely flooded sites occurred. Transposition and classification of the biological databases in all cases produced significant groupings of taxa, often including significant separation of rare and common taxa. However partitioning of the data according to these groups and reclassification based on these data provided no consistent improvement in the separation of waterbodies (Puckridge & Walker 1996).

4.3.6 Ordination of hydrological and biological data (waterbody and flow history scales)

4.3.6.1 Ordination plots

All ordinations showed adequate stress levels (0.1-0.2) using 2 or 3 dimensions. Examples of plots of ordination of the hydrological and biological data for the 20m seine are given in Figs 62-65 below. Ordination plots for other datasets (not shown) gave similar results (Puckridge & Walker 1996).

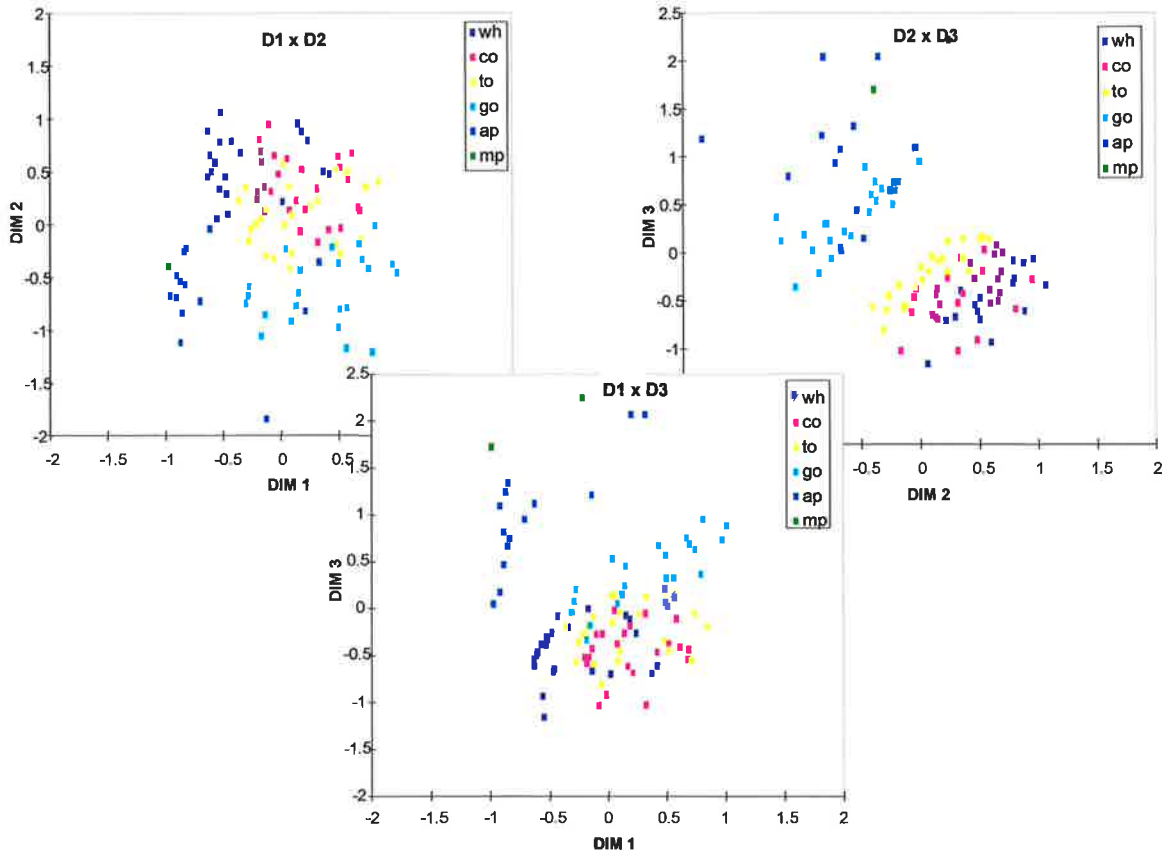


Figure 62 SSH MDS ordination of values of 30 hydrological measures corresponding to the 20m seine fish abundance samples. Values labelled by waterbody.

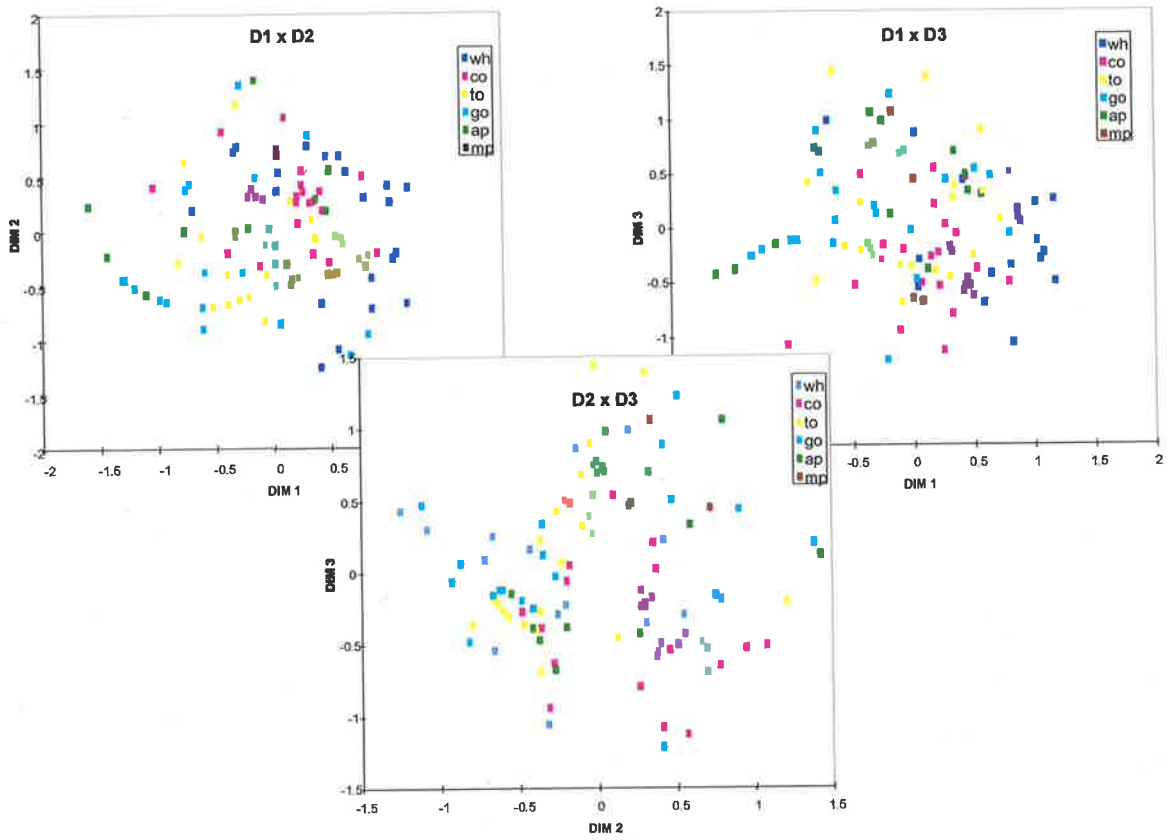


Figure 63. SSH MDS ordination of samples of abundance of juvenile and adult fish species in the deep littoral. Samples labelled by waterbody.

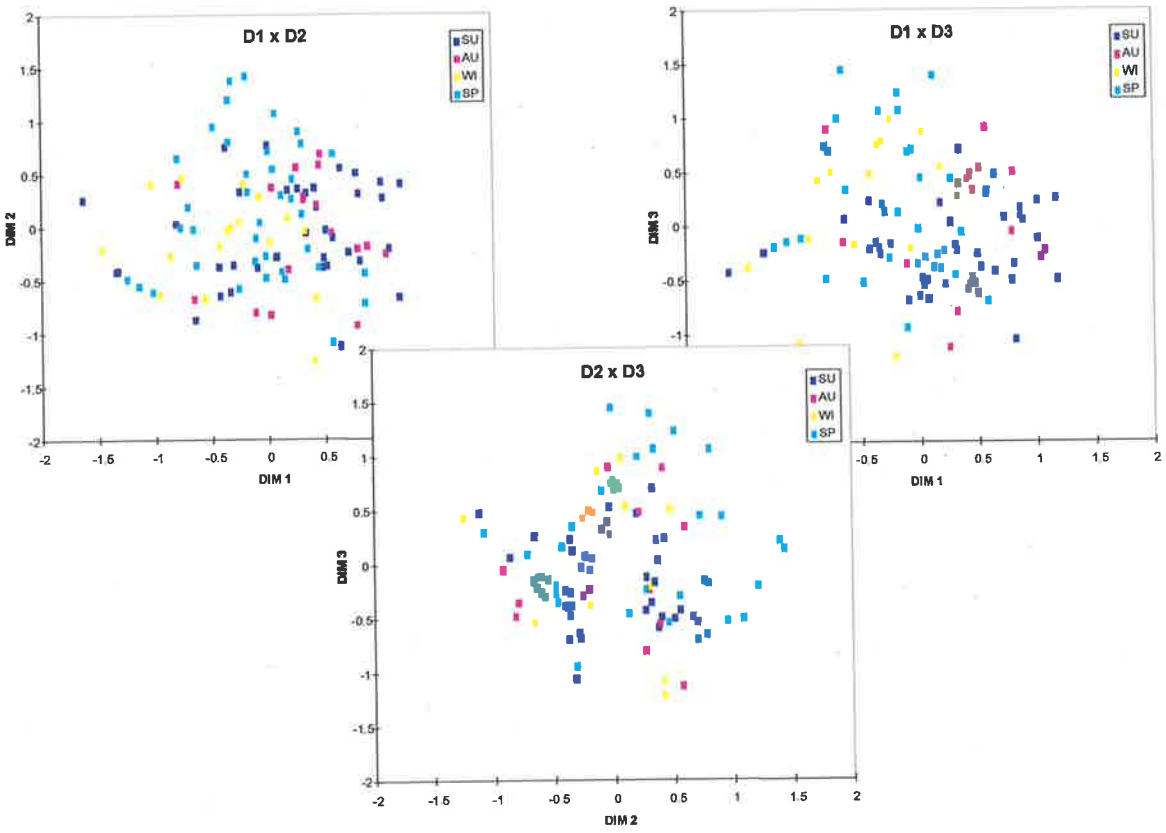


Figure 64. SSH MDS ordination of samples of abundance of juvenile and adult fish species in the deep littoral. Samples labelled by season.

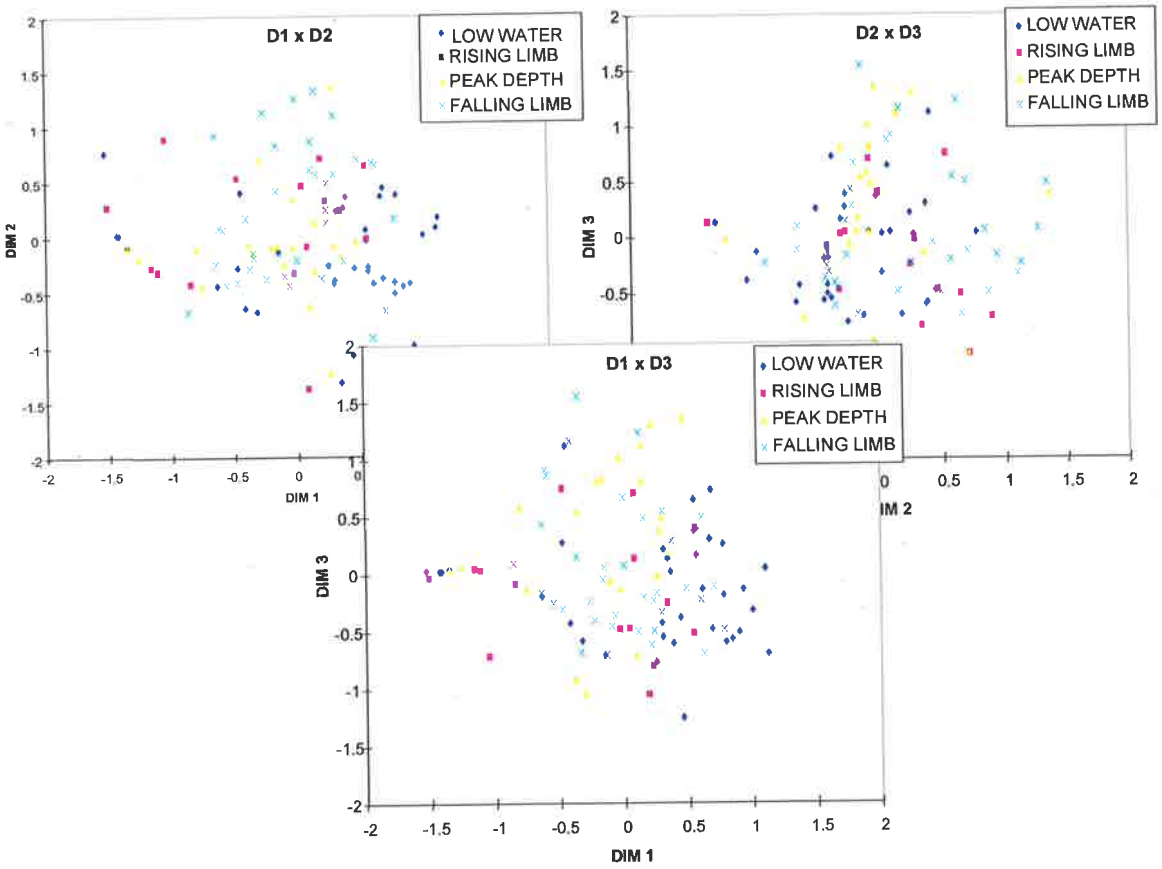


Figure 65. SSH MDS ordination of samples of abundance of juvenile and adult fish species in the deep littoral. Samples labelled by flood phase.

The 20m seine data included 110 samples in six major waterbodies - the Coongie Crossing channel (*wh*), Coongie Lake (*co*), Lake Toontoowaranie (*to*), Lake Goolangirie (*go*), Lake Apanburra (*ap*) and Lake Maroopootanie (*mp*). There was a clear grouping of hydrological values in waterbodies from the ordination of 30 hydrological measures (Fig. 62). There was separation of *wh*, *ap* and *go* in the first two dimensions, strong separation of *ap* and *mp* from the other waterbodies in dimensions 1 and 3, and in dimensions 2 and 3 the major separation was between *go*, *ap, mp* from *wh*, *co*. These separations were principally along the gradient of decreasing permanency: *wh-co-to-go-ap-mp*.

However, the ordination by 10 fish species did not produce clear grouping of samples labelled by waterbodies (Fig. 63). In dimensions 1 by 2, there was an approximate gradient

of ephemeral to more permanent waterbodies along dimension 1, but this gradient was less apparent in dimensions 1 by 3, and there was no clear grouping or gradient in dimensions 2 by 3. The ordinations of samples for the 5 common fish species and for the 5 rare fish species (not shown) gave similar results to the ordination of all fish species (Puckridge & Walker 1996).

The ordination of samples by 10 fish species labelled by season (Fig. 64) showed no seasonal grouping of samples, nor did the labelling of samples by flow pulse phase show grouping by this parameter (Fig 65). Ordinations labelled by month, year and flow pulse (not shown) gave similar results (Puckridge & Walker 1996). The findings were similar from ordinations of the other datasets (not shown).

4.3.6.2 Succession at major sites

Succession was not evident at the relatively permanent sites (such as Coongie Lake) which were already flooded at the beginning of sampling (Fig. 66). It was evident in the sites which were dry at the beginning of sampling (Lake Goolangirie, Lake Apanburra) and then were successively inundated (Figs. 67, 68). Even at these sites however, what appeared to be successional trajectories were partly obscured by shorter-term variations in assemblage structure. These findings were true of other sites and of the other fish and the invertebrate assemblages.

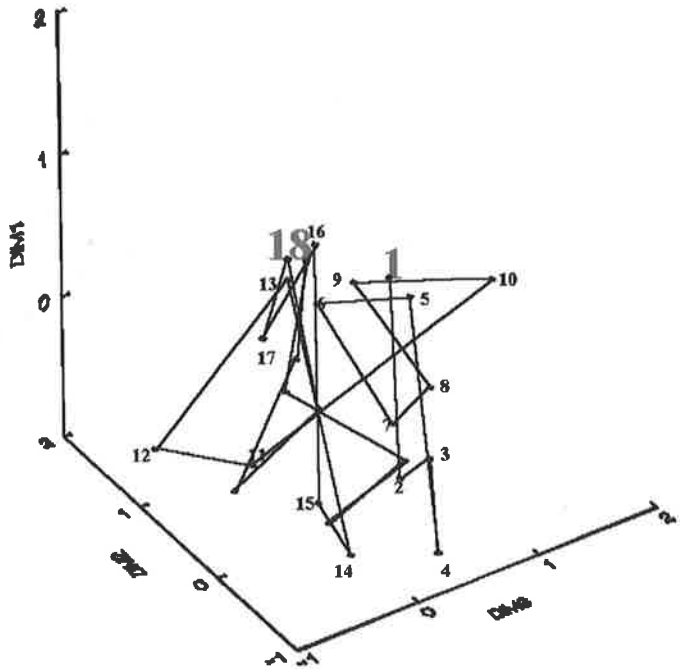


Figure 66. SSH MDS ordination of samples of fish abundance in samples of juvenile and larval fish species in the shallow littoral of Coongie Lake. Samples numbered in temporal sequence.

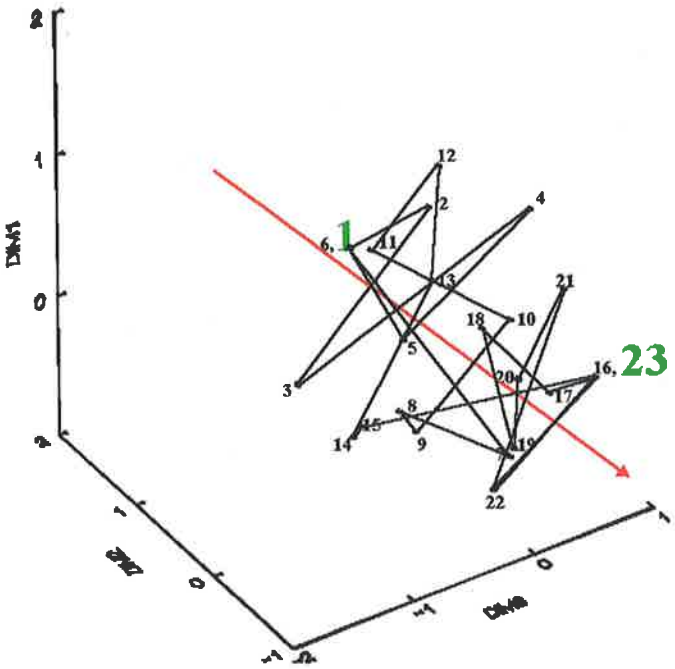


Figure 67. SSH MDS ordination of fish abundance in samples of juvenile and larval fish species in the littoral zone of Lake Goolangirie. Samples numbered in temporal sequence, red arrow indicates direction of suggested succession.

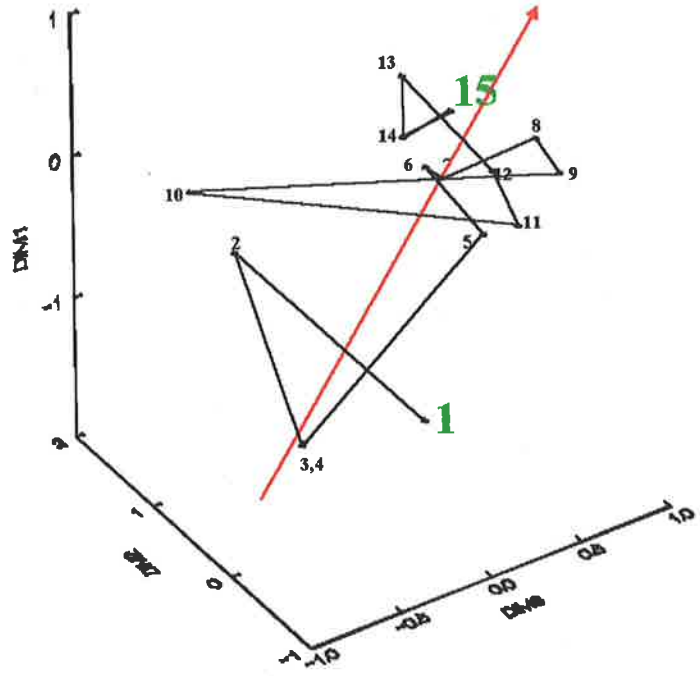


Figure 68. SSH MDS ordination of fish abundance in samples of juvenile and larval fish species in the littoral zone of Lake Apanburra. Samples numbered in temporal sequence, red arrow indicates direction of suggested succession.

4.3.6.3 Comparing biological and hydrological ordinations

Comparing ordinations by Procrustean rotation confirmed the disparity between the biological and hydrological datasets which was illustrated in both the ordination plots and the classifications (Table 56). The goodness of fit of each ordination pair is indicated by the root mean square symmetric error (RMSSE), which has a range from 0 to 1, where 0 represents a perfect fit, and 1 no fit at all. The fit between ordination pairs on this measure was poor. Deleting from the hydrological data those measures not significantly correlated with the biological ordination (not shown) did not markedly improve the RMSSE, nor did dividing the biological data base into rare and common species.

Table 56 Fit of hydrological and biological ordinations

Statistic of fit is Root Mean Square Symmetric Error (RMSSE). This ranges from 0 to 1, with fit improving toward 0

MACROINVERTEBRATES (OPEN WATER)			
	17 taxa (all)	8 common taxa	9 rare taxa
	30 measures	30 measures	30 measures
	135 samples	135 samples	120 samples
RMSSE	0.94	0.94	0.95
FISHTRAWL (JUVENILES AND LARVAE, OPEN WATER)			
	8 sp. (all)	3 common sp.	5 rare sp..
	30 measures	30 measures	30 measures
	140 samples	139 samples	43 samples
RMSSE	0.96	0.97	0.94
20M SEINE (JUVENILE AND ADULT SMALL SPECIES, SUB-LITTORAL ZONE)			
	10 sp. (all)	5 common sp.	5 rare sp..
	30 measures	30 measures	30 measures
	110 samples	110 samples	32 samples
RMSSE	0.93	0.93	0.91
2M SEINE (LARVAE AND JUVENILES, LITTORAL ZONE)			
	11 sp. (all)	5 common sp.	6 rare sp..
	30 measures	30 measures	30 measures
	134 samples	134 samples	27 samples
RMSSE	0.96	0.96	0.98
MULTIMESH GILLNETS (ADULT AND JUVENILE LARGE SPECIES, OPEN WATER)			
	9 sp. (all)	3 common sp.	6 rare sp..
	30 measures	30 measures	30 measures
	139 samples	135 samples	17 samples
RMSSE	0.98	0.97	0.95

4.3.7 Regression of flow history hydrological measures on biological ordinations at the waterbody spatial scale

However, significant results did result from the multiple regression of hydrological measures on the biological ordinations and evaluation of these correlations by Monte Carlo randomisation. To compensate for the multiple comparisons made in correlation of hydrological measures with each ordination, only measures correlated at $P < 0.01$ were

retained. This gave a suite of hydrological measures correlated significantly with the biological ordinations for each dataset (Tables 57-63).

Table 57. Flow history measures (waterbody scale) correlated with assemblage structure of zooplankton in the shallow littoral.

Code	Facet	Measure
DPNFL	Flow	Duration of present cessation of flow (if any)
DLNFL	Flow	Duration of cessation of flow at one remove from present
PSDEP	Amplitude	Present standard depth
DLFAL	Pulse shape	Duration of falling limb at one remove from present
DPDCO	Connection	Duration of present downstream connection (if any)

Table 58. Flow history measures (waterbody scale) correlated with assemblage structure of macroinvertebrates in open water.

Code	Facet	Significantly correlated measures (P<0.01)
DPFLO	Flow	Duration of present flow (if any)
DPNFL	Flow	Duration of present cessation of flow (if any)
DLNFL	Flow	Duration of cessation of flow at one remove from present
DLNF1	Flow	Duration of cessation of flow at two removes
PSDEP	Amplitude	Present standard depth
LMAD1	Amplitude	Maximum depth at one remove from last
DPRLM	Pulse shape	Duration of present rising limb (if any)
DLRL1	Pulse shape	Duration of rising limb at two removes
DPFAL	Pulse shape	Duration of present falling limb (if any)
DLFAL	Pulse shape	Duration of falling limb at one remove from present
DLINU	Duration	Duration of inundation at one remove from present
DLUCO	Connection	Duration of upstream connection at one remove from present

Table 59. Flow history measures (waterbody scale) correlated with assemblage structure of larval and juvenile fish in open water.

Code	Facet	Significantly correlated measures (P<0.01)
DPFLO	Flow	Duration of present flow (if any)
DPNFL	Flow	Duration of present cessation of flow (if any)
PSDEP	Amplitude	Present standard depth
LMID1	Amplitude	Minimum depth at one remove from last
DPRLM	Pulse shape	Duration of present rising limb (if any)

Table 60. Flow history measures (waterbody scale) correlated with assemblage structure of larval and juvenile fish in the shallow littoral.

Code	Facet	Significantly correlated measures (P<0.01)
LMIDE	Amplitude	Last minimum depth
DLFA1	Pulse shape	Duration of falling limb at two removes
DPINU	Duration	Duration of present inundation (if any)

Table 61. Flow history measures (waterbody scale) with assemblage structure of juvenile and adult small fish in the deep littoral.

Code	Facet	Significantly correlated measures (P<0.01)
MXTIM	Timing	Departure of peak waterbody depth from long-term average timing
PSDEP	Amplitude	Present standard depth
LMAD1	Amplitude	Maximum depth at one remove from last
LMIDE	Amplitude	Last minimum depth
DLINU	Duration	Duration of inundation at one remove from present
DPUCO	connection	Duration of present upstream connection (if any).
DPDCO	connection	Duration of present downstream connection (if any)
RFDRY	permanence	Relative frequency of drying

Table 62. Flow history measures (waterbody scale) correlated with assemblage structure of juvenile and adult large fish in the deep littoral.

Code	Facet	Significantly correlated measures (P<0.01)
MXTIM	Timing	Departure of peak waterbody depth from long-term average timing
DPFLO	Flow	Duration of present flow (if any)
DPNFL	Flow	Duration of present cessation of flow (if any)
PSDEP	Amplitude	Present standard depth
LMAD1	Amplitude	Maximum depth at one remove from last
LMIDE	Amplitude	Last minimum depth
DPINU	Duration	Duration of present inundation (if any)
DLDRY	Duration	Duration of dry at one remove from present

Table 63. Flow history measures (waterbody scale) correlated with assemblage structure of juvenile and adult large fish in open water.

Code	Facet	Significantly correlated measures (P<0.01)
MNTIM	Timing	Departure of minimum waterbody depth from long-term average timing
DPFLO	Flow	Duration of present flow (if any)
DLFLO	Flow	Duration of flow at one remove from present (last flow)
DPNFL	Flow	Duration of present cessation of flow (if any)
PSDEP	Amplitude	Present standard depth
DPRLM	Pulse shape	Duration of present rising limb (if any)
DPFAL	Pulse shape	Duration of present falling limb (if any)
DLINU	Duration	Duration of inundation at one remove from present
DPUCO	connection	Duration of present upstream connection (if any).
DLDCO	connection	Duration of downstream connection at one remove from present

4.3.7.1 The flow history and season *facets* at the waterbody scale significantly correlated with biological assemblage structures

The facets shown below (Table 64) are derived by merging those measures which (a) are significantly correlated (above) with one or more of the biological assemblage structures, and (b) which quantify the same facet at different temporal lags.

Table 64. Flow history facets and measures (waterbody scale) significant for biological assemblage structures, all biological databases combined.

Facets (derived by merging measures)	*Measures*
Pulse shape	Duration of falling and duration of rising limbs of the depth pulse
Flow duration	Duration of flow and duration of no-flow
Inundation duration	Duration of drying and duration of inundation
Pulse amplitude	Present depth
Pulse amplitude (extremes)	Maximum depth and minimum depth
Connectivity	Duration of upstream connection and duration of downstream connection
Timing	Timing of depth maximum and timing of depth minimum
Permanence	Long-term relative frequency of drying

One or more of the hydrological measures within each of the facets of timing, flow, amplitude, pulse shape, duration, connectivity and permanence (Table 64), correlated significantly with one or more of the seven biological ordinations. The facet *pulse amplitude* had the highest number of significantly correlated measures, the facet of *permanence* the lowest. The highest total score of significantly correlated facets was with the ordination of samples from the gillnet database (adult and juvenile large fish in open water), the lowest with the datasets for larval and juvenile fish in the littoral and in open water (2m seine and 500 trawl datasets respectively). Correlations with ordinations of rare and common taxa were fewer than for those with ordinations of all taxa in the dataset (not shown).

4.3.8 Regression of flow history hydrological *measures* on biological ordinations at the river reach scale – correlation values

The same methods as above were used to correlate hydrological measures with biological assemblage structures at the river reach scale (Tables 65-71). Values of correlations between flow history measures and the seven biological datasets provided below illustrate the relative strengths of these correlations.

Table 65. Season and flow history measures significantly correlated with assemblage structure of zooplankton in the shallow littoral.

Measure	Code	Correlation
minimum air temperature (C)	MNTEM	0.539
last minimum discharge (ML)	LMIDS	0.488
maximum air temperature (C)	MXTEM	0.465
duration of last falling limb (months)	DLFAL	0.465
Timing of maximum discharge before last (months +/- average)	LMXT1	0.465
duration of rising limb before last (months)	DLRL1	0.456
duration of last flow (months)	DLFLO	0.418
duration of flow before last (months)	DLFL1	0.418
duration of flow two before last (months)	DLFL2	0.418
amplitude of last falling limb (ML)	LFLAM	0.414
monthly total discharge (ML)	MTOTL	0.4
total discharge to date of past pulse (ML)	LTOTL	0.391
duration of present flow (months)	DPFLO	0.391
present monthly discharge (ML)	PDISC	0.389
Timing of last maximum discharge (months +/- average)	LMXTM	0.384
maximum discharge before last (ML)	LMAD1	0.381
minimum discharge two before last (ML)	LMID2	0.373
rate of last fall (Ml/month)	RLFLL	0.366
duration of falling limb before last (months)	DLFA1	0.363
total discharge to date of pulse before last (ML)	LTOT1	0.361
daylength (mins)	DLENG	0.35
amplitude of rising limb before last (ML)	LRLA1	0.346
duration of falling limb two before last (months)	DLFA2	0.346
Timing of last minimum discharge (months +/- average)	LMNTM	0.334
total discharge to date of present pulse (ML)	PTOTL	0.299
duration of present no flow (months)	DPNFL	0.295

Table 66. Season and flow history measures significantly correlated with assemblage structure of macroinvertebrates in open water.

Measure	Code	Correlation
minimum air temperature (C)	MNTEM	0.821
maximum air temperature (C)	MXTEM	0.791
daylength (mins)	DLENG	0.666
present monthly discharge (ML)	PDISC	0.609
monthly total discharge (ML)	MTOTL	0.56
total discharge to date of present pulse (ML)	PTOTL	0.422
duration of present rising limb (months)	DPRLM	0.361
minimum discharge two before last (ML)	LMID2	0.353
duration of last falling limb (months)	DLFAL	0.349
total discharge to date of past pulse (ML)	LTOTL	0.324

Table 67. Season and flow history measures significantly correlated with assemblage structure of larval and juvenile fish in open water.

Measure	Code	Correlation
minimum air temperature (C)	MNTEM	0.647
maximum air temperature (C)	MXTEM	0.631
daylength (mins)	DLENG	0.599
present monthly discharge (ML)	PDISC	0.589
monthly total discharge (ML)	MTOTL	0.572
duration of last flow (months)	DLFLO	0.447
duration of last falling limb (months)	DLFAL	0.433
amplitude of last falling limb (ML)	LFLAM	0.429
last minimum discharge (ML)	LMIDS	0.407
Timing of maximum discharge before last (months +/- average)	LMXT1	0.406
total discharge to date of past pulse (ML)	LTOTL	0.399
amplitude of rising limb two before last (ML)	LRLA2	0.381
rate of rise two before last (ML/month)	RLRS2	0.381
duration of flow before last (months)	DLFL1	0.374
rate of last fall (Ml/month)	RLFLL	0.37
maximum discharge two before last (ML)	LMAD2	0.359
duration of rising limb two before last (months)	DLRL2	0.347
duration of rising limb before last (months)	DLRL1	0.306
rate of last rise (ML/month)	RLRSL	0.282
total discharge to date of pulse before last (ML)	LTOT1	0.276
maximum discharge before last (ML)	LMAD1	0.268

Table 68. Season and flow history measures significantly correlated with assemblage structure of larval and juvenile fish in the shallow littoral.

Measure	Code	Correlation
total discharge to date of present pulse (ML)	PTOTL	0.409
last maximum discharge (ML)	LMADS	0.391
amplitude of last rising limb (ML)	LRLAM	0.388
rate of last rise (ML/month)	RLRSL	0.381
duration of last rising limb (months)	DLRLM	0.342
duration of present falling limb (months)	DPFAL	0.334
rate of fall before last (ML/Month)	RLFL1	0.318
minimum air temperature (C)	MNTEM	0.303
maximum air temperature (C)	MXTEM	0.296
duration of no flow before last (months)	DLNF1	0.288
duration of present rising limb (months)	DPRLM	0.281

Table 69. Season and flow history measures significantly correlated with assemblage structure of juvenile and adult small fish in the deep littoral.

Measure	Code	Correlation
present monthly discharge (ML)	PDISC	0.433
minimum air temperature (C)	MNTEM	0.422
total discharge to date of present pulse (ML)	PTOTL	0.413
maximum air temperature (C)	MXTEM	0.412
monthly total discharge (ML)	MTOTL	0.406
duration of present flow (months)	DPFLO	0.347
amplitude of last rising limb (ML)	LRLAM	0.315
rate of last rise (ML/month)	RLRSL	0.309
rate of last fall (Ml/month)	RLFLL	0.287

Table 70. Season and flow history measures significantly correlated with assemblage structure of juvenile and adult large fish in open water.

Measures	Code	Correlation
maximum air temperature (C)	MXTEM	0.638
minimum air temperature (C)	MNTEM	0.594
daylength (mins)	DLENG	0.492
present monthly discharge (ML)	PDISC	0.489
monthly total discharge (ML)	MTOTL	0.449
duration of no flow before last (months)	DLNF1	0.3837
duration of no flow before last (months)	DLNF2	0.3837
duration of flow before last (months)	DLFL1	0.371
duration of last rising limb (months)	DLRLM	0.368
amplitude of last falling limb (ML)	LFLAM	0.348
rate of last fall (Ml/month)	RLFLL	0.344
total discharge to date of past pulse (ML)	LTOTL	0.3379
Timing of minimum discharge two before last (months +/- average)	LMNT2	0.331
duration of last falling limb (months)	DLFAL	0.318
duration of flow two before last (months)	DLFL2	0.308
duration of last flow (months)	DLFLO	0.303
total discharge to date of present pulse (ML)	PTOTL	0.296
minimum discharge before last (ML)	LMID1	0.295
Timing of last minimum discharge (months +/- average)	LMNTM	0.27
minimum discharge two before last (ML)	LMID2	0.248
duration of rising limb before last (months)	DLRL1	0.231

Table 71. Season and flow history measures significantly correlated with assemblage structure of juvenile and adult large fish in the deep littoral.

Measure	Code	Correlation
daylength (mins)	DLENG	0.564
duration of rising limb two before last (months)	DLRL2	0.562
minimum air temperature (C)	MNTEM	0.555
maximum discharge two before last (ML)	LMAD2	0.505
maximum air temperature (C)	MXTEM	0.503
rate of last fall (Ml/month)	RLFLL	0.497
amplitude of last falling limb (ML)	LFLAM	0.475
total discharge to date of past pulse (ML)	LTOTL	0.474
Timing of maximum discharge two before last (months +/- average)	LMXT2	0.466
minimum discharge two before last (ML)	LMID2	0.464
rate of rise before last (ML/month)	RLRS1	0.463
Timing of minimum discharge before last (months +/- average)	LMNT1	0.44
amplitude of rising limb before last (ML)	LRLA1	0.433
duration of last falling limb (months)	DLFAL	0.412
rate of fall two before last (Ml/Month)	RLFL2	0.407
amplitude of rising limb two before last (ML)	LRLA2	0.401
rate of fall before last (ML/Month)	RLFL1	0.401
total discharge to date of pulse two before last (ML)	LTOT2	0.387
amplitude of falling limb before last (ML)	LFLA1	0.381
rate of rise two before last (ML/month)	RLRS2	0.377

4.3.8.1 The flow history and season *facets* at the river reach scale significantly correlated with biological assemblage structures

The facets shown below (Table 72) are derived by merging those measures which (a) are significantly correlated (above) with one or more of the biological assemblage structures, and (b) which quantify the same facet at different temporal lags.

Table 72. Flow history and season facets (river reach scale) significant for biological assemblage structure, all databases combined.

Type	Facet	Measures (timelags merged)
Season	Season	Air temp. (max.)
		Air temp. (min)
		Daylength
Flow history	Pulse shape	Duration of rising limb
		Duration of falling limb
		Rate of rise of rising limb
		Rate of fall of falling limb
	Flow duration	Duration of flow
		Duration of no flow
	Pulse amplitude	Present discharge
		Amplitude of falling limb
		Amplitude of rising limb
	Pulse amplitude (extremes)	Maximum discharge
		Minimum discharge
	Timing	Timing of discharge maximum
		Timing of discharge minimum
	Flow volume	Flow volume

Those facets of flow history (at the river reach scale) which were correlated with assemblage structure varied between databases. Zooplankton, large fish (in open water and in the deep littoral) and larval/juvenile fish in the open water showed the widest range of correlations. The values of correlations for facets of season were higher than those for flow history for some assemblages. The facets of flow history identified by correlation of river reach flow history measures with assemblage structure corresponded to their equivalents derived from correlation of waterbody flow history measures with assemblage structure. But there were three facets specific to the waterbody scale (connectivity, permanence and inundation duration), and one (flow volume) specific to the river reach scale. The data were not available to quantify the latter facet at the waterbody scale, or to accurately calculate rates of rise and fall of waterbody depth.

4.4 Discussion

4.4.1 Physicochemistry

(see also Puckridge *et al.* in press)

The increases in minimum winter afternoon water temperatures recorded over 1987–91 are surprising because the same increases did not occur in air temperatures. Floodwaters descending from Queensland in May 1990 were warmer at the surface than water remaining in the Coongie Lakes from the previous year's flood (Puckridge *et al.* in press), and may have imported thermal energy from the lower latitude catchment, increasing the winter temperatures of the lakes. Also, the greater volume of water in the wetlands following winter flooding would have increased the thermal inertia of the water bodies and so perhaps minimum water temperatures. However, a corresponding fall in temperature maxima would also be expected, and this is not evident. Another factor in winter temperature rise may have been the increased water transparency after mid-1989, which would have allowed deeper penetration of daytime infra-red energy and more rapid rise in daytime water temperatures (cf. Lillesand & Kiefer 1987, Walling & Webb 1992). Regardless of the explanation, the observed temperature increase is likely to have been biologically significant (see *Chapter 5*).

Cooper Creek water generally is turbid, owing principally to fine particles (<1 μm diam., Roberts 1988). The reason for the progressive increase in transparency (Secchi depth) after mid-1989 is unclear. Flocculation by increased salinity (Akhurst & Breen 1988) can be discounted, as conductivity rose only as the floodwaters receded. NOAA-AVHRR images on 24 May 1989 (Puckridge *et al.* in press) do not indicate a lower turbidity in the floodwaters descending from Queensland than in the residual water in Coongie Lakes. Further, the second and larger of the two pulses in the above image is more turbid than the first, so there is no evidence for subsequent pulses having less sediment available.

Big floods usually are associated with higher rather than lower sediment loads (cf. Bremner *et al* 1990, Roos & Pieterse 1994, 1995). However, the balance between sediment

settling and suspension is also influenced by floodplain storage (Olive *et al.* 1994), and the Coongie Lakes are in an area of net sediment deposition (Callen & Bradford 1992). The decrease in transparency in the wetlands became most noticeable following the 1989 flood when extensive floodplain inundation occurred (Fig. 10 in Puckridge *et al.* in press, bound in support). The smaller flows of 1987 and 1988 were confined more to channels and may have retained higher densities of sediment for this reason.

The inverse relationship between conductivity and discharge in the lower Cooper (Glatz 1985), presumably stems from the low conductivity of rainfall. The rise in conductivity at the end of the flood series in 1991 is attributable largely to the high rate of evaporation.

Some of the biological implications of these changes over the flood series will be demonstrated and discussed in Chapter 5. However the results illustrate how profound the impact of the great variability of discharge in arid zone rivers may be on the instream environment, particularly when this variability is combined with flow pulse persistence (Puckridge *et al.* in press).

4.4.2 Spatial differences between biological assemblages

Classification and ordination of hydrological data at the waterbody scale show that waterbodies are distinctive in terms of the hydrological measures used. However, classification and ordination of the biological data (fish and macroinvertebrates) suggest that the waterbodies are not markedly distinctive in biological assemblage structure. Yet ANOSIM comparisons of assemblage samples grouped by waterbody show significant differences in assemblage structure between lake and channel sites, and between individual sites.

This inconsistency may be due in part to the temporal trajectories of assemblage structure evident in the biological ordinations of the less frequently inundated sites. These trajectories show pronounced temporal variation in assemblage structure which is not synchronized between sites, and affects intersite comparisons. Further, in the previously dry waterbodies there are temporal trends suggesting assemblage succession through the flow pulse series. Given the duration of waterbody interconnection over this flow pulse series,

and the strong colonizing propensities of the fauna of intermittent streams (Puckridge & Drewien 1988, Boulton *et al.* 1991), the sites may have been converging on a common assemblage structure. If this were the case, differences in assemblage structure between sites would only be apparent in the early phase of the flow pulse series. ANOSIM's reliance on significance testing may allow it to identify diffuse but significant groupings not evident in ordination or classification.

4.4.3 Seasonal differences between biological assemblages

Ordination of the biological data for fish, zooplankton and macroinvertebrates suggests that assemblages do not differ markedly between season, month or year. Yet ANOSIM on groupings of the seven biological assemblages demonstrates significant differences between assemblage samples grouped by month, year and particularly season. The ANOSIM results are reinforced by the significant correlations between measures of season (daylength, air temperature) and the ordinations of biological assemblage samples. In an environment with an extreme range of seasonal temperatures (Kotwicki 1986, Reid 1988) biological responses timed to season are expected.

The lower Cooper has a hydrological cycle with a variable but substantial seasonal component (Puckridge *et al.* in press), so the influences of hydrology and season are to some extent confounded, and the approaches used in this thesis cannot entirely separate these influences.

4.4.4 Differences between assemblages in relation to flow history

Evidence for weakness of the match between hydrology and overall assemblage structures at the waterbody level is the poor fit obtained by the Procrustean rotation of the biological ordinations on the corresponding hydrological ordinations. On the other hand, ANOSIM on grouping of assemblages by flow pulse and particularly by flow pulse phase shows significant differences in assemblage structures. Further, the multiple regressions of hydrological measures on the fish and macroinvertebrate ordinations at both the waterbody and river reach scales demonstrate significant correlations for a broad range of hydrological measures in all hydrological facets, for all assemblages. Even assuming some redundancy in

the suites of hydrologic measures used here (see Chapter 5), these results suggest a substantial association between flow history and assemblage structures.

4.5 Summary

The results above support the contention that the biological influence of hydrology is a complex process, exerted simultaneously through a variety of factors (Walker *et al.* 1995, Puckridge *et al.* 1998). Further, in the ANOSIM comparison of the biological assemblage structures corresponding to flow pulse phases, the low water phase was the most biologically distinctive of the four phases considered. This suggests that the low water phase is biologically particularly important, and is evidence for rejecting **hypothesis 2.1**, that *the overbank phases of the flow pulse are biologically more important than the inchannel phases*.

At the river reach scale, the measures demonstrating significant correlations with biological assemblage structure (Table 72) fit into those facets of hydrology identified by others as ecologically important (Poff & Ward 1989, Junk *et al.* 1989, Richter 1996, 1997, Young 1999). At the waterbody scale, several facets – connectivity, permanence, inundation duration and flow duration are not explicitly mentioned by Junk *et al.* (1989), but are implied. However, within these facets there are several significant hydrological measures which are excluded by the focus of Junk *et al* (1989) on overbank flows – viz. duration of no-flow, duration of drying, frequency of drying, duration of connection (including between channel waterbodies). Since they are significantly correlated with assemblage structures these measures are potentially ecologically significant, so **hypothesis 2.3**, that *the facets of the flood pulse listed in Junk et al. (1989) are adequate to describe the influence of hydrology on overall structure of fish, zooplankton and macroinvertebrate assemblages*, and **hypothesis 2.4**, that *hydrological events at the scale of overbank flows are sufficient to describe biology-hydrology interactions in floodplain rivers* are rejected.

The significantly correlated measures include not only features of the current flow pulse but those of past flow pulses several removes from the present; a finding which holds even for short-lived zooplankters. This confirms that flow history plays a major structuring role in river biota (Benech *et al.* 1983, Quiros & Cuch 1989). Further, of the five major

flow pulses in the sampling period, ANOSIM indicates that the biological assemblage structures associated with the largest pulse (in 1990) were the most distinctive. So exceptional events may have a defining role in arid zone river ecology. Accordingly **Hypothesis 2.2**, that *variations in fish, zooplankton and macroinvertebrate assemblage structures are independent of flow history*, is rejected.

The fact that none of the biological ordination plots labelled for month, year, season, site, flow pulse or flow pulse phase showed clearcut groupings of samples suggests that neither seasonal factors nor annual or sub-annual hydrological factors, nor strictly site-specific characteristics were dominant in determining the biological structures of these assemblages. Further, the range of facets and measures identified differed markedly between assemblages, even between the different subsets of the lower Cooper Creek fish assemblage. Chapter 5 will focus on the detail of these differences by examining relations between hydrological measures and individual indices of assemblage structure and individual species within the fish assemblage.

5. Assemblage indices and attributes of individual species vs waterbody flow regime and river reach flow history.

5.1 Introduction

Chapter 4 explored relations between overall assemblage structure and flow history at the waterbody and river reach scales. Significant differences were demonstrated between assemblage structures at different sites and during different months, seasons, years, flow pulses and flow pulse phases. There were multiple significant correlations between flow history measures (at the waterbody and river reach spatial scales) and assemblage structures mapped by ordination. The significantly correlated measures covered a range of flow magnitudes outside the "flood" events of the Flood Pulse Concept. However, the results also suggested that neither seasonal, hydrological, nor site-specific factors were dominant in determining the biological structures of assemblages.

Chapter 4 did not explore the possibility that assemblage attributes other than structure, such as assemblage health or behaviour, might be related to hydrological change. Also, individual elements of assemblage structure may be related differently and perhaps strongly to hydrology, even when assemblage structure shows little overall relation. Further, population changes of individual species may be uniquely related to hydrology.

In this chapter, hydrology-biology relations will be explored further by deconstructing all assemblages into indices of structure, and for the fish assemblages, also into indices of health, behaviour and into individual species. These assemblage elements will be related to hydrological measures (used singly and in combination) at the flow history and flow regime temporal scales, and the waterbody and river reach spatial scales. These relations will be compared to those obtained for overall assemblage structures.

Results of these analyses are used to test the following hypotheses from Chapter 1:

1. At the flow regime temporal scale and the whole river spatial scale:

1.9. The biota of hydrologically unpredictable rivers is not adapted to the flood pulse (Junk *et al.* 1989, Bayley 1991).

2. At the flow history and flow pulse temporal scales and the river reach and waterbody spatial scales in Cooper Creek:

2.4. Hydrological events at the magnitude of overbank flows are sufficient to describe biology-hydrology interactions in floodplain rivers.

2.5 When season and flow pulse are out of synchrony, fish production falls (Bayley 1991).

2.6 Fish recruitment is not related to flow pulse magnitude.

2.7 Health of fish assemblages (disease incidence, exotic/native species ratio) is independent of hydrology.

3. At the flow history and flow pulse temporal scales and the river reach spatial scale in Cooper Creek:

3.1 Variations in indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are independent of hydrology.

3.2 Most of the seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are redundant, and could be replaced fewer, summary measures.

3.3 The seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages account for a trivial amount of the variance in these indices.

3.4 The facets of the flood pulse listed in Junk *et al.* (1989) are adequate to describe the influence of hydrology on indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages.

3.5. Relations between flow history measures and indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages have the same sign throughout flow history.

4. At the flow regime and flow history temporal scales and the river reach spatial scale in Cooper Creek:

4.1. (a) Fish spawn primarily in response to seasonal, not hydrological cues (i.e. follow a 'double or nothing' spawning strategy, *sensu* Lloyd *et al.* 1991a).

(b) Fish migrate primarily in response to seasonal, not hydrological cues.

4.2 Indices of structure of fish, zooplankton and macroinvertebrate assemblages are not related to waterbody permanence.

4.3. Indices of fish assemblage health and behaviour are not related to waterbody permanence.

5.2 Data analysis

(for other aspects of methods see Ch. 4).

The following analyses were performed on data for the seven biological assemblages, in conjunction with their corresponding hydrological data.

5.2.1 Indices of assemblage structure, health and behaviour vs hydrological measures at the flow history and river reach scales.

5.2.1.1 Assemblage indices

For each dataset, abundance (ABUND), numbers of taxa (SPRCH) and Margalef's richness (MSPRC, Margalef 1951), Shannon-Wiener diversity (SHWDV Shannon & Weaver 1949), Pielou's taxon evenness (PEVEN, Pielou 1975) and Simpson's dominance (SMDOM – Simpson 1949), were derived for all taxa for each sample. For those datasets having the appropriate data, the ratio of abundance of exotic to native taxa (EXNAT, Karr 1981, 1991), the proportion of fish running ripe (RIPEN), the proportion of fish with dermal fungal lesions (DISEA, Karr 1981, 1991), the proportion of fish migrating upstream (USIND) and downstream (DSIND), and the absolute numbers of fish migrating upstream (UPMIG) and downstream (DNMIG) were also calculated.

Table 73 Indices of biological assemblage structure, health and behaviour

Index	Code	Formula
Taxon richness	SPRCH (S)	Total number of taxa
All taxa abundance	ABUND (N)	Sum of individuals of all taxa
Margalef's taxon richness	MSPRC (d)	(S-1)/log (N)
Shannon-Wiener diversity	SHWDV (H')	The sum over all taxa of $p_i(\log p_i)$, (where p_i is the proportion of total abundance contributed by each of the taxa)
Pielou's evenness	PEVEN (J')	H'(observed)/H'(max), where H'(max) is the value of the SHWDV index (H') if all taxa were equally abundant.
Simpson's dominance	SMDOM	The sum over all taxa of the square of p_I, (where p_I is the proportion of the total abundance contributed by each of the taxa
Proportion of exotic fish	EXNAT	Numbers of exotic fish/total fish numbers.
Proportion of running ripe fish	RIPEN	Numbers of running ripe fish/total fish numbers.
Proportion of diseased fish	DISEA	Numbers of fish with fungal lesions/total fish numbers.
Proportion of upstream moving fish	USIND	Numbers of upstream moving fish/ numbers of all fish
Proportion of downstream moving fish	DSIND	Numbers of downstream moving fish/ numbers of all fish
Numbers of upstream moving fish	UPMIG	*Only from fykenets, where direction of movement of all fish was recorded.*
Numbers of downstream moving fish	DNMIG	*Only from fykenets, where direction of movement of all fish was recorded.*

5.2.1.2 Correlation of assemblage indices with single flow history measures at the river reach scale

All hydrological measures were temporally advanced to improve the fit (at two-monthly resolution) of hydrological cycles to cycles in each assemblage index. The advance was 0-6 months, depending on the lag between flow pulse peaks and subsequent peaks in biological events such as fish spawning. The effects of each advance on prediction error was tested using Neural Networks (below), and only those advances which reduced prediction error were retained.

A major concern in all environmental modelling is the selection of input variables (Maier & Dandy 1997). Reducing the number of input variables simplifies management, and the elimination of redundant variables may improve the speed and predictive power of a model. However, input selection is not a simple process. Many hydrological measures tend to be intercorrelated, and therefore could be considered redundant. But intercorrelated measures (such as the duration of the rising and falling limbs of the flow pulse) may also have distinct and separable biological effects (Puckridge *et al.* 1998), and therefore are likely to make significant and different contributions to prediction of biological outcomes.

The most effective approach to this problem is to use some kind of sensitivity analysis (Maier & Dandy 1997) where the contribution to the accuracy of prediction by each potential predictor is evaluated in conjunction with all possible combinations of others. STATISTICA Neural Networks (Statsoft 1998) performs this using a Genetic Algorithm (Goldberg 1989) in the procedure *Genetic Algorithm Input Selection* (GAIS) (So & Karplus 1996a, 1996b, Maclin & Dempsey 1994, Dinner *et al.* 1998). This algorithm tests a large number (and in simple cases all) of the possible input combinations against prediction error in a probabilistic or generalized regression neural network. The algorithm creates a population of bit-strings each of which corresponds to a list of the potential input variables. The strings (or "masks") differ in their pattern of 1s and 0s which signify inclusion or rejection of a variable. The algorithm tests each mask in the network against the prediction error, recombining masks using artificial genetic operators. Ideally, an optimum combination of input variables is the result.

GAIS was used to select those hydrological measures which made substantial contributions to prediction of the values of a given assemblage index. First, the input suite of measures was culled to those measures correlated with the index at $P < 0.05$. An alpha of 0.05 was used in this case (despite the problem of multiple comparisons, and the potential significance of Type II errors) in order to include measures which might have little influence alone but might act interdependently with others to have a strong effect. GAIS was run 10 times with these culled suites of measures for each community index in each biological community. For most indices, the ratio of *training* to *verification* data was set at approximately 8:2, *Penalty* (i.e. an addition to the error value proportional to the number of inputs) at 0 (since the input variables had already been selected by correlation), *Population* and *Generation* at 100, *Smoothing* and *Crossover* at 0.3, and *Mutation Rate* at 1. (*Penalty* is an addition to the error value proportional to the number of inputs, *Smoothing* is a coefficient which slows the updating of the gradient in the error surface, to reduce noise in the learning process. The other terms retain their biological meanings). All measures rejected by GAIS three or more times out of 10 were discarded.

Each of the ranked biological indices (Table 73) was then correlated, at both the waterbody and river reach scales, with each of the hydrological measures (ranked) selected by GAIS (cf. Clausen & Biggs 1997). The alpha significance levels of the correlations were adjusted to 0.01 to allow for multiple comparisons, and correlations were tested for adequate power using Gpower (Erdfelder *et al.* 1996). Power $(1-\beta) = 0.8$ is generally considered the acceptable minimum (Cohen 1988), but values exceeding 0.6 (for $\alpha = 0.01$) were accepted in this situation because a Type II error (in this case overlooking a significant correlation) arguably was less important than the need to minimize redundancy and simplify the environmental data set.

Because the measures selected by the above process for each assemblage index were specific for a given event in flow history, it was necessary to generalize these results so that they would apply to a broader temporal range. This meant converting the results for *measures* into results for *facets*. Facets were derived by first separating measures relating to flow pulses in progress from those relating to pulses in the past. Measures within these two temporal groups that related to the same characteristics of the flow pulse were then merged

to form two sets of facets - *present* and *past*. Hence, because some measures (particularly those related to the indices for the fish assemblages) were already advanced by 4-6 months, the set of *present* facets might sometimes relate to events which had actually occurred up to 6 months before the time of the corresponding biological sample.

The signs of the correlations between the ranked assemblage indices and the ranked hydrological measures were summarized for each facet and used to predict directions of change likely to arise from change in hydrological measures at the river reach and flow history scales.

5.2.2 Predicting assemblage indices from multiple flow history measures at the river reach scale using Neural Networks.

Neural Networks (Statsoft 1998) were used to predict magnitude and direction of change in biological community indices from change in one, a subset or all of the hydrological measures at the river reach (flow regime) scale. Neural networks are a modelling technique arising from artificial intelligence research and based in part on the structure of nerve networks in the brain (Patterson 1996). An artificial "neuron" receives a number of inputs (either from the original data or from the output of other neurons). Each input comes with a signal strength (or "weight"), which may be positive or negative. The neuron adds up the weighted sum of its inputs. From this weighted sum is subtracted a set value, the "threshold", and the difference is the "activation signal". If the activation signal is greater than zero, it is passed through a "transfer function" which transforms the output of the neuron before it is transmitted to other neurons in the sequence.

The neurons are arranged in layers (Fig. 69). Signals flow from an input layer (consisting of a number of "units" corresponding to the number of predictor variables) through one or more "hidden" layers to the output layer (the predicted variable). The input layers introduce the values of the input variables (in the present case the hydrological measures). The hidden and output layers are each connected to all of the units in the preceding layer, and each layer is progressively executed once the predictor variable values are placed in the input units.

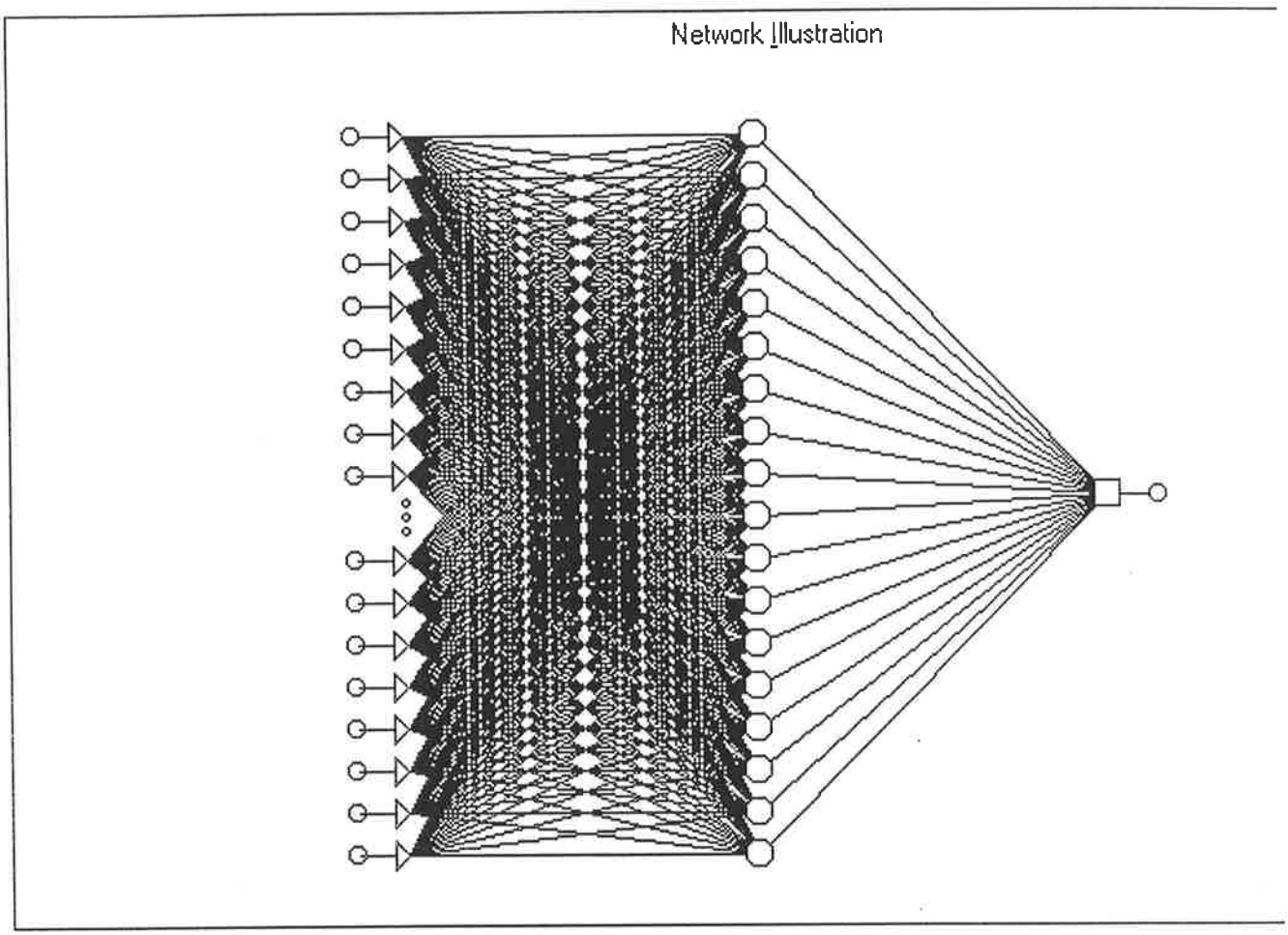


Figure 69. Structure of a Multilayer Perceptron (MLP) neural network.

Neural networks learn the input/output relationship by training. Training data consist of values of input (predictor) variables (in the present case hydrological measures) and corresponding output variables (in the present case indices of biological community structure, health or behaviour). The neural network is trained on the training data using a learning algorithm, which adjusts the network's weights and thresholds to minimize the error in its predictions. If the network has been properly trained, it has learned the (unknown) functions relating the input variables to the output variable(s), and can then be used to make predictions where the output is not known.

An advantage of neural networks (NN) over other modelling approaches (such as multiple linear regression) is that the NN model does not assume a particular distribution of

the input data or linear relationships between environmental predictors and biological responses (Maier & Dandy 1997). Neither of these assumptions can be met in the data used for this model, although hydrological inputs were log-transformed. For such data it has been demonstrated that NN modelling may have greater predictive power than multiple linear regression (Lek *et al.* 1996, Baran *et al.* 1996).

In neural network methodology there are many choices of network types, number of hidden layers and units (Bishop 1995). STATISTICA Neural Networks (Statsoft 1998) has an Automatic Network Designer which explores all of these options and optimizes the choice of network architecture. In this project, since there were many networks to train (one for each of the community indices for each of the biological communities) it was impracticable to trial all options manually, and the Automatic Network Designer was used for this purpose.

As inputs to the network training process, the hydrological measures selected by GAIS (above) were used. Because some biological responses to flow pulses (such as fish spawning) might be delayed by up to 6 months, and others (such as zooplankton blooming) were likely to be rapid, two sets of hydrological measures were trialled as inputs to network training, viz. measures with real time values and measures in which the values had been advanced by 6 months. (Measures of season were not advanced in time, since their role was to model strictly seasonal influence). From the two sets of networks trained from these data, those giving the lowest prediction errors were chosen.

Training of the networks was performed using the Automatic Network Designer in STATISTICA Neural Networks. For Network Designer training, data were allocated to training, verification and testing approximately in the ratio 7:2:1, since the databases were relatively small in proportion to the number of inputs, and in this situation it is important to maximize the number of training data. The learning algorithm used was Conjugate Gradient Descent (Shepherd 1997), the network type Multilayer Perceptron (Rumelhart & McClelland 1986), and the activation function linear. Range standardization of the input data was trialled, but made little difference to the prediction error. A *penalty* of 0.001 and number of *iterations* of 1000-5000 usually gave adequate results. The training outcomes were relatively insensitive to the settings of *window* and *epochs*.

Ten to twenty training runs were performed for each community index in each biological dataset, and the best network from these runs chosen. The effectiveness of network training was assessed by four measures

1. ***RMS*** errors of the training and the test data. During training, the algorithm (Conjugate Gradient Descent for the Multilayer Perceptron – the network type which worked best for the DRY/WET data) is guided by the RMSE error between actual and predicted output.
2. The ratios of ***Predicted Output Standard Deviation/Actual Output Standard Deviation*** for the training and test data, which are independent of the absolute error size, and so provide a useful comparison of results of repeated training runs.
3. The r^2 ***value (proportion of variance explained)*** for prediction of all values of the output data (training data + test data).
4. ***% bias = % difference between mean overall predicted output and mean overall actual output.***

Greater emphasis was placed on good performance on measures 3-4, because the primary application of the networks was to be the modelling of outcomes of flow regime change (Puckridge *et al.* 1999). This meant predicting overall (percentage) change in output from overall (percentage) change in the values of input (hydrological) variables. The networks could also be used to predict change in output from change in only a subset of input cases (derived for example by sampling at a new site), but this was not the primary intention.

5.2.3 Relating assemblage indices to waterbody permanence by regression at the flow regime scale.

The mean value of each assemblage index per waterbody was ranked and regressed (single linear regression) against ranked frequency of drying (i.e. permanence) per waterbody using sites (one site per waterbody) as replicates. Ranking was used to equalize variances. Regressions were tested for adequate power, with the minimum 1-β set at 0.6 (α = 0.05) for the same reason as given above for correlation of assemblage indices. Alpha =

0.05 was used here because the number of comparisons (regressions) per assemblage was small (for five assemblages 6 –7, for two 12,13). Significant regressions were used to predict direction and magnitude of biological change from changes in waterbody relative permanence.

5.2.4 Recruitment of single fish species in relation to waterbody depth - trends in raw data at the flow history scale.

(see also Puckridge *et al.* in press)

The lower Cooper fish fauna includes 12 native and two introduced species. For the present analysis, four species with generation times <1 year were selected to demonstrate the effects of serial floods. These were the native Australian smelt, *Retropinna semoni* (Retropinnidae), the crimson-spotted rainbowfish, *Melanotaenia splendida tatei* (Melanotaeniidae), the western carp-gudgeon, *Hypseleotris klunzingeri* (Gobiidae), and the introduced gambusia ('mosquitofish'), *Gambusia holbrooki* (Poeciliidae). The exotic goldfish, *Carassius auratus* (Cyprinidae), occurred in some samples, but in numbers too small for analysis. Comparative data for bony herring, *Nematalosa erebi* (Clupeidae), were added because this species may spawn in its first year of life (e.g. in the Murray-Darling Basin: Puckridge & Walker 1990).

Fish < 20mm TL were regarded as larvae (Gehrke *et al.* 1999), or juveniles and adults in the case of gambusia. The 2m seine and trawl catches were dominated by larval and small juvenile fish, but only adults of the early-maturing species (or juvenile bony herring) were captured in the 20m seine (13 mm mesh). The gillnets captured only bony herring, among the species considered here.

Trends in abundance of these species are of interest because they are likely to reflect recruitment over the flow pulse series 1987-1991. Because the cycles of abundance of each species differed in magnitude and timing between sites, measures of central tendency per date for all sites, or time series analysis to identify trends across sites, were likely to be misleading. Rank correlations of abundance and depth per species per site do not represent trends accurately as they are sensitive to variation in the timing of cycles. Accordingly, raw data are presented, by species and waterbody. As peak larval abundance and flow pulse

peaks do not coincide, to better illustrate their concordance the data for species were lagged so that peak abundances matched peak water depth.

5.3 Results

5.3.1 Fish health

Outbreaks of ulcerative fungal disease occurred frequently and were sometimes widespread over the study period. Ten species (*Nematalosa erebi, Retropinna semoni, Hypseleotris klunzingeri, Macquaria sp., Bidyanus welchi, Carassius auratus, Melanotaenia splendida tatei, Leiopotherapon unicolor, Neosilurus argenteus* and *Neosilurus hyrtlii*) were affected, and juveniles as well as adults. Foci of infection were the head and fins. From the characteristic encysting of zoopores at the sporangium mouth in most isolates, it is likely the principal fungal pathogen was *Achlya* sp. (Willoughby 1978), although further work would be needed to confirm this. Histopathology on the lesions revealed a fungal dermatitis extending to myositis in specimens of bony bream, callop and rainbowfish (pers. comm. Dr. J.S. Langdon, Fish Health Reference Laboratory, Benalla). Hyphae penetrated epidermis, dermis and muscle, and were associated with haemorrhage and moderate inflammation.

5.3.2 Correlation of season and flow history measures with indices of assemblage structure. Redundant measures culled by GAIS

There was a close correspondence between measures selected by rank correlation ($P<0.01$) and measures selected by GAIS. GAIS selected all measures selected by correlation, but selected also some measures correlated at $P<0.05$. Tables 74-80 list all measures which are both rank correlated (at $P<0.01$) and selected by GAIS.

Table 74 Season and flow history measures significantly correlated with assemblage indices for littoral zooplankton

Real Time Only				*Real Time Only*			
MEASURE	ABUND	MSPRC	SMDOM	MEASURE	ABUND	MSPRC	SMDOM
MXTEM		-0.36	0.42	DPNFL		-0.41	0.32
MNTEM		-0.41	0.47	PDISC		0.35	-0.31
DLENG		-0.3	0.34	LMADS	-0.42		
MTOTL		0.35	-0.31	LMAD1	-0.26	-0.38	
LTOTL	-0.34	-0.44	0.48	LMAD2	-0.49	-0.28	0.4
LTOT1	-0.49	-0.31	0.48	LMIDS	0.44	0.42	-0.48
LRLAM	-0.42			LMID1	-0.25		0.27
LRLA1		-0.38		LMID2	0.32	0.46	-0.49
LRLA2	-0.53		0.47	DLRL1		-0.35	0.44
LFLAM	-0.34	-0.44	0.48	DLRL2	-0.46		0.32
LFLA1			0.26	DLFAL	-0.33	-0.45	0.48
LFLA2			-0.27	DLFA1		-0.24	
RLRSL	-0.38			DLFA2	0.32		-0.31
RLRS2	-0.53		0.47	LMXTM	0.27	0.35	
RLFLL	-0.32	-0.41	0.47	LMXT1	0.53	0.33	-0.47
RLFL1			0.26	LMXT2			-0.25
DLFLO			0.31	LMNTM	0.5		-0.47
DLFL1		-0.42	0.31	LMNT2	-0.51		0.46
DLFL2			0.31				

Table 75 Season and flow history measures significantly correlated with assemblage indices for macroinvertebrates in open water.

	Real Time		*6 Mths Adv.*
MEASURE	SHWDV	SMDOM	ABUND
MXTEM	-0.35	0.25	
MNTEM	-0.28		
DLENG	-0.34	0.26	
MTOTL	0.45	-0.38	
LTOTL	-0.23		
LTOT2			0.33
LRLAM		0.26	
LRLA1			-0.26
LFLAM	-0.23		
LFLA2			0.38
RLRS1	-0.25		-0.24
RLFL2			0.34
DLFL1	-0.23	0.26	
PDISC	0.45	-0.38	
LMADS	-0.23	0.29	
DPRLM	0.26		
DLRLM	-0.24	0.32	
DPFAL	-0.31	0.34	
LMXTM		-0.26	0.23

Table 76 Season and flow history measures significantly correlated with assemblage indices for larval and juvenile fish in open water.

	6 Mths Adv. Only	
MEASURE	ABUND	SPRCH
MXTEM	0.57	0.44
MNTEM	0.59	0.49
DLENG	0.58	0.37
MTOTL	0.43	0.31
PTOTL	0.53	0.31
LRLAM	0.33	0.30
LRLA1	0.22	
RLRSL	0.33	0.27
RLRS1	0.23	
DLFL1	0.25	
PDISC	0.44	0.32
LMADS	0.29	0.36
LMID1	-0.42	-0.36
DLRLM	0.27	
LMXTM	-0.28	-0.26

Table 77 Season and flow history measures significantly correlated with assemblage indices for larval and juvenile fish in the shallow littoral.

	Real Time	*6 Mths Adv.*
MEASURE	EXNAT	ABUND
DLENG		0.41
MTOTL		0.25
PTOTL	-0.34	0.32
LRLAM	-0.32	
LRLA2		-0.41
RLRSL	-0.34	
RLRS1		0.25
RLRS2		-0.40
DLFLO	-0.26	0.23
DLFL2	0.26	
DLNF1	0.28	
DLNF2	-0.28	
PDISC		0.28
LMADS	-0.34	
LMAD2		-0.40
LMID1	0.3	
LMXTM		-0.30
LMNT2	-0.23	

Table 78 Season and flow history measures significantly correlated with assemblage indices for juvenile and adult small fish in the deep littoral.

	Real Time	*6 Mths Adv.*	
MEASURE	PEVEN	ABUND	MSPRC
MXTEM	-0.44	0.30	
MNTEM	-0.35	0.36	
DLENG	-0.36	0.29	
MTOTL	0.3		
PTOTL		0.27	
LTOT1	-0.31		
LTOT2	-0.29		
LRLA1			-0.26
LFLA2	-0.31		
RLRSL		0.26	
DPFLO	0.31		
PDISC	0.31		
LMADS		0.30	
LMAD1			-0.32
LMIDS			0.35
DPRLM			0.27
DPFAL			-0.28
DLFAL	-0.32		-0.30
DLFA1			-0.26
LMXTM		-0.28	0.28

Table 79 Season and flow history measures significantly correlated with assemblage indices for juvenile and adult large fish in open water.

	Real Time	*6 Mths Adv.*			
MEASURE	PEVEN	ABUND	RIPEN	SPRCH	USIND
MXTEM		0.53	0.26	0.23	0.32
MNTEM		0.56		0.21	0.30
DLENG		0.50	0.29		0.28
MTOTL		0.35		0.23	0.34
PTOTL		0.38			0.27
LTOTL				-0.23	
LRLAM		0.27			
LFLAM				-0.23	
LFLA1				0.22	
LFLA2	-0.31				
RLRSL		0.28			
RLFLL				-0.28	-0.27
DPFLO	0.42				
DLFLO				-0.32	
DLFL1				-0.32	
DLNF1				0.31	
DLNF2				-0.31	
PDISC		0.36		0.23	0.34
LMADS		0.29			
LMID1		-0.32		-0.19	-0.34
DLRLM	0.32				
DLRL1			0.21		
LMXTM		-0.27			
LMXT2	0.28				
LMNT2	0.3				

Table 80 Season and flow history measures significantly correlated with assemblage indices for juvenile and adult large fish in the deep littoral.

	Real Time			*6 Mths Adv.*		
MEASURE	SPRCH	SMDOM	RIPEN	ABUND	DNMIG	UPMIG
MXTEM		0.29			0.38	0.46
MNTEM					0.43	0.48
DLENG					0.37	0.45
MTOTL						0.37
PTOTL	-0.37				0.32	0.48
LTOTL				-0.36		
LRLAM			0.35			0.32
LRLA1				-0.28		
LFLAM				-0.46		
RLRSL			0.33	0.38		0.35
RLFLL				-0.50		
PDISC		-0.33			0.43	0.37
LMADS			0.36			0.29
LMAD1				-0.42		
LMID1				-0.44	-0.35	-0.49
LMID2				0.38		
DLRLM			0.33			
DLRL1				-0.35		
DPFAL	-0.29	0.38				
DLFAL				-0.39		
DLFA2				0.38		
LMXTM				0.29		
LMNTM				0.46		

5.3.3 Relations between biological assemblage indices and *facets* of flow history and season at the river reach scale.

Table 81 lists the *facets* of flow history that summarize over all assemblages the *measures* tabled above. Seasonal measures are also significantly correlated with most indices, particularly with indices for the fish assemblages, but seasonality is not included here. These facets are the same as those significantly correlated with overall assemblage structures in Chapter 4.

Table 81 Relations between biological assemblage indices and facets of flow history and season at the river reach scale.

Facet Code	Facets of Flow Regime
TOTL	total volume of pulse (ML)
RLAM	amplitude of rising limb (ML)
FLAM	amplitude of falling limb (ML)
RRSL	rate of rise (ML/month)
RFLL	rate of fall (ML/month)
DFLO	duration of flow (months)
DNFL	duration of no flow (months)
MADS	maximum discharge (ML)
MIDS	minimum discharge (ML)
DRLM	duration of rising limb (months)
DFAL	duration of falling limb (months)
MXTM	advance of timing of last maximum discharge (months)
MNTM	advance of timing of last minimum discharge (months)

5.3.4 Directions of change in assemblage indices in relation to change in facets of flow history and season.

The directions of change in assemblage indices are indicated by the signs of correlations between the index and the facet of flow history in Tables 82-88.

- suggests ↑ in the index for ↓ in the facet

+ suggests ↑ in the index for ↑ in the facet

+/- suggests that the direction of response depends on the time between the hydrological event and the response.

Given the multiplicity of correlations, only notable examples are discussed in the text following each table.

Table 82 Direction of change in assemblage indices of zooplankton in the littoral in relation to change in facets of flow history and season.

FACETS (PRESENT) Real Time Only				*FACETS (PAST) Real Time Only*		
FACET	ABUND	MSPRC	SMDOM	ABUND	MSPRC	SMDOM
SEAS		-	+			
TOTL		+	-	-	-	+
RLAM				-	-	+
FLAM				-	-	-/+
RRSL				-		+
RFLL				-	-	+
DFLO					-	+
DNFL					-	+
DISC		+	-			
MADS				-	-	+
MIDS				-/+	+	-/+
DRLM				-	-	+
DFAL				-/+	-	-/+
MXTM				+	+	-
MNTM				-/+		-/+

In the short term (Table 82), zooplankton abundance (ABUND) showed little response to hydrological change, but species richness (SPRCH) was higher and dominance (SMDOM) lower with higher flow volume and discharge (LTOTL, DISC). In the longer term lower zooplankton abundance (ABUND), lower taxon richness (MSPRC) and higher taxon dominance (SMDOM) were associated with past larger flow volumes, higher amplitudes of rising and falling limbs, higher rates of falling limbs and higher maximum discharge (TOTL, RLAM, FLAM, RFLL, DFLO,MADS).

Table 83 Direction of change in assemblage indices of macroinvertebrates in open water in relation to change in facets of flow history and season.

FACETS (PRESENT)				*FACETS (PAST)*		
	Real Time		*6 Mths Adv.*	*Real Time*		*6 Mths Adv.*
FACET	SHWDV	SMDOM	ABUND	SHWDV	SMDOM	ABUND
SEAS	-	+				
TOTL	+	-		-		+
RLAM					+	-
FLAM				-		+
RRSL				-		-
RFLL						+
DFLO				-	+	
DISC	+	-				
MADS				-	+	
DRLM	+			-	+	
DFAL	-	+				
MXTM					-	

Macroinvertebrate abundance (ABUND) showed no significant association with immediately preceding hydrological events (Table 83), but in the longer term higher abundance was associated with past higher flow volume, lower falling limb amplitude and rate (TOTL, FLAM, RFLL). Lower abundance was associated with past higher rising limb amplitude and rate (RLAM, RRSL).

In the short term, macroinvertebrate diversity (SHWDV) was higher and dominance (SMDOM) lower with higher flow volume and discharge (TOTL, DISC). In the longer term lower macroinvertebrate diversity (SHWDV) was associated with past higher flow pulse volumes, falling limb amplitudes, rates of rising limbs, duration of flows, maximum discharges and duration of rising limbs (TOTL, FLAM, RRSL, DFLO, MADS, DRLM).

In the longer term, higher macroinvertebrate dominance (SMDOM) was associated with past higher rising limb amplitude, duration of flow, maximum discharge and duration of rising limb (RLAM, DFLO, MADS, DRLM).

Table 84 Direction of change in assemblage indices of larval and juvenile fish in open water in relation to change in facets of flow history and season.

FACETS (PRESENT)			*FACETS (PAST)*	
6 Mths Adv.			*6 Mths Adv.*	
FACET	ABUND	SPRCH	ABUND	SPRCH
SEAS	+	+		
TOTL	+	+		
RLAM			+	+
RRSL			+	+
DFAL			+	
DISC	+	+		
MADS			+	+
MIDS			-	-
DRLM			+	
MXTM			-	-

In the short term (Table 84), abundance and species richness (ABUND, SPRCH) of larval and juvenile fish in open water (ABUND, SPRCH) were higher with higher flow pulse volume and discharge (TOTL, DISC). In the longer term, abundance and species richness were associated with past higher amplitude and rate of the rising limb, and maximum discharge (RLAM, RRSL, MADS). These increases in abundance reflected increases in relative density, since this sampling gear is volumetric. They occurred in spite of the dilution effect of an increase in inundated area (over the sampling period) of nearly two orders of magnitude (Puckridge *et al.* 1999)

Table 85 Direction of change in assemblage indices of larval and juvenile fish in the shallow littoral in relation to change in facets of flow history and season.

FACETS (PRESENT)			FACETS (PAST)	
	Real Time	6 Mths Adv.	Real Time	6 Mths Adv.
FACET	EXNAT	ABUND	EXNAT	ABUND
SEAS		+		
TOTL		+	-	+
RLAM			-	-
RRSL			-	-/+
DFLO			-/+	+
DNFL			+/-	
DISC		+		
MADS			-	-
MIDS			+	
MXTM				-
MNTM			-	

As for larval and juvenile fish in open water, abundance (ABUND) of larval and juvenile fish in the shallow littoral (Table 85) was higher in the short term with higher flow volume and discharge (TOTL, DISC), and was associated in the longer term with past higher flow volume and duration of flow (TOTL, DLFLO). As for the previous table, these increases in abundance reflected increases in relative density, and occurred in spite of an increase in inundated area of nearly two orders of magnitude.

In the longer term, a lower proportion of exotic juvenile fish to native fish in the littoral (EXNAT) was associated with past higher flow volume, greater amplitude of the rising limb of the flow pulse, greater rate of rise of the rising limb, higher maximum discharge and later timing of the flow pulse minimum (TOTL, RLAM, RRSL, MADS, MNTM).

Table 86 Direction of change in assemblage indices of juvenile and adult small fish in the deep littoral in relation to change in facets of flow history and season.

FACETS (PRESENT)				*FACETS (PAST)*		
	Real Time	*6 Mths Adv.*		*Real Time*	*6 Mths Adv.*	
FACET	PEVEN	ABUND	MSPRC	PEVEN	ABUND	MSPRC
SEAS	-	+				
TOTL	+	+		-		
RLAM						-
FLAM				-		
RRSL					+	
DFLO	+					
DISC	+					
MADS					+	-
MIDS						+
DRLM	+					
DFAL	-			-		-
MXTM					-	+

In the short term (Table 86), evenness of abundance of the juvenile/adult small fish species in the littoral (PEVEN) increased with increased flow volume, discharge, duration of flow, and duration of the rising limb (TOTL, DISC, DFLO, DRLM). In the longer term, lower evenness was associated with past higher flow volume, amplitude and duration of the falling limb (TOTL, FLAM, DFAL).

In the longer term, lower species richness of juvenile/adult small fish species in the littoral (MSPRC) was associated with past higher amplitude of the rising limb, maximum discharge and duration of the falling limb (RLAM, MADS, DFAL). In the short term, abundance of juvenile/adult small fish species (ABUND) in the littoral was higher with higher flow volume (TOTL), and in the longer term was associated with past higher rate of the rising limb and maximum discharge (RRSL, MADS).

Table 87 Direction of change in assemblage indices of juvenile and adult large fish in open water in relation to change in facets of flow history and season.

FACETS (PRESENT)							FACETS (PAST)					
	Real Time		6 Months Advance				Real Time		6 Months Advance			
FACET	PEVEN	DSIND	ABUND	RIPEN	SPRCH	USIND	PEVEN	DSIND	ABUND	RIPEN	SPRCH	USIND
SEAS			+	+	+	+						
TOTL			+		+	+					-	
RLAM									+			
FLAM							-				+/-	
RRSL									+		-	-
DFLO	+										-	
DNFL								+/-			+/-	
DISC			+		+	+						
MADS									+			
MIDS									-		-	-
DRLM							+			+		
MXTM							+		-			
MNTM							+	-				

In the short term (Table 87), abundance, species richness and upstream migration intensity of juvenile and adult large fish in open water (ABUND, SPRCH, USIND) were higher with higher flow volume and discharge (TOTL, DISC). In the longer term, higher abundance was associated with past higher amplitude and rate of the rising limb and maximum discharge (RLAM, RRSL, MADS). These responses in abundance may be related to the enhanced recruitment noted in tables 84 and 85 above.

Also in the longer term, lower species richness of juvenile and adult large fish was associated with past higher flow volume, rate of rising limb, duration of flow and minimum discharge (TOTL, RRSL, DFLO, MIDS), and lower upstream migration was associated with past higher rate of rising limb and higher minimum discharge (RRSL, MIDS).

Higher spawning intensity of juvenile and adult large fish (RIPEN) was associated in the longer term with past longer duration of the rising limb (DRLM).

Table 88 Direction of change in assemblage indices of juvenile and adult large fish in the deep littoral in relation to change in facets of flow history and season.

FACETS (PRESENT)							*FACETS (PAST)*					
	Real Time			*6 Months Advanced*			*Real Time*			*6 Months Advanced*		
FACET	SPRCH	SMDOM	RIPEN	ABUND	DNMIG	UPMIG	SPRCH	SMDOM	RIPEN	ABUND	DNMIG	UPMIG
SEAS		+			+	+						
TOTL	-				+	+				-		
RLAM									+	-		+
FLAM										-		
RRSL									+	+		+
RFLL										-		
DISC		-			+	+						
MADS									+	-		+
MIDS										+/-	-	-
DRLM									+	-		
DFAL	-	+								-/+		
MXTM										+		
MNTM										+		

In the short term (Table 88), upstream and downstream migration (DNMIG, UPMIG) of juvenile and adult large fish in the deep littoral increased with higher flow volume and discharge (TOTL, DISC). Species richness (SPRCH) decreased with increasing flow volume and duration of the falling limb (TOTL, DFAL). In the longer term, greater upstream migration was associated with higher amplitude and rate of the rising limb, and higher maximum discharge (RLAM, RRSL, MADS).

In the longer term, higher spawning intensity (RIPEN) was associated with higher past amplitude, duration and rate of the rising limb and higher maximum discharge (RLAM, RRSL, DRLM, MADS).

Also in the longer term, lower abundance (ABUND) was associated with higher flow volume, amplitude of the rising and falling limbs, rate of the falling limb, maximum discharge and duration of the rising limb (TOTL, RLAM, FLAM, RFLL, MADS, DRLM).

5.3.5 Results of training neural networks to predict biological change from GAIS -selected flow history and season measures (Tables 89-90).

Table 89 Variance explained in prediction of biological assemblage indices by neural networks trained using real time hydrological and seasonal measures.

Networks trained using real time hydrological measures			
Biological Assemblage	**Assemblage Index**	**Bias = % (mean actual output - mean predicted output)**	**Variance explained (r^2)**
Zooplankton in the littoral	ABUND MSRPC SMDOM	-0.31 0.084 0.059	0.38 0.53 0.79
Macroinvertebrates in open water	SHWDV SMDOM	0.2 1.1	0.49 0.51
Larval and juvenile fish in the shallow littoral	EXNAT	-0.37	0.42
Juvenile and adult small fish in the deep littoral	PEVEN	-1.17	0.52
Juvenile and adult large fish in open water	PEVEN	1.13	0.36
Juvenile and adult large fish in the deep littoral	SMDOM RIPEN SPRCH	0.55 -1.5 0.15	0.48 0.39 0.35

Table 90 Variance explained in prediction of biological assemblage indices by networks trained using hydrological measures 6 months advanced, and real time seasonal measures.

Networks trained using hydrological measures 6mth advanced			
Biological Assemblage	**Assemblage Index**	**Bias = % (mean actual output - mean predicted output)**	**Variance explained (r^2)**
Macroinvertebrates in open water	ABUND	2.2	0.53
Larval and juvenile fish in open water	ABUND SPRCH	0.15 0.25	0.71 0.51
Larval and juvenile fish in the shallow littoral	ABUND	-1.2	0.43
Juvenile and adult small fish in the deep littoral	ABUND MSPRC	-0.45 -0.04	0.53 0.47
Juvenile and adult large fish in open water	SPRCH ABUND RIPEN USIND	-2.1 -0.13 1.9 -2.1	0.36 0.47 0.51 0.33
Juvenile and adult large fish in the deep littoral	ABUND DNMIG UPMIG	1.0 0.6 0.94	0.4 0.47 0.68

Some assemblage indices could not be predicted with more than 0.3 proportion of variance explained, and so are not listed in Tables 89 and 90. Zooplankton assemblage indices were all best predicted using real time hydrological measures (Table 89). Indices for larval and juvenile fish in open water were all best modelled using hydrological measures six months advanced (Table 90). For all other assemblages, some indices were best modelled using real time hydrological measures, some with measures six months advanced. ABUND for macroinvertebrates and all fish assemblages, and the fish migration indices (USIND, DNMIG, UPMIG) were best modelled using measures six months advanced. The indices PEVEN and SMDOM were best modelled using measures in real time.

Taking real time and six month advanced models together, all assemblage indices (except one - DSIND for juvenile and adult large fish in open water) which had been significantly correlated with one or more individual hydrological measures, were also successfully modelled by Neural Networks using the suites of hydrological measures selected by GAIS. The three indices for which the Neural Networks models explained the greatest proportion of variance were SMDOM for littoral zooplankton, ABUND for larval and juvenile fish in open water, and UPMIG for large fish in the deep littoral.

5.3.6 Regressions of assemblage indices on ranked permanence of waterbody (flow regime scale).

5.3.6.1 Abundance

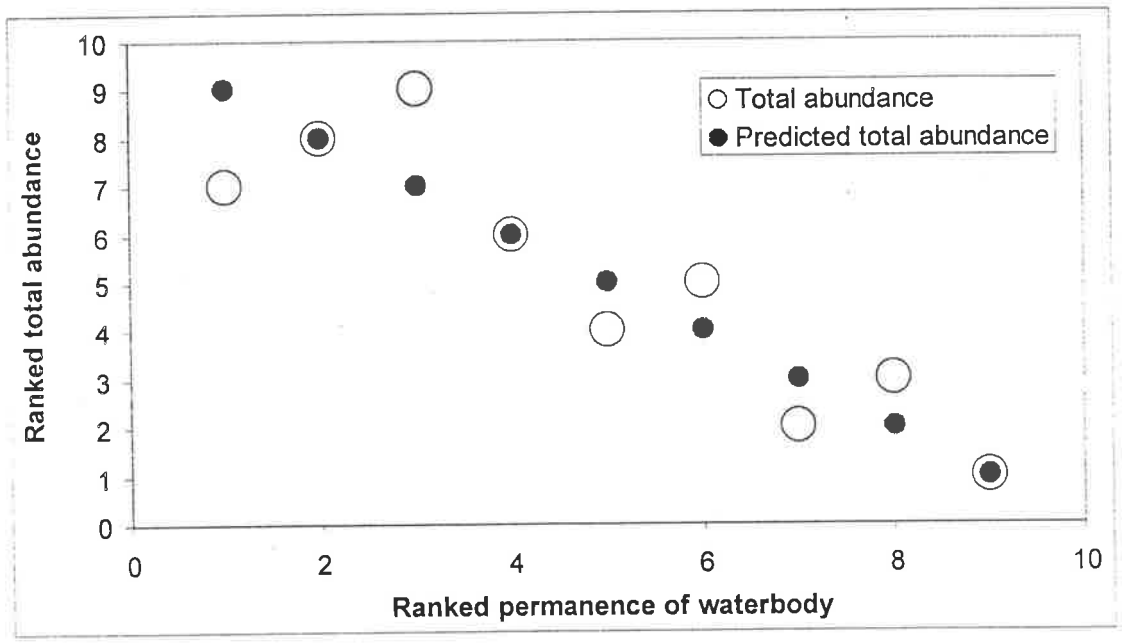


Figure 70 Quantitative relation between abundance of macroinvertebrates in open water and ranked permanence of waterbody ($r^2 = 0.78$, P=0.0009)

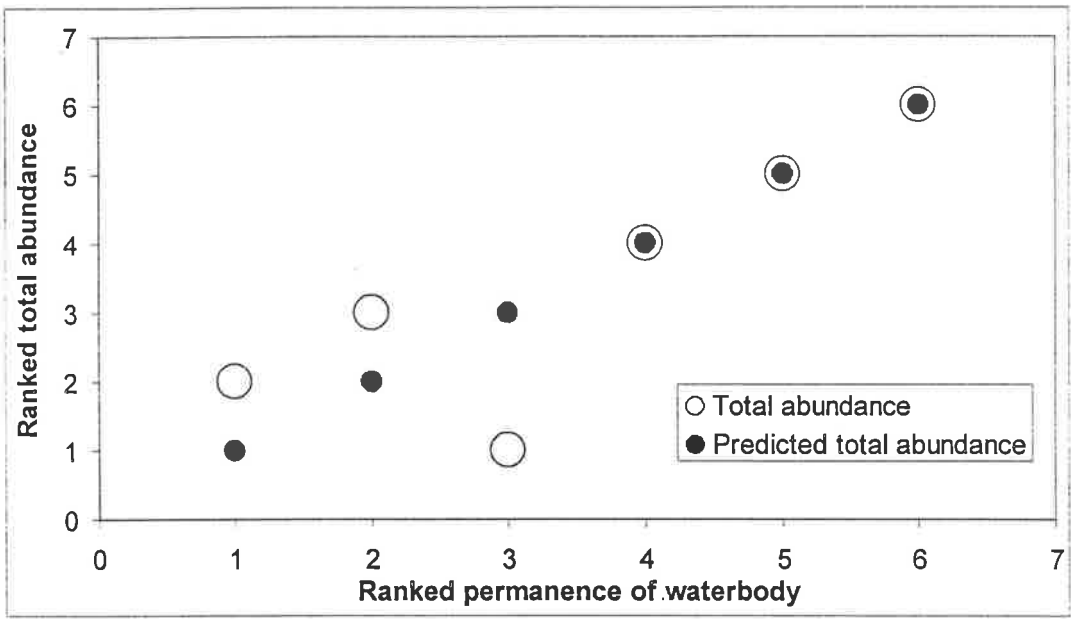


Figure 71. Quantitative relation between abundance of juvenile and adult small fish in the deep littoral and ranked permanence of waterbody ($r^2 = 0.61$, $P = 0.04$)

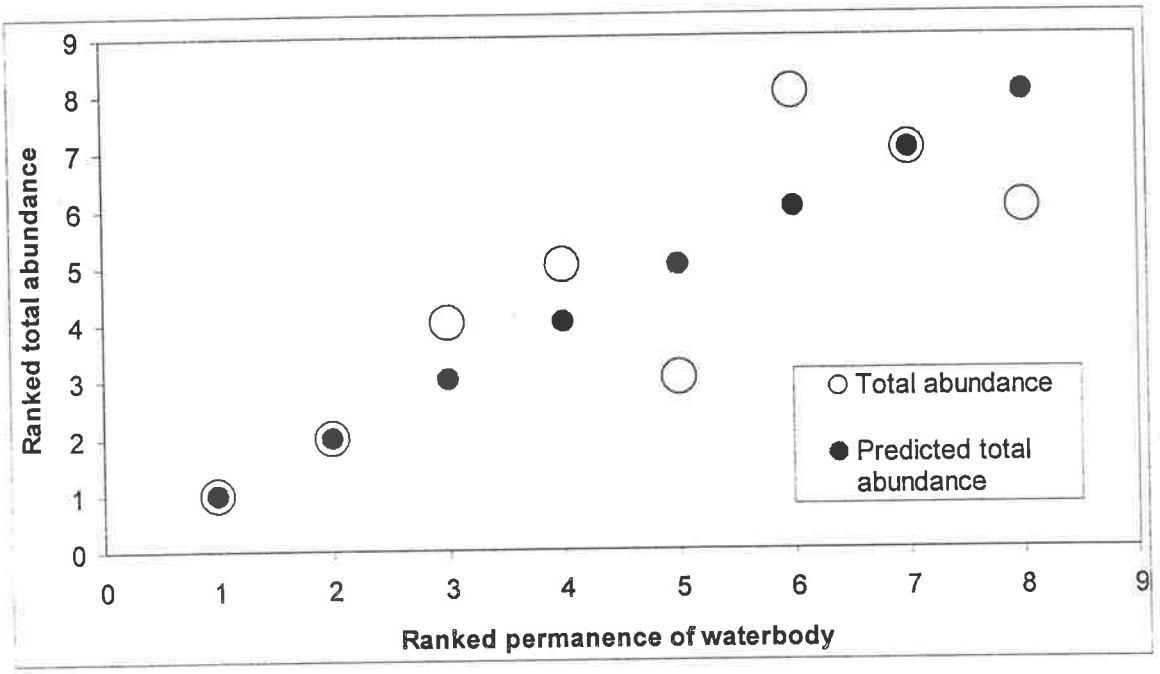


Figure 72. Quantitative relation between abundance of juvenile and adult large fish in the deep littoral and ranked permanence of waterbody ($r^2 = 0.64$, $P = 0.01$).

5.3.6.2 Species richness

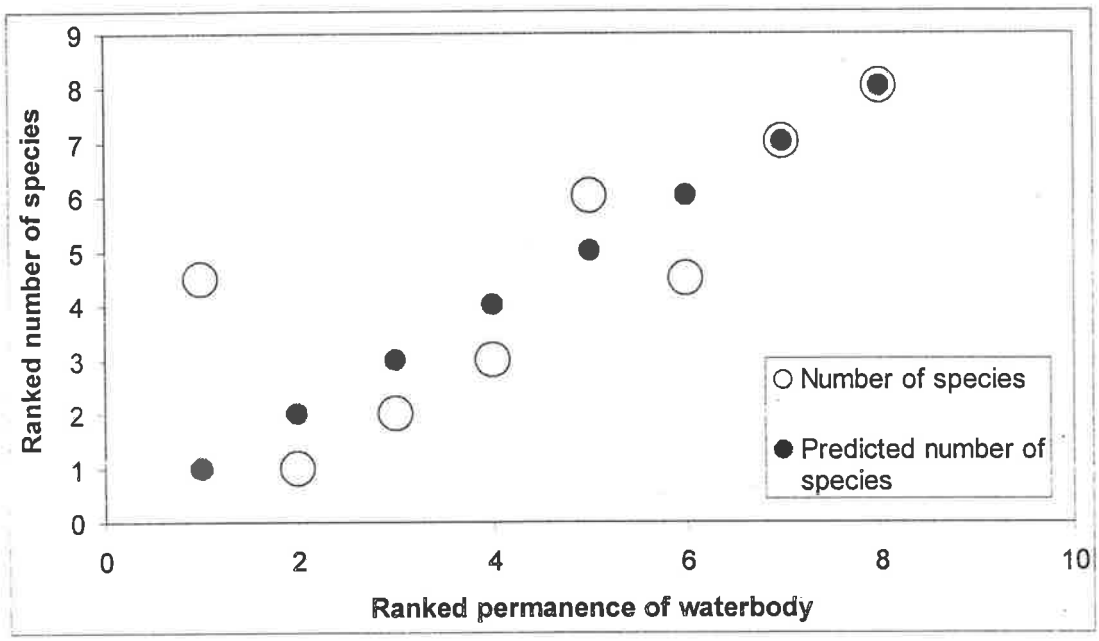


Figure 73. Quantitative relation between species richness of larval and juvenile fish in the shallow littoral and ranked permanence of waterbody ($r^2 = 0.54$, $P = 0.02$).

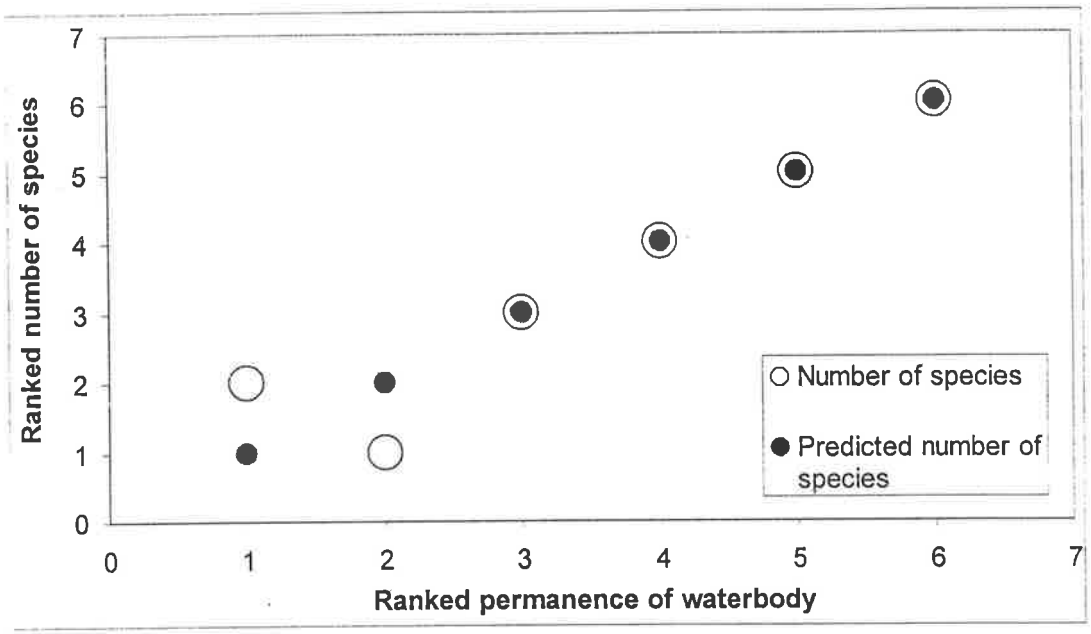


Figure 74. Quantitative relation between species richness of juvenile and adult small fish in the deep littoral, and ranked permanence of waterbody ($r^2 = 0.86$, P = 0.005).

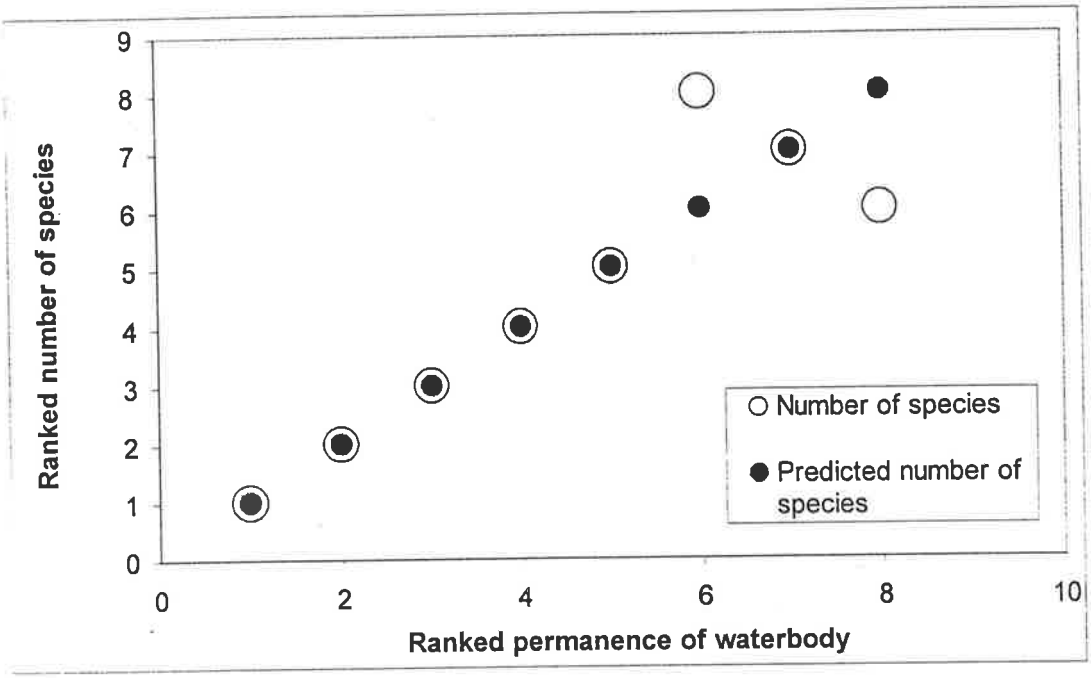


Figure 75. Quantitative relation between species richness of juvenile and adult large fish in the deep littoral, and ranked permanence of waterbody ($r^2 = 0.79$, $P = 0.002$).

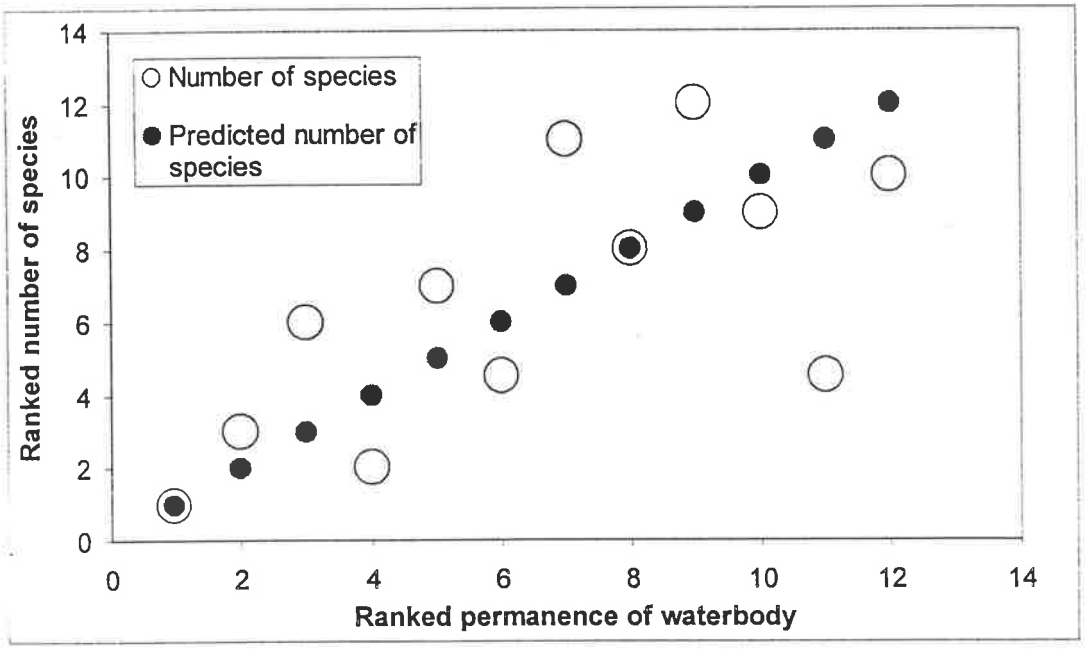


Figure 76. Quantitative relation between species richness of juvenile and adult large fish in open water, and ranked permanence of waterbody ($r^2 = 0.4$, $P = 0.016$).

5.3.6.3 Species diversity

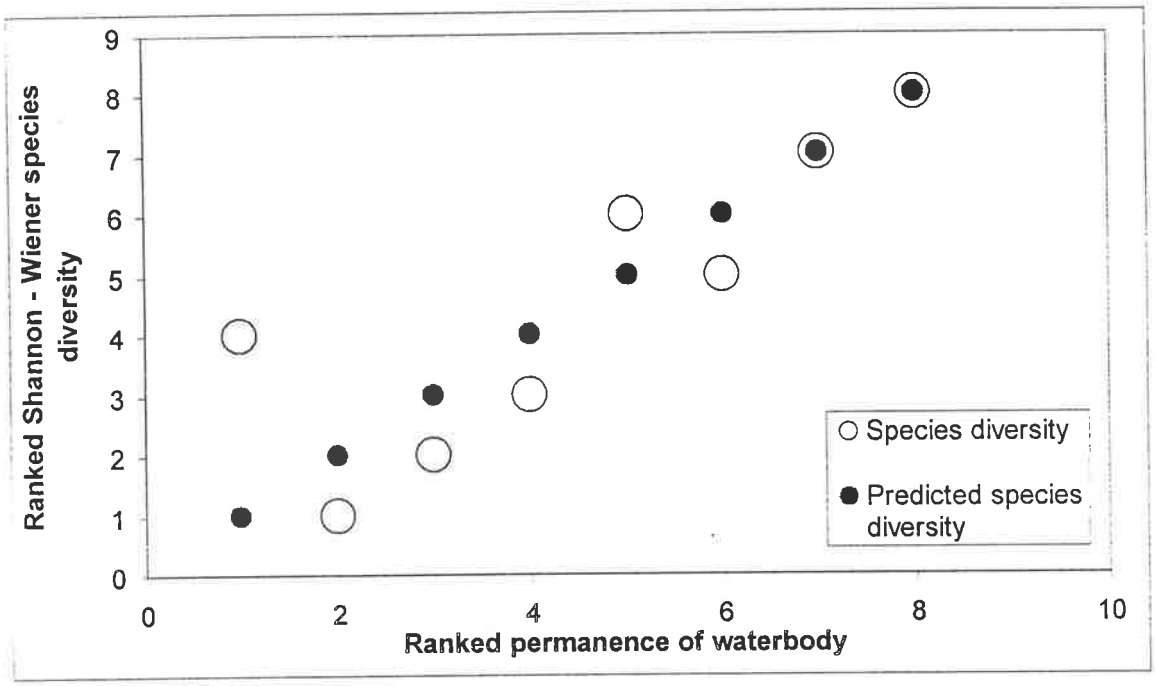


Figure 77. Quantitative relation between species diversity of larval and juvenile fish in the shallow littoral, and ranked permanence of waterbody ($r^2 = 0.64$, $P = 0.01$).

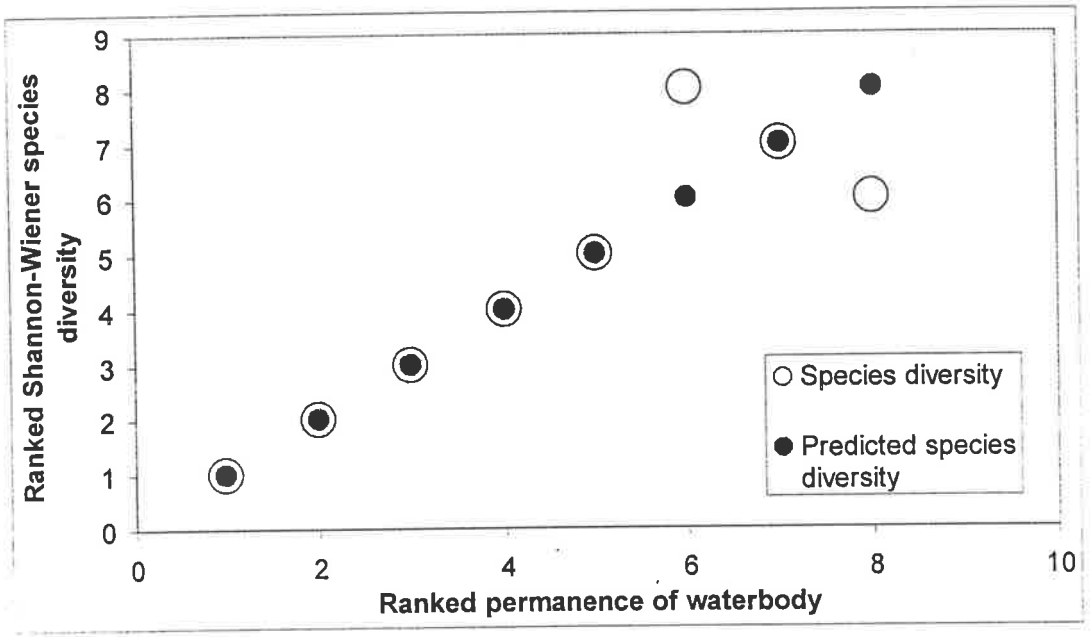


Figure 78. Quantitative relation between species diversity of juvenile and adult large fish in the deep littoral, and ranked permanence of waterbody ($r^2 = 0.79$, $P = 0.002$).

5.3.6.4 Species evenness

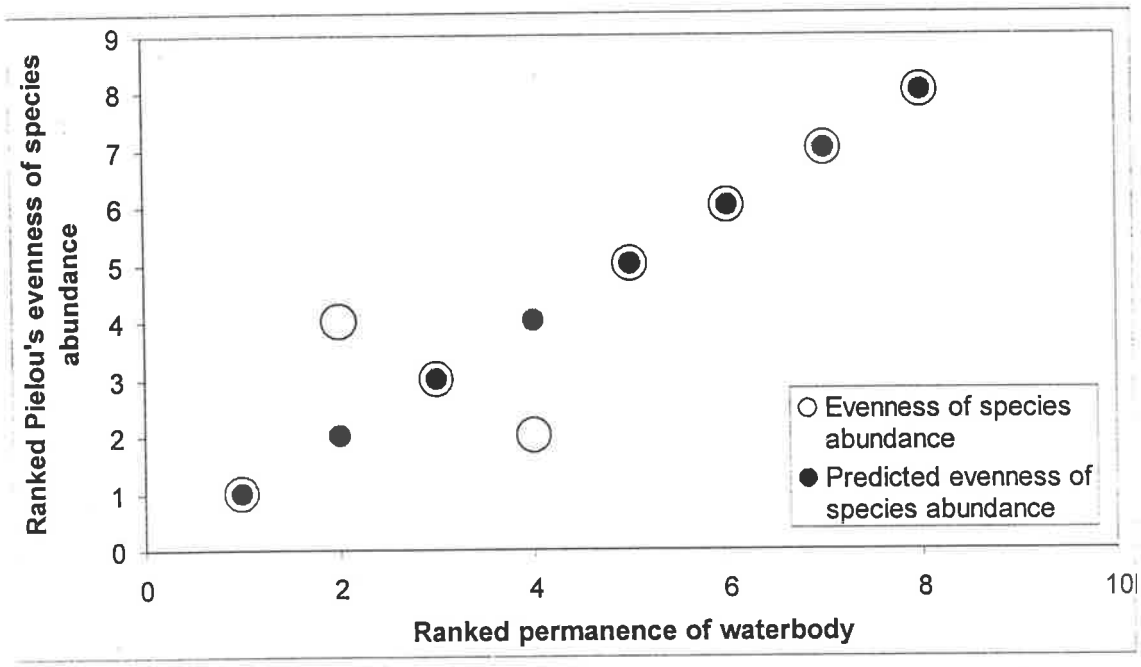


Figure 79. Quantitative relation between species evenness of larval and juvenile fish in the shallow littoral, and ranked permanence of waterbody ($r^2 = 0.79$, $P = 0.002$).

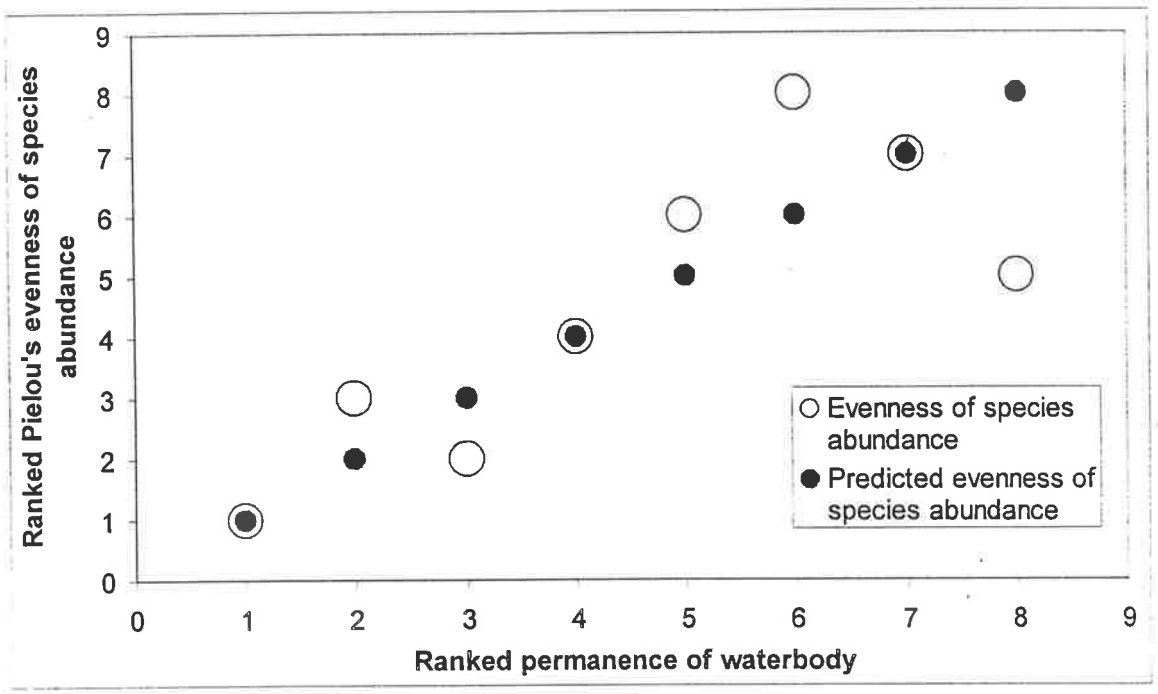


Figure 80. Quantitative relation between species evenness of juvenile and adult large fish in the deep littoral, and ranked permanence of waterbody ($r^2 = 0.60$, $P = 0.014$).

5.3.6.5 Species dominance

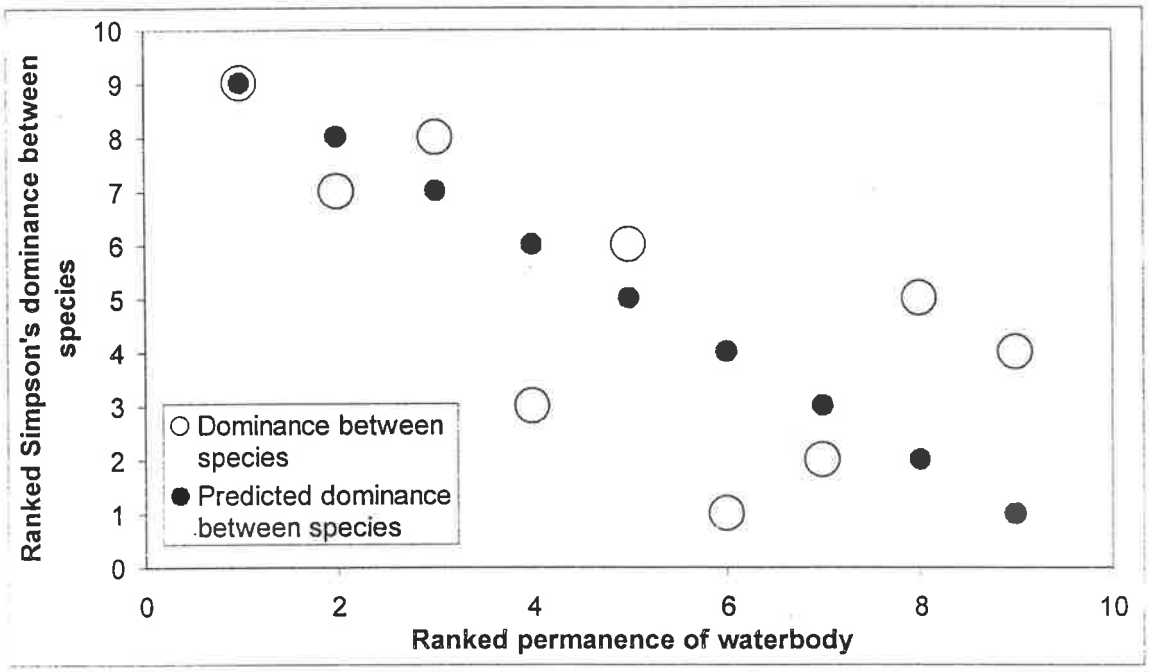


Figure 81. Quantitative relation between species dominance of larval and juvenile fish in open water, and ranked permanence of waterbody ($r^2 = 0.37$, $P = 0.049$).

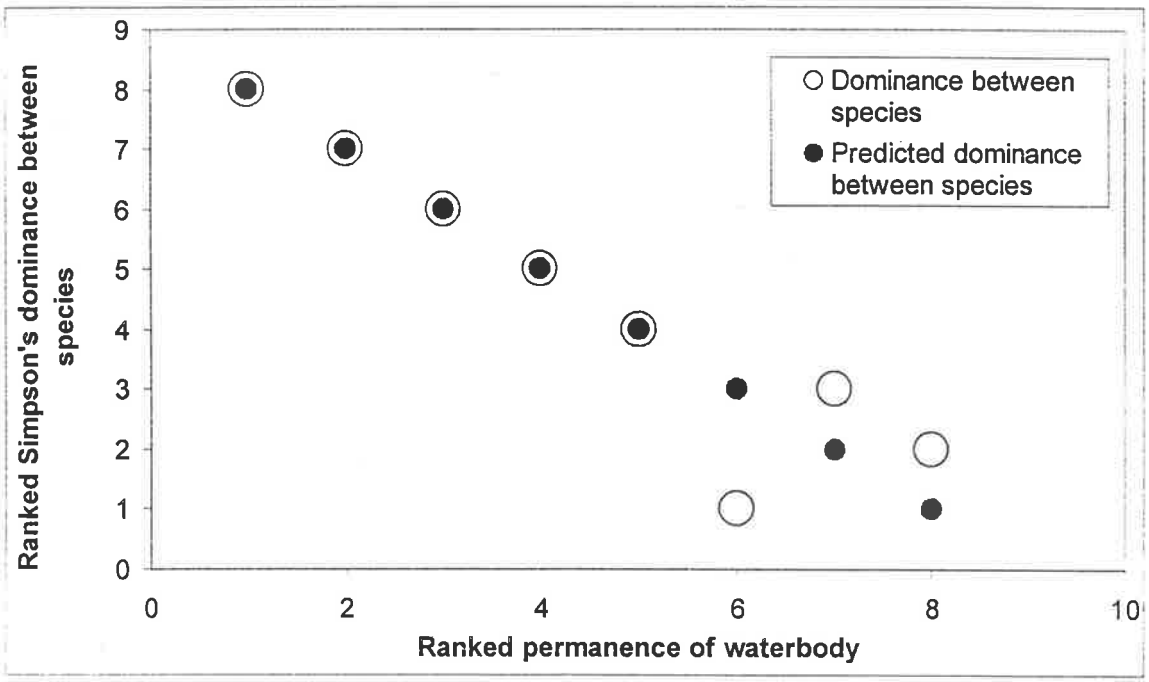


Figure 82. Quantitative relation between species dominance of juvenile and adult large fish in the deep littoral, and ranked permanence of waterbody (r^2 = 0.84, P = 0.0008).

5.3.6.6 Fish disease

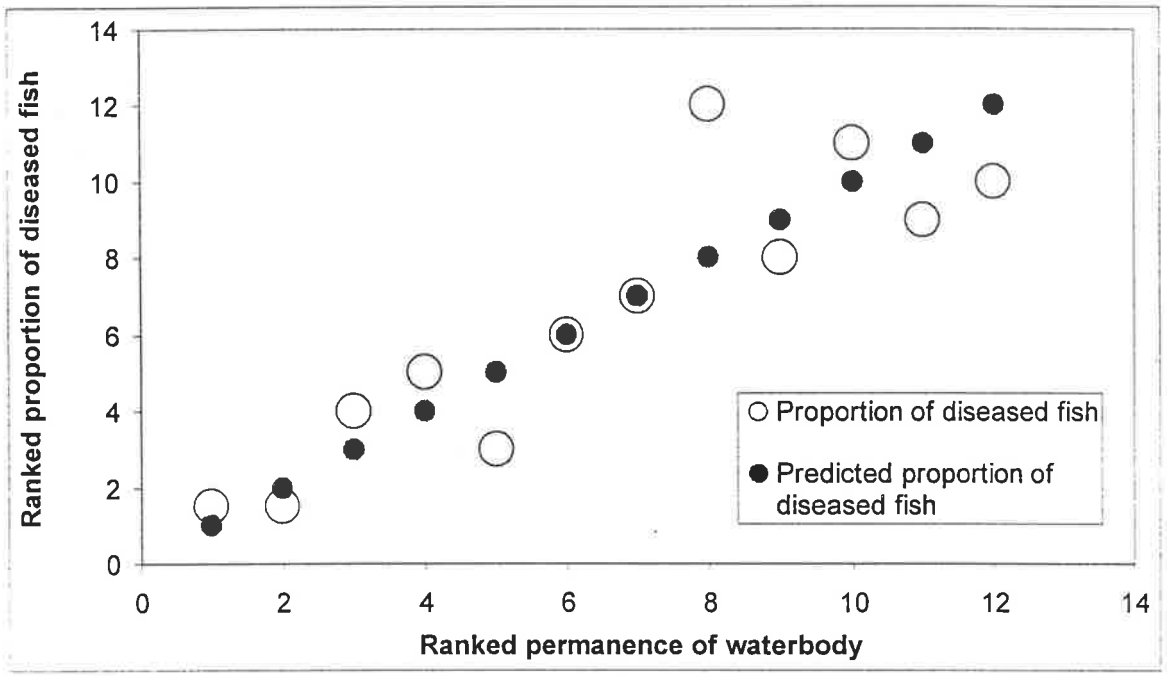


Figure 83. Quantitative relation between disease incidence of juvenile and adult large fish in open water, and ranked permanence of waterbody ($r^2 = 0.76$, P = 0.0001).

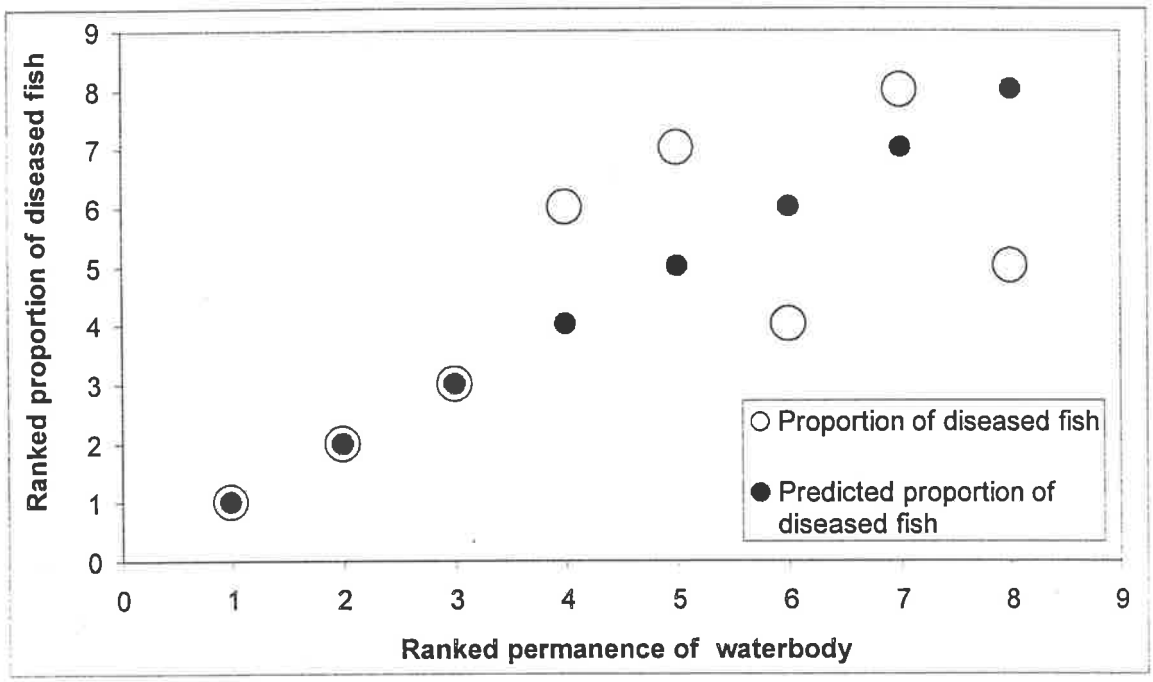


Figure 84. Quantitative relation between disease incidence of juvenile and adult large fish in the deep littoral, and ranked permanence of waterbody ($r^2 = 0.47$, P = 0.037).

Table 91 Summary of regressions of assemblage indices on waterbody relative permanence

Index	Assemblage	Sign of slope	r^2	P
Abundance	Macroinvertebrates in open water	-	0.78	0.0009
	Juvenile and adult small fish in the deep littoral	+	0.61	0.04
	Juvenile and adult large fish in the deep littoral	+	0.64	0.01
Species richness	Larval and juvenile fish in the shallow littoral	+	0.54	0.02
	Juvenile and adult small fish in the deep littoral	+	0.86	0.005
	Juvenile and adult large fish in the deep littoral	+	0.79	0.002
	Juvenile and adult large fish in open water	+	0.4	0.016
Species diversity	Larval and juvenile fish in the shallow littoral	+	0.64	0.01
	Juvenile and adult large fish in the deep littoral	+	0.79	0.002
Species evenness	Larval and juvenile fish in the shallow littoral	+	0.79	0.002
	Juvenile and adult large fish in the deep littoral	+	0.6	0.014
Species dominance	Larval and juvenile fish in open water	-	0.37	0.049
	Juvenile and adult large fish in the deep littoral	-	0.84	0.0008
Disease incidence	Juvenile and adult large fish in open water	+	0.76	0.0001
	Juvenile and adult large fish in the deep littoral	+	0.47	0.037

Each assemblage except zooplankton showed at least one significant regression. As waterbody relative permanence increased:

- Fish abundance, species richness, species diversity, species evenness and disease incidence rise, and species dominance fell.
- Macroinvertebrate abundance fell.

The highly significant increase in macroinvertebrate abundance (in open water) with decreasing permanence of inundation, contrasts with the decrease in juvenile and adult fish abundance in the deep littoral. The increasing disease incidence in juvenile and adult large fish (in open water) with increasing waterbody permanence is also highly significant.

5.3.7 Relations between individual species larval/juvenile abundance and waterbody depth at the flow history scale.

(from Puckridge *et al.* in press).

Remarkable changes occurred in fish abundance in 1987-90 (Figs 85-89), in concert with increasing water depth. Catches (2m seine) of larval and juvenile bony herring, carp-gudgeons and smelt in the littoral zones of the four main lakes increased strongly in 1987-89, and in some cases continued to increase in 1990-91 (Figs. 16-18). Data for larval rainbowfish (Fig. 88) and gambusia (Fig. 89) did not show strong trends.

Adult bony herring in open water, and adult smelt and carp-gudgeons in sub-littoral zones, showed trends similar to those for the juveniles and larvae of these species (Figs. 85-87). Juvenile bony herring numbers in the 20m seine appeared not to increase, but gillnet catches were substituted as large juveniles and adults easily evaded the seine. Adult rainbowfish (Fig. 88) increased like the other native species. Gambusia (in the 2m seine) showed no trends of the magnitude observed for the native species (Fig. 89).

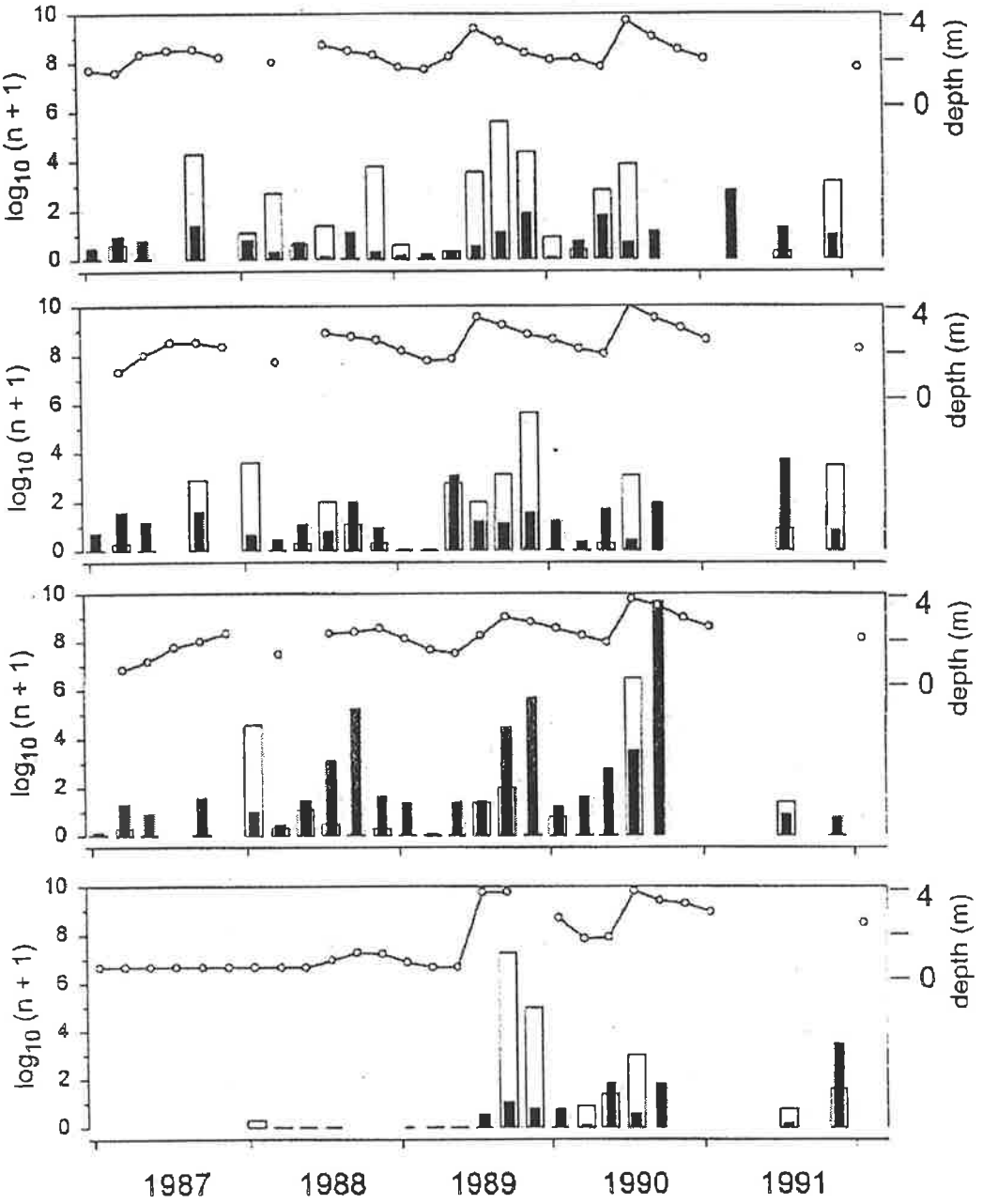


Figure 85. Concordance between water depth (right axes: m) and *Nematalosa erebi* larval/juvenile and adult abundance (left axes: sum of five randomly-selected hauls, each $\log_{10}$ CPUE) in 4 of the Coongie lakes (Coongie, Toontoowaranie, Goolangirie, Apanburra), 1987-91. Abundance lagged 6 months to fit depth peaks. White bars are larvae/juveniles, black bars are adults.

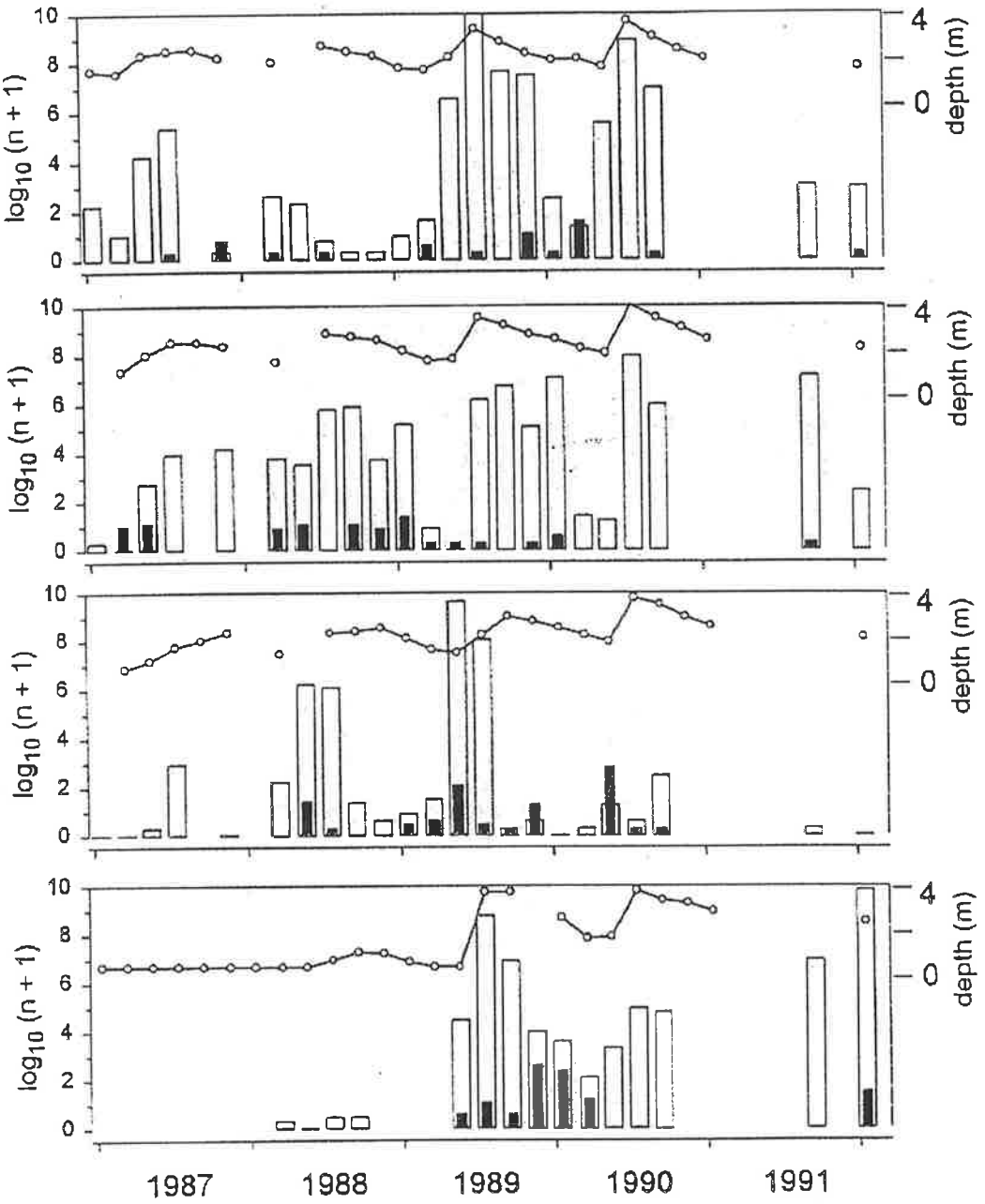


Figure 86. Concordance between water depth (right axes: m) and *Retropinna semoni* larval/juvenile and adult abundance (left axes: sum of five randomly-selected hauls, each $\log_{10}$ CPUE) in 4 of the Coongie lakes (Coongie, Toontoowaranie, Goolangirie, Apanburra), 1987-91. Abundance lagged 4 months to fit depth peaks. White bars are larvae/juveniles, black bars are adults.

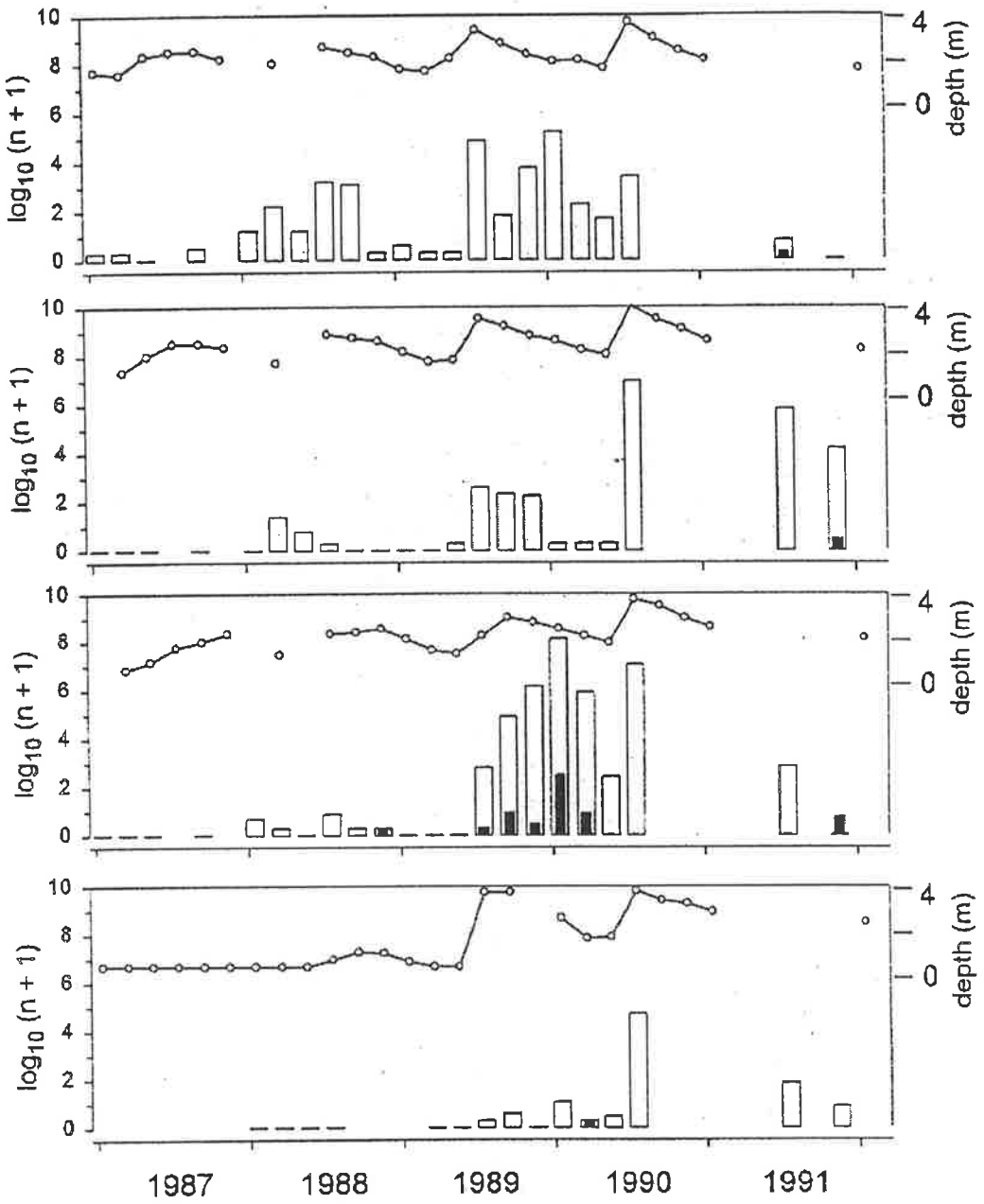


Figure 87. Concordance between water depth (right axes: m) and *Hypseleotris klunzingeri* larval/juvenile and adult abundance (left axes: sum of five randomly-selected hauls, each $\log_{10}$ CPUE) in 4 of the Coongie lakes (Coongie, Toontoowaranie, Goolangirie, Apanburra), 1987-91. Abundance lagged 6 months to fit depth peaks. White bars are larvae/juveniles, black bars are adults.

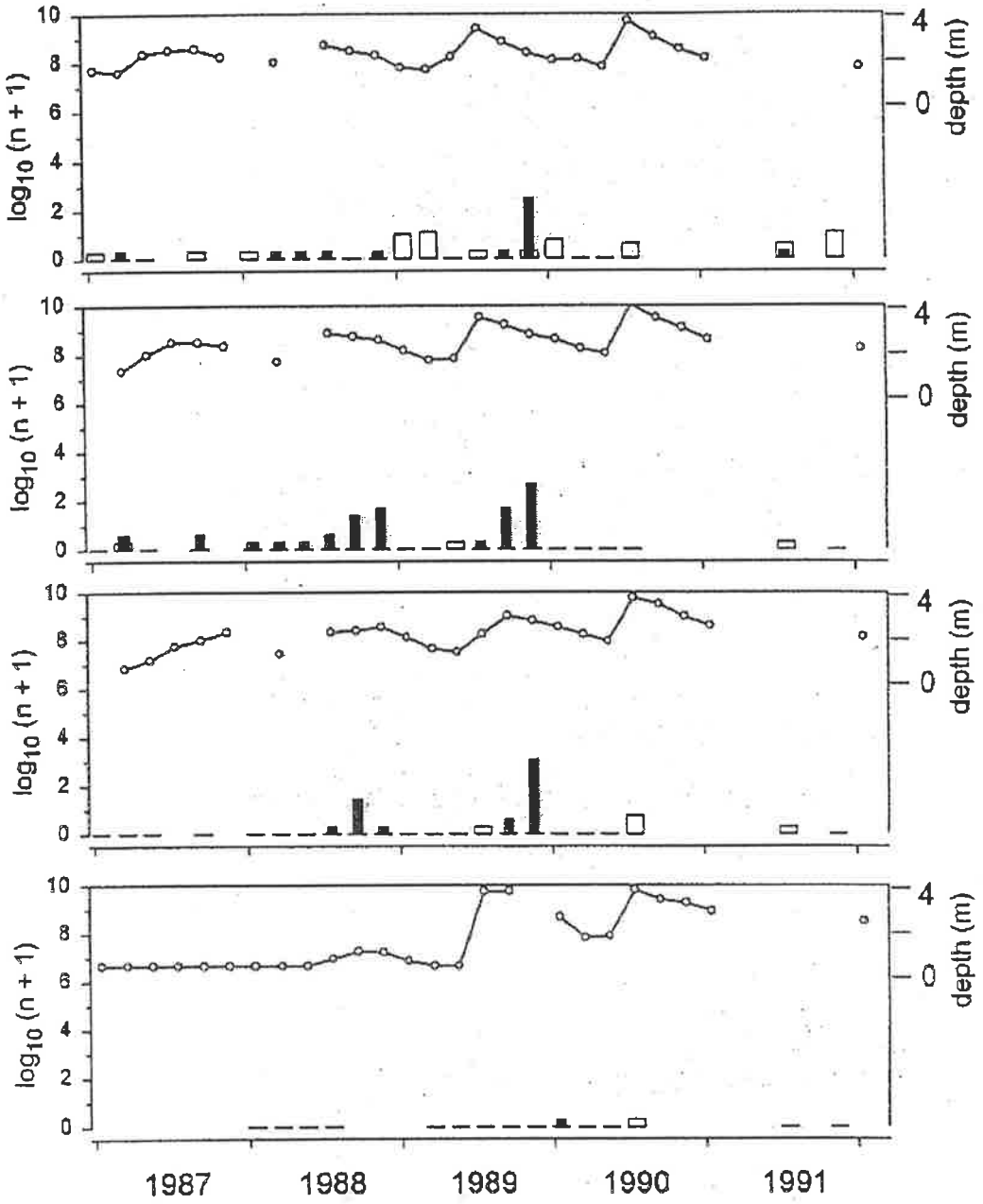


Figure 88. Concordance between water depth (right axes: m) and *Melanotaenia splendida tatei* larval/juvenile and adult abundance (left axes: sum of five randomly-selected hauls, each $\log_{10}$ CPUE) in 4 of the Coongie lakes (Coongie, Toontoowaranie, Goolangirie, Apanburra), 1987-91. Abundance lagged 6 months to fit depth peaks. White bars are larvae/juveniles, black bars are adults.

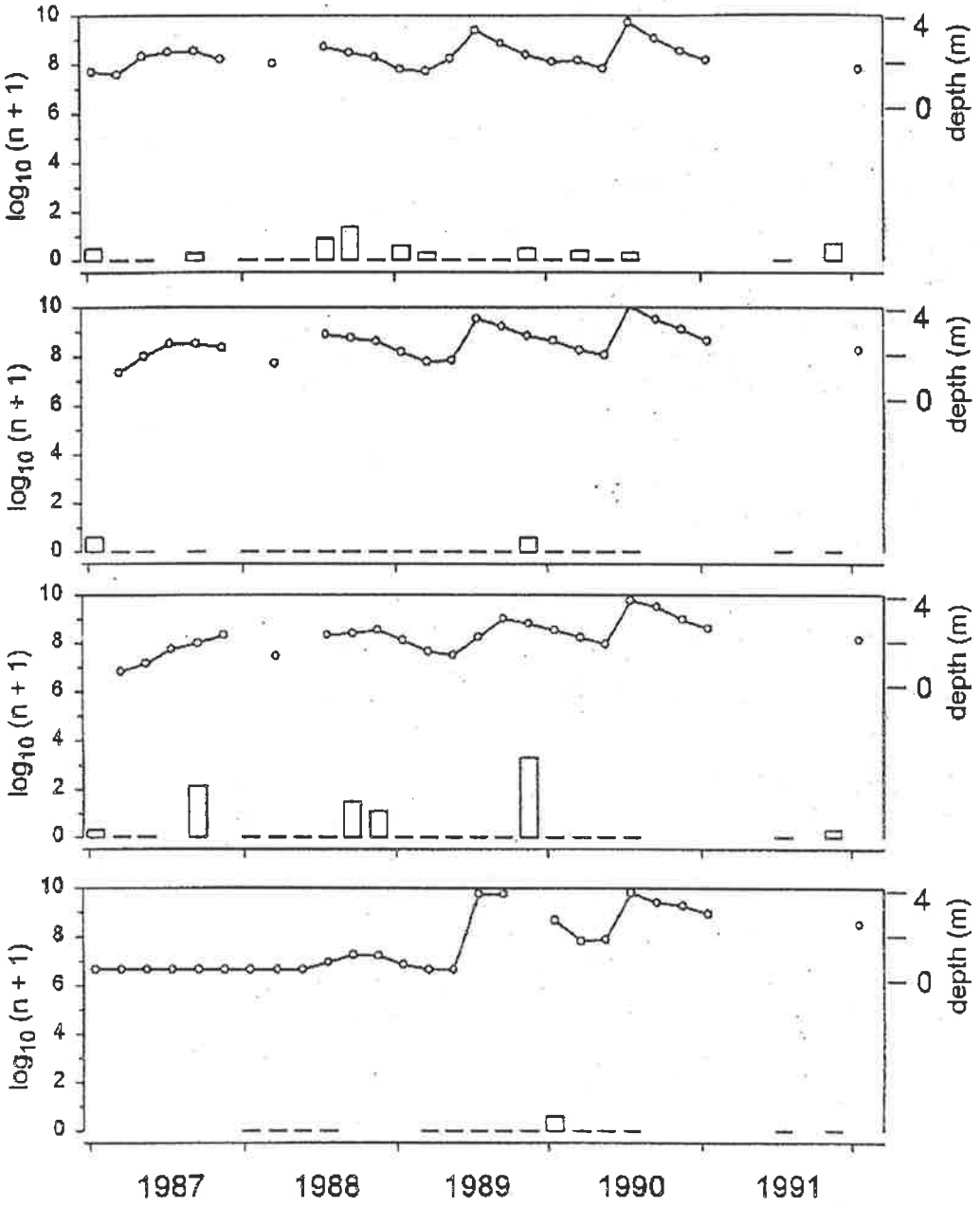


Figure 89. Concordance between water depth (right axes: m) and *Gambusia holbrooki* larval/juvenile and adult abundance (left axes: sum of five randomly-selected hauls, each $\log_{10}$ CPUE) in 4 of the Coongie lakes (Coongie, Toontoowaranie, Goolangirie, Apanburra), 1987-91. Abundance lagged 6 months to fit depth peaks. Adults and juveniles pooled in white columns.

In open water (trawl samples, not shown), the trends in the abundance of larval bony herring and carp-gudgeons were parallel to those in the littoral. Rainbowfish were rarely caught in open water, smelt increased at two sites but fell in two others, and again gambusia showed no trend. In the one channel site sampled with the same gears for the same period (data not shown), trends for larvae (littoral and open water) and adults (littoral, but bony herring in open water) matched the trends at lake sites.

5.4 Discussion

Chapter 4 demonstrated multifaceted relationships between the overall structures of seven biological assemblages and measures of flow history at the waterbody and river reach spatial scales. This chapter has extended this examination to substructures within assemblages, by relating indices of assemblage structure, health and behaviour to measures of flow history. It has shown that multifaceted relationships also exist between these indices and measures of flow history. These relationships are too various to discuss here exhaustively, and particularly the significance of each of the variety of hydrological measures correlated with each of the indices will not be dealt with. However, that the discussion is confined to some dominant themes and examples should not detract from the fact of the demonstrated complexities. Relationships shown for the fish assemblages will be considered first, because responses by the zooplankton and macroinvertebrate assemblages may be affected by these.

5.4.1 Correlations

The suite of facets of river reach flow history significantly correlated with indices of assemblage structure, health and integrity are the same as the facets found in Chapter 4 to be significantly correlated with overall assemblage structures mapped by ordination. Of course the measures input to both analyses were the same, but the fact that the same suite of facets was found to be significant at both levels of assemblage resolution encourages confidence in these results. Further, Genetic Algorithm Input Selection chose from a larger suite of measures almost exactly the measures identified by correlation. This group of measures should also be relatively free of redundancy, since GAIS is based on the additional contribution of each measure to explained variance.

The fact that measures of season were significantly correlated with most indices is expected in an environment where seasonal cycles, particularly of temperature, are very pronounced. Correlations with measures of season were particularly strong for the fish assemblages, and since this occurred in assemblages sampled by both passive and active sampling gear, it was not only a signal of temperature-dependent cycles of fish activity (Todd & Rabeni 1989, Colombini *et al.* 1995). It may also reflect the predominantly annual cycles in fish life histories (Chapter 3), in contrast to the briefer cycles for zooplankton and for some macroinvertebrates (Hamilton *et al.* 1990). However at the level of assemblage structure zooplankton and invertebrates also show annual cycles (Crome & Carpenter 1988, Bruns & Minshall 1986)

The positive correlation of abundance of larval and juvenile fish (in open water and in the shallow littoral) with total volume and discharge of the last flow pulse probably reflected increased spawning intensity and improved survival derived from the increased habitat area. The finding is supported by the concordance between larval/juvenile relative densities for individual fish species and waterbody depth, discussed below (***Per species larval abundance vs lake depth,*** see also Puckridge *et al.* in press), and the positive correlation between spawning intensity (for large fish in the deep littoral) and total volume and discharge of the last flow pulse. That increases in abundance of larval and juvenile fish resulted in improved recruitment is supported by the finding that flow pulse volume, flow duration and discharge are positively correlated with abundance of adult small fish (in the deep littoral) and adult large fish (in open water) (see also ***per species larval abundance vs lake depth*** below).

However, these increases in recruitment do not appear to be reflected in the abundance of juvenile and adult large fish in the deep littoral. This may be because sampling of large juvenile and adult large fish in the deep littoral (like the zooplankton sampling), was confined to the years 89-91, during the largest floods, so there were no contrasts with the low flow years 1986-88. Also during 89-91 dilution and dispersal effects were extreme, and this sampling was confined to channel habitats, where the dilution and dispersal effects would have been exacerbated. These factors may have contributed to the differences between results for this database and those for juvenile and adult large fish in

open water, which covered the period 86-92. Such discrepancies underline the dependency of results on the length of record used, and the importance of long-term databases for highly variable systems.

Responses in fish species richness and evenness are probably largely due to the balance between downstream and upstream movement during flooding. For example in the relation to the current pulse, assemblage evenness of juvenile and adult small fish in the deep littoral was positively correlated with total volume, maximum discharge and pulse duration. In the longer term, assemblage evenness and species richness were negatively correlated with total volume, maximum discharge and falling or rising limb amplitudes of past pulses. The latter effects may have been due to differential displacement and migration of individual small fish species during different floods and flood phases, particularly during 1989-91, when inundated area increased by nearly two orders of magnitude (Puckridge *et al.* in press). For example one small species (*Ambassis mülleri*), which is relatively common upstream in the Channel Country, first appeared in the Coongie Lakes region after the large 1989 flood. The results for juvenile and adult large fish in the deep littoral and in open water indicate that movement of large fish species was also positively associated with the immediate past flow pulse volume and discharge.

The negative correlations of the exotic/native fish ratio for larval and juvenile fish (in the shallow littoral) with the volume, amplitude and rate of rising limbs and maximum discharge of past flow pulses, indicate that the most abundant exotic (the mosquitofish *Gambusia holbrooki*) was disadvantaged by the large floods (See below under ***per species larval abundance vs lake depth***, and Puckridge *et al.* in press).

For littoral zooplankton, Margalef's species richness was positively and Simpson's dominance negatively correlated with current flow pulse volume and discharge. For nektonic macroinvertebrates, Shannon –Wiener diversity was positively, Simpson's dominance negatively correlated with volume, discharge and duration of the rising limb of the current flow pulse. These effects may have been due to a flood-induced influx of upstream zooplankters and perhaps macroinvertebrates of the Channel Country lotic assemblages into the more lentic assemblages of the Coongie system (c.f. Cellot &

Bournaud 1988, Saunders & Lewis 1988, Cronberg *et al.* 1996), but higher taxonomic resolution of the data would be required to confirm this.

These relationships were reversed in the longer term, and zooplankton abundance also showed a negative correlation in the longer term. Such effects were probably due to increased fish predation (Qin & Culver 1996, Jeppesen *et al.* 1996, Brett 1989) brought about by the strong recruitment of small fish (and the planktivorous bony herring) associated with large floods (above, and below under ***per species larval abundance vs lake depth***). Interestingly, macroinvertebrate abundance increased in the longer term, so fish predation on macroinvertebrates, if it increased, may have been selective for certain taxa, and advantaged others (Butler 1989, Closs 1996). Curiously flood dilution, which would have acted most obviously in the short rather than the long term, does not seem to have had a major influence on zooplankton density (cf Van Dijk & Van Zanten 1995, Thorp *et al.* 1994).

5.4.2 Neural Networks modelling

Results for Neural Networks modelling demonstrate that the suites of measures of flow history and season chosen by GAIS can explain a substantial proportion of the variance (average 48%) in indices of structure, health and behaviour for all assemblages. That the proportion of variance explained was not higher is probably due to the approximations inherent in assemblage indices (which cannot account fully for species level differences), to the approximations made in adjusting the Cullyamurra discharge record to waterbody level hydrology, and to approximations in adjusting for lags between hydrological events and biological responses. The three most successful models (for taxon dominance in littoral zooplankton, abundance of larval and juvenile fish in open water, and upstream migration of large fish in the deep littoral) reinforce themes discussed above viz. the sensitivity of zooplankton structure to hydrology, fish recruitment responses to pulse magnitude, and changes in fish assemblage structure through migration and displacement. The fact that, with only one exception, the same indices significantly correlated with individual measures of hydrology were also modelled (with an $r^2 > 0.3$) by Neural Networks using all measures together, suggests the results are robust.

5.4.3 Regressions

There were no significant regressions between waterbody permanence and indices of littoral zooplankton assemblage structure, and only one for the nektonic macroinvertebrate assemblage. This was not expected, since both assemblages showed a multitude of correlations with other hydrological measures, though at the flow history temporal scale. The results are more readily explicable for the zooplankton assemblage, because this database covered only the years 1989-92, when all sampled waterbodies but two had been flooded for at least a year, and perhaps had converged toward a common structure. The results are more surprising for the macroinvertebrate assemblage, however, which was sampled from 1986. The findings suggest that, with the exception of overall abundance (discussed below), these assemblages must very rapidly establish the same assemblage structures in newly inundated waterbodies as exist in the more permanent source waterbodies. Perhaps zooplankton and nektonic macroinvertebrate assemblages are washed into new waterbodies relatively intact, and certainly the more mobile macroinvertebrate taxa colonize rapidly (Larson 1997). Yet elsewhere the macroinvertebrate and zooplankton assemblages of the newly inundated phase are quite different from those in the later phase of inundation (Crome & Carpenter 1988, Bazzanti *et al.* 1996, Garcia & Niell 1993), and across a gradient of permanence, assemblage structure shows distinct patterns (Wellborn *et al.* 1996).

The fish assemblages however showed a variety of relations to waterbody permanence. The regressions demonstrated that in waterbodies with higher relative permanence, mean fish abundance, fish species richness, fish species diversity and fish species evenness were higher, and fish species dominance lower. This agrees with other work showing that higher fish density, species richness and diversity are more evident in the fish assemblages of permanent (or persistent) habitats than of temporary habitats (Kushlan 1976, Meador *et al.* 1990, Snodgrass *et al.* 1996, Bowen *et al.* 1998). The fact that Coongie Lake is the downstream limit of permanent waters on the Northwest Branch of Cooper Creek, and fish moving with floodwaters downstream of this point risk stranding and death (Ruello 1976), may have, by inhibiting migration of some species, exacerbated the above characteristics. Certainly a few colonists (*N. erebi*, *R. semoni, H. klunzingeri*,

Macquaria sp., *B. welchi*) dominated assemblages in the newly flooded waterbodies downstream, and some species (*Neosilurus sp.*, *A. mülleri*, *S. barcoo*) were captured rarely (if at all) in these waterbodies.

That mean littoral zone fish abundance also was higher in the more permanent waterbodies may have been because of the greater complexity of the littoral habitats, created by a dense and diverse riparian flora, in the permanent waterbodies. It may also have been a product of colonization lags, which were far more pronounced for fish than for zooplankton or macroinvertebrates. Initial abundance was low in the newly flooded waterbodies, but as recruitment built up, peak abundance of adults in these waterbodies equalled and in some cases exceeded abundance in the permanent sites. This is illustrated by comparing the patterns of adult fish abundance in lakes Coongie and Toontoowaranie with the patterns in lakes Goolangirie and Apanburra (Figs 85-88). This issue warrants more sophisticated analysis to isolate trends, for example by time series analysis of abundance cycles, but the less frequently flooded sites particularly have too few cycles to support such methods.

An interesting contrast to the above results is provided by the positive regression of disease incidence in large fish (in open water and the deep littoral) on waterbody permanence. This is likely to be due, in permanent waterbodies, to a combination of an abundance of substrata (leaf litter, macrophytes, dead invertebrates) for colonisation by phycomycete fungi (Golini & Sherry 1979, Khallil 1990, Khallil *et al.* 1991), and dense populations of fish under some physiological stress from adverse physicochemical conditions, particularly during low flow periods (Roberts 1988). The finding suggests that fish populations in the lower Cooper may rely on episodic access to newly flooded waterbodies to allow them to temporarily escape these conditions, recover from infections and avoid – at least temporarily – reinfection.

In contrast to the results for fish abundance, the regression of ranked macroinvertebrate abundance on ranked permanence of inundation is negative and highly significant. This result disagrees with findings from streams (Feminella 1996) but agrees with evidence for lentic waterbodies (Corti *et al.* 1997) that those more rarely flooded support the highest densities of macroinvertebrates. In conjunction with the finding above

about fish disease, this result strengthens the case for ephemeral waterbodies as crucial sites for episodic feeding and breeding by waterbirds (Crome 1986, Maher & Braithwaite 1992, Kingsford *et al.* 1998a) and some fish species (Ruello 1976, Benech & Quensiere 1983, Bruton & Jackson 1984).

5.4.4 Species larval abundance vs lake depth

Increases in native fish populations over the flood series from 1987 to 1990 accompanied an increase in inundated area of nearly two orders of magnitude. Two of the four native species were in substantial numbers in 1990 in Lake Blanche, 200 km downstream along the previously dry Strzelecki Creek (Puckridge & Drewien 1992), and evidently had colonised the entire flooded area. The absolute increases in larval abundance must then have been far greater than the relative increases recorded at Coongie Lakes sites.

Although only the western carp-gudgeon has been reported elsewhere as spawning in response to flooding (Lloyd *et al.* 1991a, Hume *et al.* 1983, Milton & Arthington 1984, Puckridge & Walker 1990), and all four native species spawned 3-6 months after the flood peaks, there is little doubt that increases in their larval abundances were related to flood magnitude. These increases may have been due to enhanced reproductive output derived from increased fecundity, spawning frequency and/or the abundance of breeding adults compounded over successive years. Corresponding increases in adult populations confirm that cumulative recruitment was occurring. Habitat expansion, nutrient influx and release (Briggs *et al.* 1985, Hirst & Ibrahim 1996), hence increased plankton (Crome & Carpenter 1988, Boulton & Lloyd 1992) and macroinvertebrate production (Maher & Carpenter 1984, Crome 1986), are likely to have occurred over the flood series. These changes would have increased adult condition and reproductive output, and also enhanced larval survival (Arumugam & Geddes 1987, Cowan *et al.* 1993, Culver & Geddes 1993) and recruitment (Quiros & Cuch 1989, De Merona & Gascuel 1993, Merron *et al.* 1993).

Elevated winter water temperatures may have magnified the above effects. The temperature changes would have directly affected only Australian smelt, a late winter-spring spawner at this latitude (Milton & Arthington, 1985). However, if zooplankton and macroinvertebrate production increased in response to elevated winter temperatures (Huryn

& Wallace 1986, Shuter & Ing 1997), the condition of maturing populations of later spawning fish would have been enhanced. Zooplankton abundance also might have increased in response to the rise in water transparency (Thorp *et al.* 1994).

In a river which, like the Cooper, contracts to waterholes, there may be a selective advantage in fish reproductive output being linked to flood magnitude. Such advantage would lie in the colonising potential of a proportionate number of offspring. In evolutionary time, fish with the highest colonising potential are most likely to find refugia and new habitats among the disconnected waterbodies that are typical of central Australian rivers during drought. An ecological corollary of hydrological persistence would be for the biota to extend this advantage by increasing their reproductive responses over a flood series.

Massive mortalities of fish occur by stranding in Lake Eyre, at the terminus of Cooper Creek (Ruello 1976), yet the fish move hundreds of kilometres downstream on floodwaters. These catastrophic mortalities perhaps are a trade-off against selection for high mobility of juveniles and a reproductive effort linked to floods and flood clusters. Both clearly are adaptive for life in an environment that is widely variable in space and time.

There is debate over the antiquity of ENSO (Quinn & Neal 1987, Fischer & Roberts 1991, Ripepe *et al.* 1991, Morner 1996), but even single ENSO-driven climatic extremes can be associated with evolutionary change (Grant & Grant 1993, 1995). If patterns of recruitment in Cooper Creek fish reflect adaptations to a persistent hydrological regime, they also indirectly reflect adaptations to ENSO.

The weak recruitment response of gambusia to the flood series suggests that native fish may be advantaged in unregulated rivers that exhibit flood persistence, although the mechanisms of this advantage are unclear. Gambusia reputedly is a flood-exploiting species (Ross & Baker 1983), but populations in Cooper Creek may be disadvantaged by the high velocities of big floods (Yu & Peters 1997) and by the lack of dense vegetation in the littoral zone during flooding (cf. Lloyd 1987). As drought clusters are a companion to flood clusters, it would be interesting to determine whether native fish sustain their apparent advantage over gambusia through a series of drought years.

5.5 Summary

This chapter adds to evidence from Chapter 4 that **Hypothesis 2.4** - *hydrological events at the scale of overbank flows are sufficient to describe biology-hydrology interactions in floodplain rivers* – should be rejected, since duration of no-flow events is a significant correlate of assemblage structure of four of the seven biological assemblages.

Hypothesis 2.5, that *when season and flow pulse are out of synchrony, fish production falls* is rejected since all major flow pulse peaks in the study period arrived 5-7 months before fish spawning peaked, yet this spawning resulted in strong recruitment for the common native species.

Hypothesis 2.6, that *fish recruitment is not related to flow pulse magnitude* is rejected, since this chapter has demonstrated a clear relationship for the common native species. The hypothesis is not rejected for the exotic species *Gambusia holbrooki*.

Hypothesis 2.7, that *health of fish assemblages is independent of hydrology* is rejected, since the index EXNAT is related to ten measures of flow history, and at the flow regime temporal scale DISEA is related to waterbody relative permanence.

Hypothesis 3.1, that *variations in indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are independent of hydrology*, is rejected.

Hypothesis 3.2, that *most of the seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages are redundant, and could be replaced fewer, summary measures* is rejected, because Genetic Algorithm Input Selection also selects the correlated measures from a larger pool.

Hypothesis 3.3, that *the seasonal and hydrological measures correlated with indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages account for a trivial amount of the variance in these indices* is rejected, since Neural Networks modelling based on these measures explains on average half (i.e. a non-trivial proportion) of the variation in the indices.

Chapter 5 adds to the evidence of Chapter 4, that **hypothesis 3.4**, *the facets of the flood pulse listed in Junk et al. (1989) are adequate to describe the influence of hydrology on indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages* should be rejected. The measure "duration of no flow" is significantly correlated with assemblage indices, but is not within the range of hydrological events considered by Junk *et al.* (1989).

Hypothesis 3.5, that *relations between flow history measures and indices of structure, health and behaviour of fish assemblages, and structures of zooplankton and macroinvertebrate assemblages have the same sign throughout flow history* is rejected. In fact the signs of these relations are often reversed at different intervals in flow history.

Hypothesis 4.1(a), that *fish spawn primarily in response to seasonal, not hydrological cues (i.e. follow a 'double or nothing' spawning strategy, sensu Lloyd et al. 1991a)* is not rejected for juvenile and adult large fish in open water, because the correlations between measures of season and indices of fish spawning, and measures of hydrology and indices of fish spawning, are too few and weak to be conclusive. But the hypothesis is rejected for juvenile and adult large fish in the deep littoral, because correlations are stronger, and all correlations are with hydrology.

Hypothesis 4.1(b), that *fish migrate primarily in response to seasonal, not hydrological cues* is rejected, because the correlations between measures of season and indices of fish migration, and measures of hydrology and indices of fish migration, are of similar magnitudes.

Hypothesis 4.2, that *indices of structure of fish, zooplankton and macroinvertebrate assemblages are not related to waterbody permanence* is not rejected for zooplankton, but is rejected for macroinvertebrates and fish. However, the indices correlated with waterbody permanence differ between assemblages, and for macroinvertebrates, only the index of abundance is significantly correlated.

Hypothesis 4.3, that *indices of fish assemblage health and behaviour are not related to waterbody permanence* is rejected, although again the indices correlated with waterbody permanence differ between assemblages.

6. An extended FPC

6.1 Introduction – summary of findings

Chapter 2 showed that hydrological variability in large rivers is not adequately summed in a single measure. Rivers have characteristic *signatures* of flow variability, and the categorical terminology of hydrological *facets* (e.g. amplitude, rate of change, timing) conceals ecologically significant complexity. Chapter 2 also demonstrated that large arid zone rivers as a group are hydrologically distinctive. Arid zone rivers have exceptionally variable flow pulse amplitudes at monthly, annual, and multi-annual scales. Their multiannual flow variability is consistent with multi-annual hydrological persistence (Puckridge *et al.* in press). It is clear that these rivers are sufficiently distinctive to warrant an elaboration of the FPC as formulated by Junk *et al.* (1989).

Chapter 3 compared the life histories of fish assemblages of the arid zone Cooper Creek and the hydrologically more predictable Magela Creek in the wet/dry tropics. The results suggested that the Cooper assemblage has a higher frequency of *r*-selected life histories. However, the assemblage does not show the degree of opportunism suggested in Chapter 1 as a hallmark of the biota of unpredictable systems. This may be a reflection of the paucity of life-history data for the Cooper Creek assemblage.

Chapter 4 showed that the low or zero flow phase of the flow pulse is biologically most distinctive. This strengthens the implication from Chapter 2 that consideration only of overbank flows (as in the FPC) overlooks crucial ecological events. This implication was strengthened further by the relations apparent between biological assemblages and the duration of zero flow and of waterbody drying. However this chapter also showed that very large flow pulses do appear to have distinctive effects on arid zone river biota, as they do on river geomorphology (Kresan 1988).

Chapter 5 examined biology-hydrology relations at two levels of resolution. At the level of individual indices of assemblage structure, health and behaviour, the findings reinforced those of Chapter 4, that fish, zooplankton and macroinvertebrate assemblage structures are related to flow history, and that isolated facets of the flood pulse are

inadequate to describe these effects. No facet is redundant, however, and all contribute predictive power to the variance in the assemblage indices.

Further, Chapter 5 demonstrated that the signs of the relations between flow history measures and indices of assemblage structure, health and behaviour may differ at different points in flow history. This finding reinforces the need, identified in Chapter 2, to conduct research at the level of particular hydrological measures and at various spatial and temporal scales and levels of biological resolution.

That the measure "duration of no flow" was found in Chapter 5 to be correlated with assemblage indices adds to evidence that hydrological events at the scale of overbank flows are not sufficient to describe biology-hydrology interactions in floodplain rivers (Chapter 4). In terms of indices of fish health and behaviour, Chapter 5 indicated that the ratio of exotic to native species, intensity of fish spawning and migration were related at least as strongly to hydrological events as to seasonal events. At the waterbody spatial scale and flow regime hydrological scale, indices of structure of fish and macroinvertebrate assemblages and disease incidence in juvenile and adult large fish were related to waterbody permanence.

At the waterbody spatial scale, the flow history temporal scale and the species level of resolution, Chapter 5 demonstrated that the recruitment of common native species but not of the exotic *Gambusia holbrooki*, was related to depth pulse magnitude. Since spawning of these species and the timing of depth pulses were out of synchrony, the fact that this spawning resulted in strong recruitment for native species conflicts with the proposal that asynchrony impairs floodplain fish production (Bayley 1991).

The multiple correlations between hydrological events and biological assemblage structure, health and behavior (Chapters 4-5), and the contrast in recruitment between native and exotic fish species (Chapter 5) suggest that the biota of hydrologically unpredictable rivers are adapted to the flood pulse (cf. Junk et al. 1989, Bayley 1991).

6.2 Limitations of this study.

6.2.1 Scale

Chapter 2 was focussed at the flow regime temporal scale and the whole river spatial scale. However, the available data were limited to 20 years and monthly flows, and most rivers were represented by only one gauging station. The findings should be tested against longer records, daily flows and (more extensively) multiple gauges per river. Chapter 2 also found that, although large rivers could be grouped climatically on a suite of measures of hydrological variability, individual rivers had distinctive patterns of flow variability (*signatures*) on measures that play an important part in their ecology, so findings from one large river should not be applied uncritically to another.

Data in Chapters 4-5 were constrained in spatial scale to the Strzelecki Desert reach of Cooper Creek, and in temporal scale to the years 1986-92 (or for waterbody relative permanence to the years 1974-1992). Implications for upstream reaches of Cooper Creek, for other arid zone rivers and for the longer term can be drawn, but with caution. Findings should be tested in several reaches of several arid zone rivers.

6.2.2 Analysis

Seasonal factors (air temperature, daylength) are correlated with features of several biological assemblages. Distinguishing the influences of hydrology and season is complicated by the overlap of their cycles, and this study has not quantified their different contributions to biological variance, although some impression of their relative importance can be gained from the values of their correlations with assemblage structures.

The analyses in this study involve mapping patterns, testing differences between groups, correlation, regression and "black box" modelling. These approaches support hypothesis testing, but reveal little about causation or the nature of processes underlying pattern. For example, biological interactions undoubtedly influence the results of this study, but there was not time to explore these interactions. However, each of the hydrology-biology relations presented above is a potential field for study of underlying processes and

causation, and the findings taken together present a strong case for review of the conceptual framework for floodplain river studies.

6.3 Testing predictions arising from this thesis

The limitations of scale – particularly of spatial scale and of taxonomic scope - in the database on which this thesis is based, suggest that the predictions of the thesis should be tested at extended scales and for other biological assemblages. A scheme for such a project is set out below, using the Diamantina and Neales rivers in the Lake Eyre Basin as locations for additional sites.

1 ASSEMBLAGES TO BE SAMPLED

- Littoral zooplankton
- Littoral and nektonic macroinvertebrates
- Littoral, benthic and pelagic fishes, all age-classes
- Aquatic vegetation
- Waterfowl

2 PARAMETERS TO BE MEASURED OR DERIVED

2.1 Littoral zooplankton

Abundance, species richness, evenness, diversity, proportions of functional groups

2.2. Littoral macroinvertebrates.

Abundance, species richness, evenness, diversity, proportions of functional groups

2.3. Nektonic macroinvertebrates.

Abundance, species richness, evenness, diversity, proportions of functional groups

2.4. Larval and juvenile fishes in the pelagic.

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species.

2.5. Larval and juvenile fishes in the littoral.

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species.

2.6. Juvenile and adult small fishes in the littoral.

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species, spawning intensity (adults), disease incidence.

2.7. Juvenile and adult large fishes in the pelagic and benthic

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species, spawning intensity (adults), disease incidence.

2.8. Juvenile and adult large fishes in the littoral.

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species, intensity and direction of movement, spawning intensity (adults), disease incidence.

2.9. Aquatic vegetation.

Distribution, abundance, species richness, evenness, diversity, ratio of exotic to native species.

2.10. Waterfowl.

Distribution, abundance, species richness, evenness, diversity, breeding intensity, feeding intensity, proportions in different categories of conservation importance

2.11. Ecosystem Processes

Production and respiration

3 HYPOTHESES TO BE TESTED AT THE FLOW HISTORY AND FLOW REGIME TEMPORAL SCALES, AND AT THE RIVER REACH AND WATERBODY SPATIAL SCALES.

3.1 QUALITATIVE HYPOTHESES – HYDROLOGICAL PREDICTORS

For the period 1986-1992 at sites on lower Cooper Creek, suites of measures of hydrology were selected by rank correlation and by Genetic Algorithm Input Selection (GAIS) as important predictors of the values of each of the above parameters for assemblages 2.1, 2.3 - 2.8

Hypothesis 1 (temporal effects - flow history scale)

The suites of predictors selected for the same sites on lower Cooper Creek for the same parameters for the same assemblages will differ between the periods 2001-2003 and 1986-1992.

Hypothesis 2. (Spatial effects – river reach scale)

2.1 The suites of predictors selected for the same parameters for the same assemblages at sites on the upper Cooper will differ from those selected for sites on the lower Cooper over the same the period (2001-2003).

2.2 The suites of predictors selected for the same parameters for the same assemblages at sites on the upper Diamantina will differ from those selected for sites on the lower Diamantina over the same the period (2001-2003).

Hypothesis 3. (Spatial effects – river scale)

The suites of predictors selected for the same parameters for the same assemblages at sites on the Diamantina, Cooper and Neales over the same period (2001-2003) will differ in each river.

Hypothesis 4. (Spatio-temporal effects – generality of DRY/WET)

The suites of predictors selected for the same parameters for sites on the upper Cooper Creek and on the upper and lower Diamantina and on the Neales for the period 1999-2001 will differ from those selected for the lower Cooper sites for the period 1986-1992.

Hypothesis 5. (Taxonomic effects)

The suites of predictors selected for the same parameters for sites on the lower Cooper Creek for the period 2001-2003 will differ from those selected for the biotic parameters of assemblages 2.2 and 2.9-2.10 at the same sites for the same period.

3.2 QUALITATIVE HYPOTHESES – DIRECTIONS OF EFFECTS

For the period 1986-1992 at sites on lower Cooper Creek, directions of effects on values of the parameters in assemblages 2.1, 2.3 - 2.8 from given percentage changes in facets of hydrology were predicted by rank correlation and by Multilayer Perceptron neural networks.

Hypothesis 1 (temporal effects – flow history scale)

The directions of effects predicted for the same sites on lower Cooper Creek for the same parameters for the same assemblages will differ between the periods 2001-2003 and 1986-1992.

Hypothesis 2. (Spatial effects – river reach scale)

2.1 The directions of effects predicted for the same parameters for the same assemblages at sites on the upper Cooper will differ from those predicted for sites on the lower Cooper over the same the period (2001-2003).

2.2 The directions of effects predicted for the same parameters for the same assemblages at sites on the upper Diamantina will differ from those predicted for sites on the lower Diamantina over the same the period (2001-2003).

Hypothesis 3. (Spatial effects – river scale)

The directions of effects predicted for the same parameters for the same assemblages at sites on the Diamantina, Cooper and Neales over the same the period (2001-2003) will differ between these rivers.

Hypothesis 4. (Spatial and temporal effects – generality of DRY/WET)

The directions of effects predicted for the same parameters for sites on the upper Cooper Creek, on the upper and lower Diamantina and on the Neales for the period 2001-2003 will differ from those predicted for the lower Cooper sites for the period 1986-1992.

Hypothesis 5. (Taxonomic generality)

The directions of effects predicted for the same parameters for sites on the lower Cooper Creek for the period 2001-2003 will differ from those predicted for the biotic parameters 2.2 and 2.9-2.10 at the same sites for the same period.

3.3 QUANTITATIVE HYPOTHESES – REGRESSIONS

For the period 1986-1992 at sites on lower Cooper Creek, significant linear regressions were found for the values of parameters in assemblages 2.1, 2.3-2.8 as a function of waterbody relative permanence.

Hypothesis 1 (temporal effects – flow regime scale)

The regression equations for the same waterbodies on lower Cooper Creek for the same parameters for the same assemblages will differ significantly between the periods 2001-2003 and 1986-1992.

Hypothesis 2. (Spatial effects – river reach scale)

2.1 The regression equations for the same parameters for the same assemblages in waterbodies on the upper Cooper will differ from those for waterbodies on the lower Cooper over the same the period (2001-2003).

2.2 The regression equations for the same parameters for the same assemblages in waterbodies on the upper Diamantina will differ from those for waterbodies on the lower Diamantina over the same the period (2001-2003).

Hypothesis 3. (Spatial effects – river scale)

The regression equations for the same parameters for the same assemblages in waterbodies on the Diamantina, Cooper and Neales over the same the period (2001-2003), will differ between these rivers.

Hypothesis 4. (Spatial and temporal effects – generality of results)

The regression equations for the same parameters for the same assemblages in waterbodies on the upper Cooper Creek, on the upper and lower Diamantina and on the Neales for the period 2001-2003 will differ from those for the lower Cooper waterbodies for the period 1986-1992.

Hypothesis 5. (Taxonomic generality)

The regression equations for the same parameters for waterbodies on the lower Cooper Creek for the period 2001-2003 will differ from those for the biotic parameters 2.2 and 2.9-2.10 at the same waterbodies for the same period.

3.4 QUANTITATIVE HYPOTHESES – MAGNITUDES OF EFFECTS

For the period 1986-1992 at sites on lower Cooper Creek, magnitudes of effects (% change) on values of the parameters in 2.1, 2.3-2.8 from given percentage changes in measures of hydrology were predicted by Multilayer Perceptron neural networks.

Hypothesis 1 (temporal effects – flow history scale)

The magnitudes of effects predicted for the same sites on lower Cooper Creek for the same parameters for the same assemblages will differ by >20% between the periods 2001-2003 and 1986-1992.

Hypothesis 2. (Spatial effects – river reach scale)

2.1 The magnitudes of effects predicted for the same parameters for the same assemblages at sites on the upper Cooper will differ by >20% from those predicted for sites on the lower Cooper over the same the period (2001-2003).

2.2 The magnitudes of effects predicted for the same parameters for the same assemblages at sites on the upper Diamantina will differ by >20% from those predicted for sites on the lower Diamantina over the same the period (2001-2003).

Hypothesis 3. (Spatial effects – river scale)

The magnitudes of effects predicted for the same parameters for the same assemblages at sites on the Diamantina, Cooper and Neales over the same the period (2001-2003) will differ by >20% between these rivers.

Hypothesis 4. (Spatial and temporal effects – generality of DRY/WET)

The magnitudes of effects predicted for the same parameters for sites on the upper Cooper Creek, on the upper and lower Diamantina and on the Neales for the period 1999-2001 will differ by >20% from those predicted for the lower Cooper sites for the period 1986-1992.

Hypothesis 5. (Taxonomic generality)

The magnitudes of effects predicted for the same parameters for sites on the lower Cooper Creek for the period 2001-2003 will differ by >20% from those predicted for the biotic parameters 2.2 and 2.9-2.10 at the same sites for the same period.

6.4 Adjustments to the floodplain / flood fish ecology model

1) The focus on overbank flows in this model needs to be widened to include inchannel events, as hydrological measures for events below overbank flows are correlated with fish assemblage structures and with indices of fish health and behaviour. For example, the strong relation between fish disease incidence and waterbody permanence in this study is an indicator of the importance of conditions in dry season

refugia. The influence of minimum water levels on recruitment has been identified (Bayley 1991), but the role of instream flows in general needs more attention in the model, particularly for highly variable systems (Bishop 1987).

This may seem a contradiction of the purpose of the model, which has been to articulate the role of floods and the floodplain in large river fish ecology. However, the case made here is that the role of flooding and the floodplain cannot be modelled in isolation from within-channel hydrological events. Much work has been done on the role of hydraulics in defining within-channel fish habitat in streams, particularly in relation to determining environmental flows (e.g. IFIM, Bovee 1982, Bovee 1986, Osborne et al. 1988, Milhouse et al. 1989, Layzer & Madison 1995, Glozier et al. 1997). Similar attention needs to be given to the role of within-channel hydrology in large floodplain rivers, and particularly to developing an integrated perspective across the full range of flows.

2) The role of the floodplain in providing macroinvertebrate blooms on which fish can fatten is supported in this study by the negative relation between macroinvertebrate abundance and waterbody permanence. However, perceptions of what constitutes floodplain need to be extended to accommodate the terminal floodplains and intermittent channels of arid zone rivers.

3) The multivariate nature of the relations between fish ecology and hydrology needs to be incorporated into the model. The common emphasis on a few hydrological parameters – magnitude, rates of rise and fall, duration and timing particularly – neglects the variety of hydrological measures which independently contribute to prediction of indices of fish assemblage structure, health and behaviour. At the waterbody spatial scale this variety should include for example measures of connectivity, depth and frequency of drying. At the flow pulse temporal scale it should include the phases of the flow pulse in Table 1 Chapter 1, and at the flow history temporal scale it should consider for example the cumulative (or conflicting) influences of antecedent events occurring at various intervals before a given biological response.

4) The role of flow variability is central to the model. However Chapter 2 demonstrates how various the measures of flow variability significant for fish biology are, and this variety needs to be incorporated into the model. The use of single summary measures of variability will restrict the applicability of the model.

5) The scale dependency of relations between hydrology and fish biology should structure the model, guiding the choices of levels of biological resolution and spatial and temporal scales.

6) The role of hydrology in promoting fish migration, spawning and recruitment is supported in this study by the relations between the latter biological parameters and various hydrological measures. Further:

(a) The massive recruitment of native species in response to floods out of synchrony with breeding seasons suggests that the model's emphasis on the synchrony of season and flow pulse should be qualified.

(b) Although most of the common fish species in Cooper Creek migrate upstream and/or downstream in response to flow, migration downstream in an endorheic system with strong transmission losses carries a high risk of stranding and recruitment failure (Ruello 1976, Puckridge & Drewien 1992) Whether such migration is deliberate or inadvertent, and whether it succeeds in the very long term in facilitating colonization of new habitat, the implications for the fish of systems like Cooper Creek need to be incorporated into the model.

In the following section some of these adjustments to the flood-floodplain fish ecology model are applied more generally to river ecology, and incorporated into an extended Flood Pulse Concept.

6.5 Towards a new Flood Pulse Concept

To understand, predict and manage the ecological impacts of development on large rivers we need a paradigm that characterizes all major flow-biology relations, including all biologically significant facets of flow (Richter *et al.* 1996, 1997). The Flood Pulse Concept of Junk *et al.* (1989) is a seminal contribution, but it has limitations.

6.5.1 Limitations of the FPC

6.5.1.1 The floodplain

A floodplain usually is defined as a low-lying area subject to periodic inundation by lateral overflow from fluvial channels or lakes (Junk *et al.* 1989, Junk & Welcomme 1990). This conforms with traditional geomorphology, in which lowland fluvial systems are represented by *active channels* which carry flow, and *floodplains* (here designated *geo-floodplains*) are formed by sediment deposition during overbank flows (Gregory *et al.* 1991). However from an ecological viewpoint the critical functional distinction between "channel" and "floodplain" is the alternation of wetting and drying. If this is so, then the main channels of rivers with highly variable pulse amplitudes may, in being alternately dry or inundated, function as floodplain (Puckridge *et al.* 1999). Moreover, the FPC model of "floodplain" – "channel" exchange by lateral overflow and withdrawal may be too restrictive, since:

a) in large floods the geo-floodplain may be subject to longitudinal rather than lateral flows (Lewis *et al.* 1990, Puckridge *et al.* 1999).

b) in localized floods there may be inflow from the geo-floodplain to the channel (Welcomme 1979, Lewis *et al.* 1990).

c) parts of the geofloodplain may act as a drainage terminus rather than as an area of exchange with the channel (Rodier 1985, Falkenmark 1989).

To accommodate this diversity, particularly apparent in arid zone rivers, *floodplain* needs to be redefined in ecologically relevant terms. Junk *et al.* (1989) propose an ecological definition of a floodplain as an Aquatic-Terrestrial Transition Zone, ATTZ) that excludes permanent lentic and lotic habitats. The ATTZ has features common to terrestrial and permanent aquatic habitats, and links the two. The title highlights the role of wetting and drying in floodplain dynamics but may obscure the fact that the biota of the "aquatic" phase has characteristics (e.g. abbreviated life cycles, capabilities for aestivation and migration) that are quite different from those of the biota of permanent lotic or lentic habitats. Similarly, the fauna and flora of the "terrestrial" phase differ from those of a

terrestrial habitat not subject to flooding (e.g. in having water-borne seeds, tolerance of submergence). However the most serious limitation of the ATTZ model is that its application to the variety of transition zones actually encountered in large rivers is constrained by the range of hydrological events considered by the FPC.

6.5.1.2 The flood

The FPC is concerned with variation in overbank flows, although as shown throughout this thesis, variations in in-channel flows also are biologically significant. Study of the pulsing of river discharge should be scale-dependent, as variations in discharge at any spatial or temporal scale are likely to be significant for at least some organisms. For example, a brief spate in a dry channel will produce a biological response (Stanley *et al.* 1997) and small stage-fluctuations affect littoral biofilms (Sheldon 1994, Burns 1997).

The importance of inchannel flows is particularly apparent for those arid zone rivers which have such variable flow amplitudes that channel flows may cease or channel reaches dry. Such rivers may also be endorheic and have such large transmission losses (Knighton & Nanson 1994a), that downstream reaches are only intermittently inundated, and function in this respect as floodplain. The Coongie Lakes, which are connected by the Northwest Branch channel of Cooper Creek and fill in sequence, act as floodplain in this way (Chapter 3). Lateral "overbank flows" in such systems are less important.

Further, there is evidence (Bunn & Davies 1999) that carbon production and foodweb linkages in the permanent waterholes and ephemeral floodplain pools of Cooper Creek are dominated by littoral bands of filamentous algae, not by riparian and floodplain litter. Inchannel flows, which govern waterlevel and physicochemistry of the channel waterholes in which this algal production occurs, may play a major role in mediating river production.

Proponents of the FPC may reasonably argue that the concept does not purport to be a comprehensive account of the role of flow in river ecology. But river flow, although multifaceted, is also integrated, as are its biological responses, and neither are sensibly partitioned between overbank and inchannel. Moreover, world-wide the modifications of river flow patterns occur across the whole range of flow magnitudes, and there is an urgent practical need for an integrated model.

6.5.1.3 Predictability and variability

The Group A rivers identified in Chapter 2 are distinctive in their extreme values on many measures of flow variability. The review in Chapter 2 and the results of Chapters 4 and 5 demonstrate that many measures of flow variability, including persistence at ENSO frequency, have biological significance. The FPC recognizes a role for flow variability, but understates its complexity, and deals with it at a range of temporal scales which is far exceeded in arid zone rivers.

The FPC focuses on systems where "the pulse is regular and of long duration" (Junk *et al.* 1989, p 122). Further, Bayley (1991, p 84) stated that "a predictable annual flood pulse is essential for the survival of the system". Junk *et al.* consider that unpredictable pulses impede biological production and the adaptations of organisms, but this is too narrow a perception of biotic adaptation and ecological response because life-history attributes like opportunism, flexibility and trophic generalism arguably are adaptations to unpredictable hydrological regimes (Kodric-Brown 1981, Winterbourn *et al.* 1981, Robinson *et al.* 1992, Poff & Allan 1995, Walker *et al.* 1995).

The biota of Cooper Creek, a hydrologically unpredictable river, shows manifold relations between hydrology and biology. Whether these are adaptive relations it is not within the scope of this study to determine, and the review of information on life-histories for the Cooper Creek fish assemblage (Chapter 3) was inconclusive because of the paucity of data. But at least one of these relations – the recruitment response of native fish to flow pulse amplitude – is likely to be an adaptation to the particular long-term hydrological variability and extreme spatial patchiness of this river basin (Puckridge *et al.* in press).

In a corollary to the FPC, Bayley (1991) argues that rivers with large floodplains have higher fish production (the flood pulse advantage), but only when season and flood pulse are in synchrony. However, Chapter 2 showed that the Cooper and Diamantina have high long-term variability in flow pulse timing, yet Chapter 5 demonstrates that in the Cooper there was a massive recruitment response of early maturing native fish to flow pulses over 1988-91. These pulses arrived at times varying from 5-8 months before the breeding

seasons of these fish. The results suggest that synchrony between flood and season is not necessary for high fish production.

6.5.1.4 Hydrological complexity

Although the FPC recognises that "the system responds to the rate of rise and fall and to the amplitude, duration, frequency, and regularity of the pulses" (Junk *et al.* 1989, p 122), the results of this study suggest that, even for overbank flows, large rivers are ecologically more complex. In the analysis of Chapter 2, eleven hydrological measures, each with potential biological significance, acted relatively independently to distinguish between groups of large rivers. Change in any of these measures could affect system responses at the scale of overbank flows. In subsequent chapters, a recurring result has been the multiplicity of relations between hydrological measures and biology. These measures have been shown not to be redundant, and to account for a substantial proportion of the biological variance.

The restriction of the FPC to overbank flows is also a distraction from the complexity at the scale of the flow pulse. Chapter 1 presented a 10 - phase model of the flow pulse, (including hyporheic, inchannel and overbank flows) which integrates all the levels of flow processes which shape river ecology.

6.5.1.5 Scale

Another recurring theme in this study is the role of scale. In terms of temporal scale the FPC focusses on the flood pulse and its long-term, predictable pattern. This distracts from the fact that hydrology-biology relations vary over scales from hours to decades (Ch. 2, Erskine & Warner 1988, Puckridge *et al.* in press). Further, hydrology-biology relations vary greatly over flow history – i.e. depending on the intervals between hydrological events and biological responses. On the one hand, single events in flow history may transform the structure of a riverine community (Fisher & Grimm 1988) and the geomorphic environment (Graf 1988, Kresan 1988, Pickup 1991). On the other, pulses are interdependent in their effects as Chapter 5 illustrates, and if they are hydrologically persistent may have striking biological consequences (Puckridge *et al.* in press) .

Spatial patchiness in arid zone floodplain rivers may also be more complex than the floodplain – channel dichotomy of the FPC suggests. Arid zone floodplain rivers (and those in the wet-dry tropics, Bishop 1987) may contract to disconnected channel waterholes (Knighton & Nanson 1994b) or lakes (Puckridge *et al.* 1999) which function as refugia during drought. This adds an additional spatial element to the river channel, and to the range of riverine connectivity (Bishop 1987).

The FPC needs a more explicit treatment of temporal and spatial scales and their implications for hydrology-biology relations, following for example Walker *et al.* (1995).

6.6 A revised FPC

6.6.1 Applicability of current models

It has been suggested (Thorp & Delong 1994, Walker *et al.* 1995) that the FPC, RCC and RPM are complementary concepts, reflecting respectively lateral and longitudinal linkages, and local autochthonous production. Certainly each model may be more readily applicable to particular river types – the FPC to large lowland floodplain rivers, the RCC to small upland systems, the RPM to large rivers with constricted channels. The preliminary model of Bunn and Davies (1999) (which could be named – using the authors' phrase – the Algal Bathtub Ring Model, ABRM) has to date been developed from work in only one river, although it is likely to apply to similar rivers in the Lake Eyre Basin of central Australia. Each model may also apply in particular reaches (or *patches, sensu* Sedell *et al.* 1989) of a given large river, and it has been suggested (Walker *et al.* 1995) that identification of sources and net movements of carbon and nutrients in each patch could be used to identify the model which has the locally dominant influence. The relative importance of each model may also vary between temporal patches – e.g. the ABRM may be dominant in arid zone rivers during low or zero flow, but be eclipsed by floodplain processes (modelled by the FPC) during high flows.

Of course the models may not necessarily be complementary. The RPM and ABRM challenge the dominance in large floodplain rivers of carbon derived from the floodplain (the Aquatic Terrestrial Transition Zone, Junk *et al.* 1989). Both assert the importance of

local instream production, and the RPM also questions the role of the flood pulse in mediating this production. Bunn and Davies (1999) however, concede the role of the flood pulse in mobilizing nutrients from the floodplain, enlarging habitat and dispersing organisms.

The focus of this thesis is on extending the FPC as a model of the role of flow in large floodplain rivers, not on the development of an all-embracing hybrid model for river ecosystems (cf. Walker *et al* 1995). However the RPM and ABRM models, in highlighting the contributions of instream production, imply that hydrological events within the river channel could, particularly in highly variable rivers, disrupt or enhance this production. This has major implications for ecosystem function (Sheldon 1994, Burns 1997). Accordingly, if the FPC is to be a comprehensive and integrated account of the role of flow in large floodplain rivers, it must be extended to encompass instream hydrological events.

6.6.2 The Flow Pulse Model (FPM)

The FPC is the most substantial formulation to date of the role of flow in large floodplain rivers, but this study has identified the following ways in which the FPC should be extended. I will call this extended version the Flow Pulse Model (FPM), to indicate its inclusion of inchannel hydrology.

6.6.2.1 Defining the eco-floodplain

Instead of the ATTZ, I define an *eco-floodplain* as the area periodically inundated by a river, including all areas of the channel and *geo-floodplain* except permanent pools in the channel bed and permanent lakes and billabongs (oxbows). The spatial limits of the eco-floodplain are defined by the limits of inundation in the lifetime of the longest-lived flood-dependent species (cf. Naiman *et al.* 1993). In the case of certain tree species, the appropriate temporal scale may be hundreds of years.

6.6.2.2 Including all magnitudes of flow

The FPC is concerned only with overbank or *flood* flows, although as demonstrated in Chapters 2, 4 and 5, implied by the RPM and ABRM, and implied above in the definition of *eco-floodplain*, variations in inchannel flows also have biological significance. The Flow

Pulse Model replaces the *flood pulse* with the *flow pulse*, which includes the full range of possible hydrological events, from hyporheic flow to peak flood - a ten-phase flow pulse (Table 1, Chapter 1).

6.6.2.3 Encompassing variability

The FPM treats flow variability as the major structuring process in river-floodplain ecology, and recognizes its multi-faceted nature and the broad range of scales over which it should be considered, particularly in arid zone rivers.

6.6.2.4 Including unpredictability

Junk *et al.* (1989) and Bayley (1991) consider that unpredictable flood pulses impede biological production and the adaptations of river organisms. The FPM suggests that the biota of rivers with low predictability may still be adapted to their hydrological environments. The FPM also recognizes that predictability is scale-dependent. Events which appear unpredictable at an annual scale may be cyclic (variable) over a scale of decades, and so still exert selective pressure, depending on the organisms considered. Accordingly the FPM applies to all large floodplain rivers, irrespective of the predictability of their hydrological regimes.

6.6.2.5 Encompassing hydrological complexity

Chapters 2, 4, and 5 demonstrate that large floodplain rivers show a multiplicity of relations between hydrological measures and biology (Richter *et al.* 1996, 1997, 1998). Accordingly the FPM incorporates a multivariate view of river hydrology, in which many hydrological measures are related to biological responses in patterns which may be distinctive for each river, and at temporal and spatial scales appropriate to particular organisms.

6.6.2.6 Extending scales

The FPM makes considerations of scale explicit by using a model of scales for large rivers adapted from Walker *et al.* (1995). The FPM is concerned principally with hydrological, not hydraulic scales, but the latter cannot be omitted. Extending temporal and

spatial scales in this way will also better accommodate the wider ranges characteristic of arid zone systems, particularly with respect to flow history.

Table 92 Temporal and spatial scales appropriate to large rivers (adapted from Walker *et al.* 1995).

Feature			Response	Scale	
Geomorphic	**Hydrological**	**Biological**	**Biological**	**Space (m^2)**	**Time**
catchment	Flow regime	Ecosystem	*Evolutionary:* Selection of life-history strategies	$>10^{11}$	$>10^{2}$ y
reach	Flow history	Community, population	*Ecological:* Succession, recruitment, mortality	10^{8}-10^{11}	1-10^{2} y
waterbody	Flow pulse	organism	*Physiology, behaviour:* disease, dispersal, breeding	10^{2}-10^{8}	days –1yr
microhabitat	hydraulics	macroinvertebrates, colonies of microorganisms	*Ecology, physiology, behaviour*	$<10^{2}$	hours - days

6.7 Management implications

6.7.1 The impacts of flow regime change

Human intervention alters flow regimes. Catchment clearance and flow regulation alter flow duration, amplitude, pulse shape (Grubaugh & Anderson 1988, Walker & Thoms 1993), minimum flows (Thomson 1992) and pulse frequencies (Carlson & Muth 1989, Walker & Thoms 1993). Regulation may reduce variability at one scale (Schneider *et al.* 1989, Grossman *et al.* 1990, Bayley & Li 1992) but increase it at another (Carlson & Muth 1989) and may modify the interactions of temporal and spatial variations. Changes in amplitude variability may affect the pattern of floodplain inundation and thus habitat heterogeneity (Copp 1989, Ward & Stanford 1995b). The results may be permanent shifts in ecosystem or community structure and function (Regier *et al.* 1989, Walker *et al.* 1992, Gehrke *et al.* 1995). The FPM is an attempt to provide a conceptual model of flow –

biology relations which may guide management in mitigating and perhaps avoiding these impacts. Some examples of the management implications of the FPM follow.

6.7.2 Implications of the FPM – particular features

6.7.2.1 The eco-floodplain

Defining the extent of the eco-floodplain as above (*in terms of the limits of inundation in the lifetime of the longest-lived flood-dependent species, and including all areas within these limits which are subject to alternating drying and inundation from river flow)*, strengthens the role of flow in governing the functional ecology of rivers, and challenges dichotomies between elements like channel and floodplain, which in the past have led to the undervaluing of atypical rivers like those of the arid zone.

The definition also conveys to managers the importance, in arid zone rivers particularly, of extreme hydrological events and of the episodically flooded outlying floodplains of such rivers. Such outliers may seem wastelands, but in fact produce, in response to rare great floods, biological events of exceptional scale and continental significance (Simmons 1996, Drewien & Best 1992, Kingsford *et al.* 1999). Although extreme floods are generally beyond human constraint, the remote eco-floodplains they inundate may be impacted by a range of uses (Gillen & Drewien 1993, Simmons 1996, Landsberg *et al.* 1997) which affect their capacity to support these exceptional biological responses.

6.7.2.2 Inchannel flows

Including the full range of flow events in the FPM makes explicit the importance of instream flow patterns (including zero flow and waterbody drying), which have crucial implications for refugia, connectivity and floodplain processes in variable rivers, and which are especially vulnerable to flow regulation, withdrawals and diversions. It also raises the status of intermittent and episodic river systems (where low and zero flows are the rule), which are often dismissed as not *real* rivers (e.g. Cooper "Creek"). Combining hyporheic and surface flows in one model also encourages a more comprehensive and integrated approach to flow management.

6.7.2.3 Unpredictability

Admitting unpredictable systems under the umbrella of the FPM also enhances the status of arid zone rivers. It emphasizes the necessity of long-term data for management of such rivers, and the need to conserve the stochasticity to which their fauna are adapted (Kingsford *et al.* 1999). Stochasticity is not compatible with the economics of most water resource use, and is commonly a casualty of such use (Walker *et al.* 1997).

6.7.2.4 Flow variability

Measures of flow variability used in hydrological analyses generally are few, and are sometimes reduced to a simple summary index (Walker *et al.* 1995, Poff 1996). Some water resource development proposals and assessments ignore flow variability altogether (e.g. Hawkins *et al.* 1995, Independent Audit Group 1996, Queensland Department of Natural Resources & Queensland Department of Local Government and Planning 1996), as users usually require fixed, seasonal allocations (Petts 1996, Walker *et al.* 1997). Even sophisticated flow management models, hydrological impact assessments or environmental flow determinations often pay less regard to variability than to central tendency (e.g. Arthington *et al.* 1992, Petts 1996, Thoms *et al.* 1996). Placing variability at the core of flow – ecology relations in the FPM implies that it should be given corresponding attention in river resource use and management.

6.7.2.5 Persistence

The ecological correlates of persistence are not well understood, but there is sufficient evidence for waterbirds (Kingsford & Porter, 1993, Kingsford 1995) and fish (Puckridge *et al.* in press) to suggest that it is biologically important, particularly for rivers in arid and semi-arid regions.

River management typically concerns the timing, shape and magnitude of the flow pulse and the frequencies of flows of various magnitudes, based on modelling of long-term patterns (e.g. Department of Natural Resources, 1998a, b). When biological factors are considered, attention generally is devoted to the impacts of changes in facets of the flow regime, especially to patterns of low flows, seasonal timing, the slopes of the falling and

rising limbs and floodplain inundation. Hydrological persistence, and particularly its biological significance, are rarely considered in river management. Indeed, diversions from high flows, including clusters of high flows, generally are considered a strategy for minimal impact. The FPM suggests that conservation of high flows and the 'carry-over' effects associated with persistence should also be considered in river management.

6.7.2.6 Hydrological complexity

Methods of summarizing flow pattern, such as flow/flood frequency or flow/flood exceedance curves (Farquharson *et al.* 1992, Duncan 1995) are useful in hydrological management and engineering. However, to manage the biological impact of flow regime change, hydrologists must be able to use hydrological measures which relate as directly as possible to biological responses. These responses are various and complex, necessitating a multivariate approach, which does not accord with summary measures such as *a general flow index* (*sensu* Clausen & Biggs 1997). The challenge put to managers by the FPM is to model for each river the multiple hydrological measures which biological scientists have related to particular responses of the biota.

6.7.2.7 Scale

Large rivers, particularly those in arid zones, operate over extensive spatial and temporal scales. The FPM, by setting a framework for addressing scale, highlights such issues as the paucity of hydrological data and the more severe paucity of biological data at scales appropriate to management questions. It is also a reminder of the need for impact assessment and monitoring at these scales.

6.8 Implications for arid zone rivers

The rivers identified in Chapter 2 as "Group A" are highly variable on many hydrological measures. Most have dry-climate influences, but some are dominated by mid-latitude rainy climates and a few by continental climates. These rivers are usually situated in regions where human needs for water are extreme (Kingsford *et al.* 1998b), and consequently many have undergone considerable hydrological modification (Kingsford *et al.* 1998b). For example, in the past 70 years the ecological health of the Darling River

(Australia) and the Great Fish River (South Africa) has declined due to flow diversions and abstractions which have reduced natural flow variability (O'Keeffe & De Moor 1988, Thoms *et al.* 1996). The variability of these rivers makes them particularly vulnerable to ecological changes consequent on regulation, such as invasion by exotic species (Meffe 1984, O'Keeffe & De Moor 1988, Gehrke *et al.* 1995).

This study has indicated that large arid zone floodplain rivers may be the most hydrologically complex, variable and unpredictable of all river systems, and are also geomorphically distinctive. Effective management of such rivers cannot be based on research from more humid regions. It must be based on studies of the rivers themselves, and these studies need to be exceptionally long-term. Yet because such rivers are often remote from research centres, the data available usually are less than for most temperate and tropical systems (Puckridge 1998). Resources need to be committed to redressing this imbalance, and until it is redressed, further development of the water resources of these rivers seems foolhardy. When substantial data become available, it is suggested the protocol below be followed.

6.9 Towards a protocol for assessing water resource use impacts on river systems

6.9.1 The context

It has been argued that there is water excess to long-term ecological requirements in unmodified large rivers (Arthington *et al.* 1992, Arthington *et al.* 1995, Arthington 1998). In the absence of convincing evidence for this contention, and in the light of the ecological significance of extreme floods (Kingsford *et al.* 1998a, Puckridge *et al.* in press), this thesis assumes that there is no such excess. I contend that all changes to long-term patterns of flow are likely to have biological impacts. If this is so, the terms "environmental flows" and "minimum flow requirements" (Ferrar 1989, Arthington *et al.* 1992, Sutton *et al.* 1997) are misleading, since they imply that a component of river flow is not *environmental*, and can be used for economic gain without environmental cost. The task of science is to determine these environmental costs, rather than to guess at minimum threshold flows above which

river ecology may be resilient to change. The task of society at large is to weigh, in a social and economic context, the likely ecological costs demonstrated by science . However scientists also have a responsibility to promote community debate on these issues (Puckridge 1998).

Water resource agencies should collaborate with ecologists to base hydrological analyses on the biologically significant facets of flow regime. This call has been made repeatedly (Fausch & Bramblett 1991, Molles *et al.* 1992, Richter *et al.* 1996), but rarely heeded (e.g. Walker *et al.* 1997). Habitat restoration in modified rivers should include reinstating the natural hydrograph as far as possible (Bayley 1991), allowing natural hydrological variability, stochasticity and persistence as well as median or minimum flows (Naiman *et al.* 1993). This is in keeping with the protection of ecosystem processes (Regier *et al.* 1989, Bayley & Li 1992), and should take precedence over designing flow regimes for particular species groups or segments of the system (cf. Bovee 1982, 1986, Cambray 1991, Lubinski *et al.* 1991). Given the declining integrity of the world's large rivers, conservation of the few remaining unregulated rivers deserves a high priority (Naiman *et al.* 1993, Sparks 1993, Welcomme 1995).

6.9.2 The protocol

Determination of impacts of potential or actual flow regime change should begin with characterizing the natural flow regime (Arthington *et al.* 1992) and the spatial patterns of inundation from natural flows. The flow regime should initially be described using as comprehensive a range of ecologically significant facets of hydrology as possible, developed from the literature on relations between hydrology, geomorphology, ecological processes, biotic structures and responses (e.g. Ch. 2), in accordance with an holistic view of river ecosystems (Arthington *et al.* 1992, Ward 1998).

Considering the multivariate hydrological differences between climatic groups of rivers and between individual rivers (Ch. 2), and in contrast to practice in current holistic methods (Arthington *et al.* 1992, King & Tharme 1994, Thoms *et al.* 1996), the relations above should be derived from refereed research on the target river. Where such work has not been done and management agencies refuse to postpone intervention until it can be

done, the relations should be derived from published and refereed information on rivers similar to the target system. The facets of hydrology thus derived should be related to spatial patterns of inundation (Puckridge *et al* 1999), and quantified as measures at a range of temporal and spatial scales appropriate to the system under study.

To provide a sound basis for derivation of the relations described above, broad-scale comparisons of rivers (in terms of their hydrology, geomorphology, ecological processes and biota) to delineate regions with similar systems should be a priority. In each region, benchmark river systems, as near pristine as possible, should be reserved from development and studied intensively (Dynesius & Nilsson 1994). From these systems, ecology-hydrology relations can be extrapolated for other rivers in the region. However relations extrapolated from the benchmark river to the target system must be tested in the target system, for example as in the section "Testing predictions arising from this thesis" above.

Once hydrology-biology relations capable of predicting a significant component of variance in biological parameters have been established, the management authority should model how the predictive measures for the system (including the spatial patterns of inundation) are likely to change under potential water resource development scenarios. The changed values for the predictive measures can then be input to the established hydrology – biology relations, and likely biological impacts derived.

Implementing a new flow management regime is too often the final step. In fact it should mark the beginning of an iterative, long-term process of genuinely adaptive management (e.g. Merritt *et al.* 1996), in which predictions of the original model are tested against ecological outcomes, and flow management is adjusted accordingly. Sadly, adaptive management practices have rarely matched their rhetoric (Walters *et al.* 1993, McLain & Lee 1996), and given the complexity and long-term nature of many responses to flow regime change, adaptation, if it occurs at all, may come too late. The complete protection of benchmark rivers is all the more important in this situation. Such rivers provide not only a guide to rehabilitation (where this is possible) but an essential testament to the splendour of a pristine river, and what we risk in meddling with the few we have left.

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