Littoral Ecology of a Regulated Dryland River (River Murray, South Australia) with Reference to the Gastropoda

Fran Sheldon, B.Sc. (Hons)

River Murray Laboratory
Department of Zoology
University of Adelaide

Submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy.

-April 1994-

Table of Contents

Chapter 8: Conclusion

Chapter 9: Recommendations for Management

Abstract

The riverine littoral zone is a boundary between terrestrial and lotic aquatic ecosystems, corresponding to the "wetted perimeter" when the river is within its banks and the advancing or receding water's edge in times of flood. It is a patchy habitat whose spatial complexity reflects the geomorphological nature of the floodplain, and whose temporal complexity is related to variations in the timing and duration of floods.

Flow regulation modifies the scale of littoral habitat patches. Spatially, it decreases lateral gradients and enhances longitudinal gradients, alienating channel and floodplain habitats. Temporally, it may reduce the frequency, amplitude and duration of floods, or increase the frequency of short-term water-level fluctuations. Such changes are apparent in the River Murray, a regulated dryland river in south-eastern Australia. The regulated regime in the lower Murray is governed by a series of 10 weirs, and is distinguished by increases in summer-autumn flows, long-term flow constancy and short-term flow fluctuations.

This thesis explores the ecological impacts of regulation on the littoral zone of the lower Murray, South Australia. It first describes the spatial patterns of benthic macroinvertebrate assemblages at macro-, meso- and micro-scales. Particular attention is given to the gastropod fauna, a group likely to be sensitive to changes in the littoral environment, and one of the few groups for which there are some, albeit sparse, historical data.

In summer 1990, littoral habitats of the lower Darling and lower Murray rivers supported 103 macroinvertebrate taxa, dominated by insects and crustaceans, but with uneven distributions of individuals among taxa. In each river there was a wide diversity of meso- and micro-habitats. Distinctive assemblages were apparent across the entire range of spatial scale in each river, and the complexity of microhabitats influenced patterns at meso- and macro-scales. The relative abundances of "functional feeding groups" in all habitats indicated utilisation of diverse resources of organic detritus. Generalist *collector-gatherers* were commonest, with few *filterers* and *scrapers*; suggesting that organic matter inputs in these lowland reaches come principally from the floodplain rather than from downstream transport.

Regulation may diminish lateral water-level changes and impose strong longitudinal gradients on the littoral zone. The weirs on the lower Murray impose sequential water-level and trophic gradients, and disrupt the distribution of vegetation. These gradients are reflected in the invertebrate assemblages of the upper, middle and lower weir pools. In all littoral pool environments snags (fallen wood) and emergent macrophytes are common, and invertebrate assemblages include highly abundant shrimps, chironomids and other taxa. In the upper pools submerged macrophytes are common, with assemblages containing amphipods and coleopterans. In lower pools unvegetated reaches and sedge microhabitats predominate, each with distinctive invertebrate assemblages dominated by dipterans.

The biology of the prosobranch gastropods were therefore examined to determine the reasons for the virtual local extinction of some 18 species over the past 30-40 years.

Increases in the rate and magnitude of daily or weekly water-level fluctuations may have contributed by stranding snails when levels fall suddenly. Experiments showed, however, that *Notopala hanleyi* and *Thiara balonnensis* were able to accommodate to fluctuations even greater than those that normally occur in the regulated river. Decreased seasonal fluctuations may have contributed to the decline by changing available food sources. Both *Notopala* and *Thiara* are detritivores, assimilating carbon from detrital sources even when algae are abundant. They are also viviparous, requiring an abundant supply of nitrogen for breeding and growth, particularly for females. Compared with algal periphyton, microbial biofilms have a high food quality, measured as the ratio of carbon to nitrogen (C:N). *Notopala* is unable to select detritus in the presence of abundant filamentous algae. Thus, if faced with a food resource consisting entirely of algae, these species may be unable to obtain sufficient nitrogen. This is supported by the persistence of snail populations in environments where food resources are rich in nitrogen, notably the irrigation pipelines of the Riverland in South Australia.

Algal biofilms are prevalent in all pool environments associated with the lower Murray, but this may not have always been so. Regulation has stabilised the photic zone and enhanced the growth of attached algae, whereas in unregulated, turbid rivers, as the Murray was prior to about 1920, the constant movement of the water levels causes the photic zone also to move constantly, preventing prolific algal growth. In unregulated rivers, the community is likely to be predominantly heterotrophic (bacterial/microbial). A shift from bacterial-microbial towards algal food sources in the Murray may have affected many aquatic invertebrate species, including the gastropods.

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 had been made in the text.

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

Signed:

Date: 14th April 1994

Acknowledgments

I would like to express my sincere thanks to the following people who assisted in various ways.

Dr Keith Walker, my supervisor, for his support, patience and optimism throughout the project, and for insights the noisy, fast moving, luggage laden, steam driven freight trains. He also displayed amazing stamina in providing critical comments on many drafts of this thesis.

An ecology project would be impossible without field assistance. Tim Doherty is especially thanked for sacrificing many of his well-earned school holidays to haul boats on and off cars and travel long distances, his help was greatly appreciated. Others who survived the weather include: Lance Lloyd, Sandi Poland, Andrew Boulton, Jim Puckridge, Robyn Molsher, Catherine Watt, Terry Bertozzi, Jason John, Denise O'Keefe, Kerry and Rod Derrington, Michelle Jenkins and Thomas Flöttmann.

Landholders who allowed access to their properties are also thanked for their cooperation. A special thanks to Ann and Roger Green of 'Fiddlers Green' (Morgan) who allowed repeated access to Scott Creek backwater, John Chappel of Chowilla Station and Alan Davies of Culpaulin Station.

Financial support from the Natural Resources Management Strategy, Murray-Darling Basin Ministerial Council was greatly appreciated and made field work possible. A University Research Grant through the Department of Zoology funded the carbon stable-isotope analyses. A visit to the Australian Museum, Sydney, was assisted by a Keith Sutherland Award.

The staff of the Zoology Department, University of Adelaide, also assisted in many ways, special thanks to Sandi Poland and Helen Vanderwaude (for help in far too many ways to express here), Terry MacKenzie (the construction of various pieces of field equipment) and Phil Kempster (photography and computer advice). Thanks also to Dr Keith Turnbull, Department of Geology and Geophysics, University of Adelaide, for use of the 'perchloric-acid-proof' fume hood, making the phospholipid analyses possible. Dr Stuart Bunn, Division of Environmental Sciences, Griffith University, conducted the carbon stable-isotope analyses. Mr Colin Rivers, Division of Soil Sciences, Waite Agricultural Research Institute, University of Adelaide,

analysed the total carbon and nitrogen samples. Fellow postgrads are thanked for sharing coffee, beers, and occasionally, providing sanity.

Several people read drafts of this thesis and provided useful and critical comments, these include, Dr David Dudgeon (Department of Zoology, University of Hong Kong), Dr Keith Walker, Dr Thomas Flöttmann, Stuart Blanch and Adrienne Burns. Many others contributed through discussions along the way.

A big thanks to my grandmother, Mrs R. Faunt, who sparked an interest in studying biology at uni, and to my crazy family Staff, Kerry, Rod, Janey, Kimi and Rishi for continual encouragement - and for never letting life become too boring.

A special thanks to Thomas for his friendship, support and laughs at a time when life got just a bit tough.

List of Tables

Chapter 4

Chapter 5

Chapter 6

Chapter 7

List of Figures

Chapter 4

Chapter 1

General Introduction

1.1 INTRODUCTION

Boundaries (ecotones) between adjacent ecological systems are regions of high productivity and diversity with characteristics dependent upon their transitional position (cf. Wiens *et al.,* 1985; Holland, 1988; Naiman *et al.,* 1988; Pinay *et al.,* 1990; Risser, 1990). The structural and functional characteristics of land-water boundaries are primarily influenced by hydrologic regimes (Holland *et al.,* 1990), and in freshwater lotic systems the *flood pulse* (Junk *et al.,* 1989) is the principal force (Décamps and Naiman, 1990).

In fluvial systems boundary habitats depend on exchanges and interactions between different elements that include aquatic, semi-aquatic and terrestrial patches (Pinay *et al.,* 1990). The riverine littoral zone is an example of an ecological boundary (Walker *et al.,* 1992). It forms the interface between terrestrial and lotic aquatic ecosystems, but is often not easily delineated as a distinct habitat. It is also complex, comprising a mosaic of different landforms (e.g. floodplain and channel) and communities (e.g. lentic and lotic) (cf. Amoros and Roux, 1988; Naiman *et al.*, 1988; Gregory *et al.,* 1991). Compared with the main-channel the littoral is a region of calm water and stable sediments, with microhabitat "structure" conferred by rocks, snags, plants, and bank irregularities (Walker *et al.,* 1992).

In pristine rivers the littoral zone is rarely static: it corresponds to the water's edge when the river is within its banks, and to the advancing or receding edge in times of flood; hence the *moving littoral* (Junk *et al.,* 1989). The extent of this boundary will depend on the periodic flooding and drying regime of the river, the configuration of the shore terrace and adjoining terrestrial areas, and on water level fluctuations and depositional and erosional processes (Pieczynska, 1990). Thus, the littoral is composed of habitat patches that vary in space and time. Most of the biodiversity associated with large rivers is likely to be concentrated within this zone (cf. Pinay *et al.,* 1990; Walker, 1992; Walker *et al.*, 1992).

Lateral linkages between main-channel and floodplain habitats are vital for the ecological processes of large rivers (cf. MacArthur, 1988; Junk *et al.,* 1989;

Puckridge *et al.,* unpublished MS). The moving littoral maintains these lateral interactions, thereby increasing the diversity of habitat types within the river, enhancing both food resources and refuges. Variations in the lateral movement of the littoral, through flow variability, further increases habitat complexity. Lateral movements also increase organic matter cycling within river systems and prevent stagnation and dominance of late successional taxa on substrata, promoting high littoral productivity (cf. Conners and Naiman, 1984; Findlay *et al.,* 1986; Edwards and Meyer, 1987; Cuffney, 1988; Junk *et al.,* 1989; Pinay *et al.,* 1990).

Flow variability is typical of rivers in arid and semi-arid regions (dryland rivers) and pervades every feature of their physical, chemical and biological environment (Walker *et al.,* 1992). Dryland rivers are characterised by wide fluctuations in discharge, oscillating between periods of flood and drought (Kotwicki, 1986; Molles *et al.,* 1992). The magnitude of the variations in water level between these phases suggests the littoral zone in dryland rivers is well developed and provides a significant habitat for littoral fauna. Further, freshwater littoral communities are particularly sensitive to landscape change (Naiman *et al.,* 1988) and thus, are likely to be adversely affected by anthropogenic disturbances such as flow regulation.

One threat to the natural character of the world's large rivers is flow regulation. This is particularly the case in arid and semi-arid regions, where the combination of variable discharge and a persistent high need for water creates a demand for intensive flow management (Graf, 1988). Regulation often results in the isolation of the main-channel from the floodplain, reducing the extent of the littoral zone (cf. Sedell and Froggatt, 1984; Pinay *et al.,* 1990) and changing the scale of its habitat patches in both space and time (Urban *et al.,* 1987; Salo, 1990). Littoral zones will therefore show marked changes in response to flow regulation.

The physical changes induced by regulation may eliminate from the river many zoobenthic species, allow the colonisation of others, and induce shifts in the abundance of those taxa able to maintain populations under the altered regime (Ward and Short, 1978). These changes may be further exaggerated in dryland rivers, because of the disparity between natural and regulated patterns of flow. In dryland rivers the natural regime is prone to droughts and floods whereas the regulated regime is engineered to provide reliable water supplies. The fauna of dryland rivers is therefore adapted to flow variability and will be affected by any change in variability.

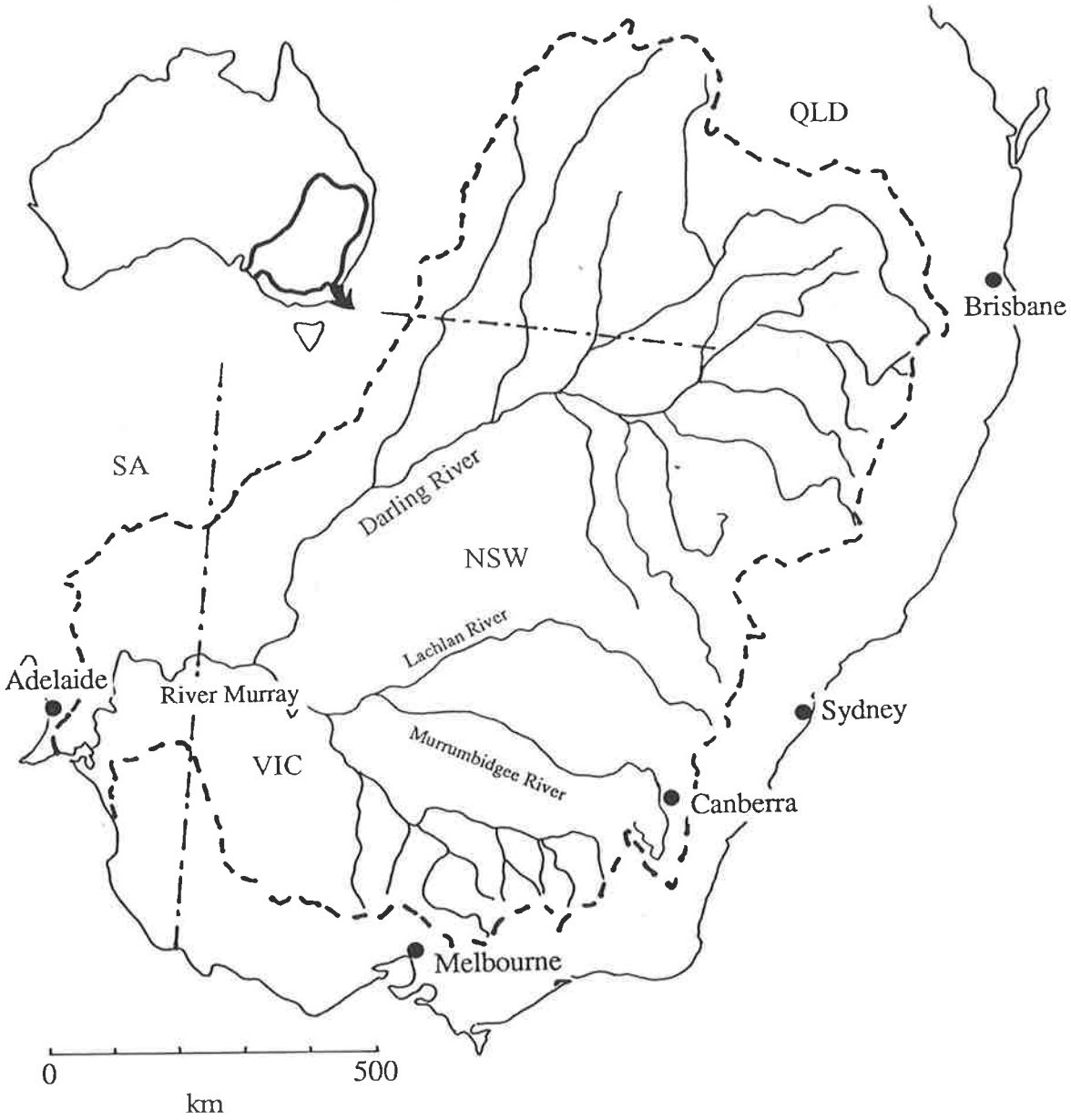


Figure 1.1 Map of the Murray-Darling Basin and river system.

The Murray-Darling Basin, in south-eastern Australia (Figure 1.1) is an ideal area in which to examine the effects of flow regulation on littoral ecology. Flows are regulated by storages in the upper catchment of the River Murray and its main tributaries, as well as low-level weirs on lowland sections. Since flow regulation commenced in the 1920's there have been marked changes in the distribution and abundance of a number of faunal groups including fish such as Murray cod (*Maccullochella peeli)* (Cadwallader and Lawrence, 1990). There have also been population changes in invertebrate taxa, for example, Murray crayfish (*Euastacus armatus)* (Geddes, 1990), the river mussel (*Alathyria jacksoni)* (Walker, 1990; Walker, 1992) and the river gastropods *Thiara balonnensis* and *Notopala* spp. (Walker, 1992; Sheldon and Walker, 1993a).

This thesis explores the impacts of flow regulation on the ecology of the littoral zone of the River Murray in South Australia. It examines the spatial patterns of benthic macroinvertebrate assemblages from meso- and micro-habitats in the littoral zone of the regulated lower Murray and an unregulated section of the Darling River in New South Wales. Special attention is given to the gastropod fauna a group likely to be sensitive to changes in the littoral environment, and one of the few groups for which there are some historical data.

1.2 Study Area: the Murray-Darling Basin

1.2.1 Physical Characteristics

The Murray-Darling Basin (cf. Figure 1.1) extends from about 24 to 38 degrees south latitude. It covers one seventh of the continental land mass and has a catchment area of 1.073 million km^2. The climate varies from inland sub-tropical in the north to cool and humid in the Eastern Highlands, temperate in the south and hot and dry inland. Average annual rainfall varies from over 1400 mm in the highlands to less than 300 mm in the north-west. The basin is also affected by the El Niño-Southern Oscillation (cf. Nicholls, 1989) which contributes to the considerable annual variability in rainfall, increasing with distance inland (MDBMC, 1987).

The lengths of the principal rivers, the River Murray and the Darling River, total 5300 km placing them among the longest systems in the world. The River Murray rises in the south-eastern Alps and flows in a north-westerly direction as the border between New South Wales (NSW) and Victoria (Vic). The Darling River rises in the north-east (NSW and Queensland (Qld)) and flows predominantly south-west across

semi-desert to meet the Murray at Wentworth, 830 river-km from the sea. Beyond this confluence no other major tributaries enter the system. Other major rivers in the basin include the Murrumbidgee, Lachlan, Goulburn, Macquarie, Culgoa and Warrego. The rivers of the basin meander over the inland plains, with the gradient of the Murray falling from 1 in 7000 in the upper region near Albury to 1 in 60000 near the Murray mouth.

Most of the Murray-Darling catchment is arid to semi-arid and consequently annual discharge is generally low and erratic (average for 1950-80 at Blanchetown, 318.3 m^3s^{-1}). The low average disguises the 'inter-year' variability which, for the period 1950-80, ranged from 0.62 to 49.3 ML annually; corresponding to the record drought of 1967-68 and floods of 1955-56 (Walker, 1986). Flows in the system are among the most variable in the world (Finlayson and McMahon, 1988). This variability is reflected in the complex physical character of the lower Murray, with a channel cross-section characterised by internal benches representing different flow configurations (Thoms and Walker, 1992).

The floodplains of both the lower Murray and the Darling River fall into the "fringing floodplain" category of Welcomme (1979); those accompanying river courses that are, in effect, the major channel during high discharge. The two rivers differ markedly, however, in the morphology of their floodplain. The floodplain of the lower Murray is well-watered, compared with the surrounding semi-arid land, and there are frequent exchanges of water between the main channel and the floodplain, so floodplain communities are well-developed (Walker, 1986; Boulton and Lloyd, 1991). In contrast, the Darling flows through a 10-metre 'trench', the floodplain is not "well-watered" and does not support significant floodplain communities (Walker, 1986). Like the lower Murray, the channel of the Darling has a complex cross-section with internal benches (Woodyer *et al.*, 1979). These benches are frequently flooded and constitute part of the littoral zone and hence the floodplain.

Descriptions of the geography, geology and hydrology of the Murray-Darling Basin are given in Walker (1986, 1992), MDBMC (1987) and Mackay and Eastburn (1990).

1.2.2 Unregulated Flow Characteristics

About half the total discharge of the Murray-Darling Basin comes from winter-spring rainfall and snow melt within the Murray catchment above Yarrawonga Weir (Walker, 1992). In contrast, the Darling catchment of northern New South Wales and Queensland (cf. Figure 1.1), comprises over 50 percent of the total basin area, but contributes only 12 percent of the flow. The Murrumbidgee catchment, covering central and southern New South Wales, adds only 3 percent (MDBMC, 1987). The lower Murray below the Darling junction yields negligible runoff.

Natural flows in the lower Murray are variable but tend towards a maximum in winter and spring and a minimum in late summer and autumn (Maheshwari *et al.*, 1993). At most stations minimum flows increase between February and October and decrease during the following months. Flows in the Darling are more variable, being governed by unreliable summer monsoons in south-eastern Queensland (MDBMC, 1987).

Differences in flow regimes of the two rivers is illustrated in Figure 1.2a. The variable nature of flow is evident in 20 year hydrographs of unregulated mean monthly discharge, with extreme high flows alternating with periods of low flow. Differences are also evident from comparisons of variability and predictability, calculated from the data used for the hydrographs (cf. Table 1.1; Puckridge *et al.*, unpublished MS). Flows in the Darling at Wilcannia are more variable than those in the lower Murray with respect to mean annual (ANX) and mean monthly (MNX) discharge (Figure 1.2b). Flows in both the lower Murray and the Darling during these 20 years were slightly skewed (mean (*SE*), 752.54 (*51.43*) and 96.92 (*7.93*) m^3s^{-1}, respectively; median 498.07 and 47.34 m^3s^{-1}, respectively). The various coefficients of variation should, therefore, be treated with some caution. Based on Colwell's index of Predictability (Colwell, 1974), flows in the lower Murray are slightly more predictable.

Flows in both rivers, however, are more variable than in corresponding rivers from tropical regions and some rivers from temperate climates (Puckridge *et al.*, unpublished MS). One noticeable feature is that discharge during the 20 years is never stable for an extended period: water levels are generally rising or falling. Continual movement of the littoral zone (cf. Junk *et al.*, 1989) is a significant feature in the ecology of dryland rivers.

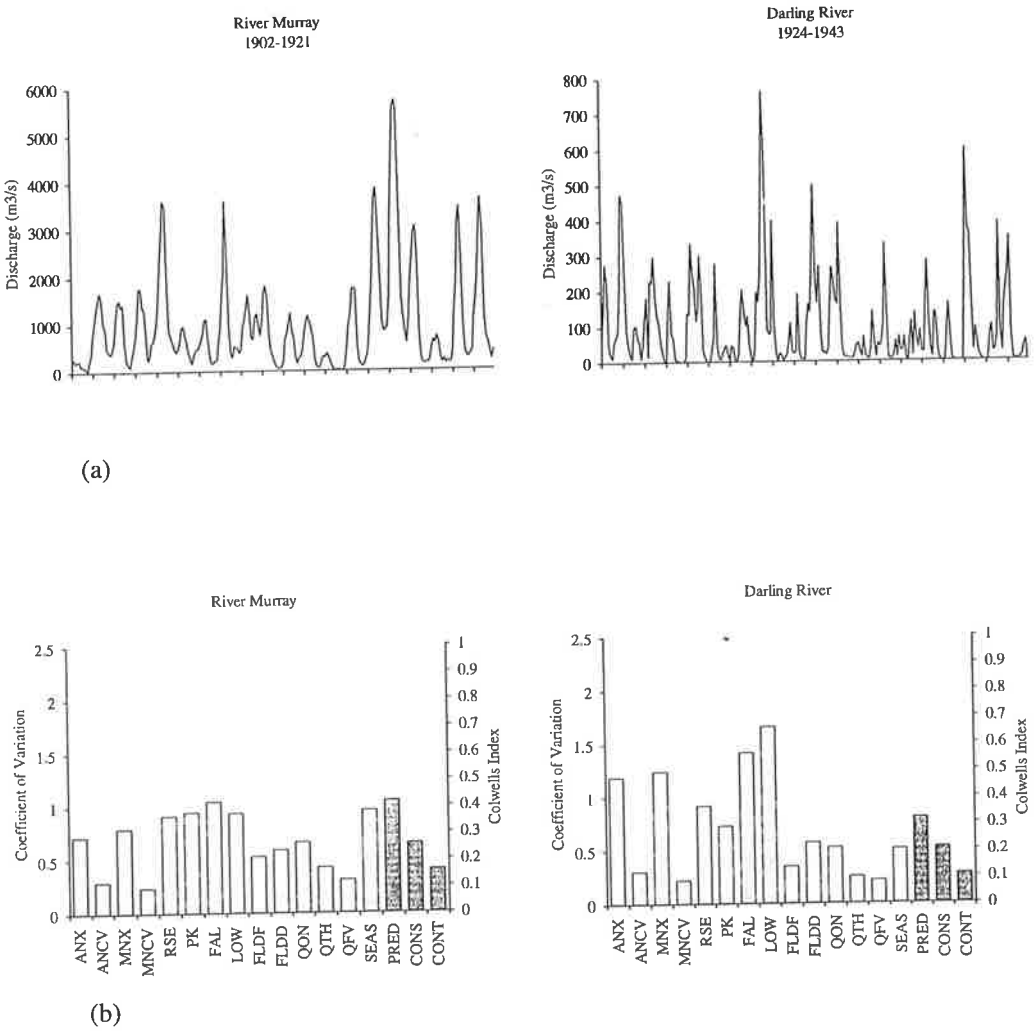


Figure 1.2 (a) Twenty-year hydrographs of mean monthly discharge for the River Murray at Lock 6 and the Darling River at Wilcannia, (b) Profiles for both rivers of the coefficients of variation (cf. Table 1.1) and Colwell's indices of predictability, constancy and contingency.

Table 1.1 The components of variability and predictability used to demonstrate aspects of flow variability in the unregulated River Murray and Darling River (CV = Coefficient of Variation). Data are mean monthly flows (m^3s^{-1}). A 'pulse' is a rise and fall in monthly discharge.

Components	Abbreviation
CV of all annual CV's	ANCV
CV of all monthly CV's	MNCV
CV of all monthly peak discharges	PK
CV of all monthly minimum discharges	LOW
CV of amplitude of falling limb of pulse	FAL
CV of amplitude of rising limb of pulse	RSE
CV of number of months between low flows (pulse duration)	FLDD
CV of number of floods per year	FLFR
CV of mean annual discharge	QON
CV of mean discharge over three years	QTH
CV of mean discharge over five years	QFV
CV of timing of flows each year	SEAS
% months of zero flow	ZERO
Mean of CV's of monthly discharge	MNX
Mean of CV's of annual discharge	ANX
Colwell's (1974) index of Predictability	PRED
Colwell's (1974) index of Constancy	CONS
Colwell's (1974) index of Contingency	CONT

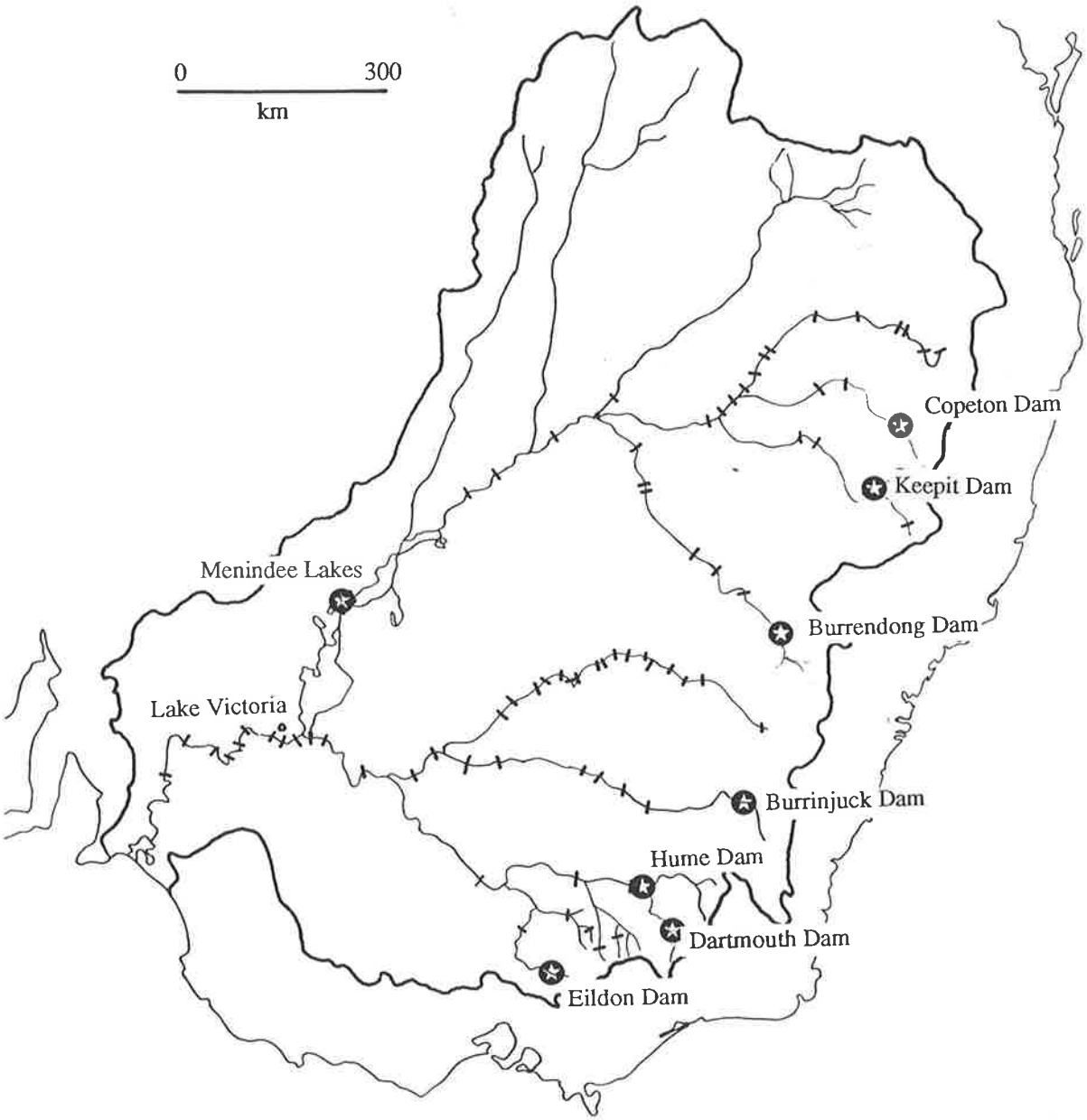


Figure 1.3 Location of ✪ major storages and / wiers in the Murray-Darling Basin.

1.2.3 Regulation and Regulated Flow Characteristics

Due to naturally variable flows in the Murray, flow regulation has been necessary to provide reliable water supplies for urban, irrigation and industrial uses. Regulation began with the River Murray Waters Agreement, ratified in 1915 by Acts of Parliament at Commonwealth and State Government levels. As part of this initial agreement a set of water-sharing principles was adopted. This ensures that flows in the River Murray are shared equally among the three riparian states, with a guaranteed minimum entitlement flow for South Australia (1850 GL) (cf. Appendix A). Flows in the basin are administered by an independent commission, the Murray-Darling Basin Commission (MDBC), which allocates the water to the three lower states (New South Wales, Victoria and South Australia) based on a yearly water resource assessment (Jacobs, 1990). The annual 'entitlement' flow to South Australia is approximately 14 percent of the mean annual flow at the state border.

Accounts of the historical development of flow regulation in the Murray-Darling Basin are given by Baker and Wright (1978), Close (1990), Jacobs (1990) and Maheshwari *et al.* (1993). Flow regulation is achieved through dams, weirs and offstream storages (cf. Table 1.2; Figure 1.3). The main storages in the Murray catchment (Eildon Dam, Hume Dam and Dartmouth Dam) were constructed to increase the security of water supply for irrigation. Water is stored during winter and spring, and released during the irrigation season, summer and autumn, when flows are low. This practice tends to decrease the frequency of small to moderate floods while increasing the level of base flows in the lower river (Maheshwari *et al.*, 1993). In the catchment of the Darling there is a number of smaller dams (e.g. Copeton Dam and Keepit Dam) that maintain water supplies for local needs and small scale irrigation.

Below the Darling confluence the mainstem of the Murray is regulated by a series of 10 Boulé weirs (Figure 1.4). These lock and weir structures (hereafter referred to as 'locks') make the river permanently navigable and provide steady pools for irrigation diversions, enabling irrigation by gravity feed. Flows across the weirs are regulated by the addition or removal of 0.4 m deep concrete 'stoplogs' in the sluice section and 1 m^2 Boulé panels in the navigable pass section (Figure 1.5a). The water level above the weir is maintained within ±50 mm of a design level (Figure 1.5b). This operational target is accomplished by the lockmaster adjusting the panels or removing the stoplogs as necessary (Maheshwari *et al.*, 1993). The effect is to cause variations in both flows and water levels downstream of each weir.

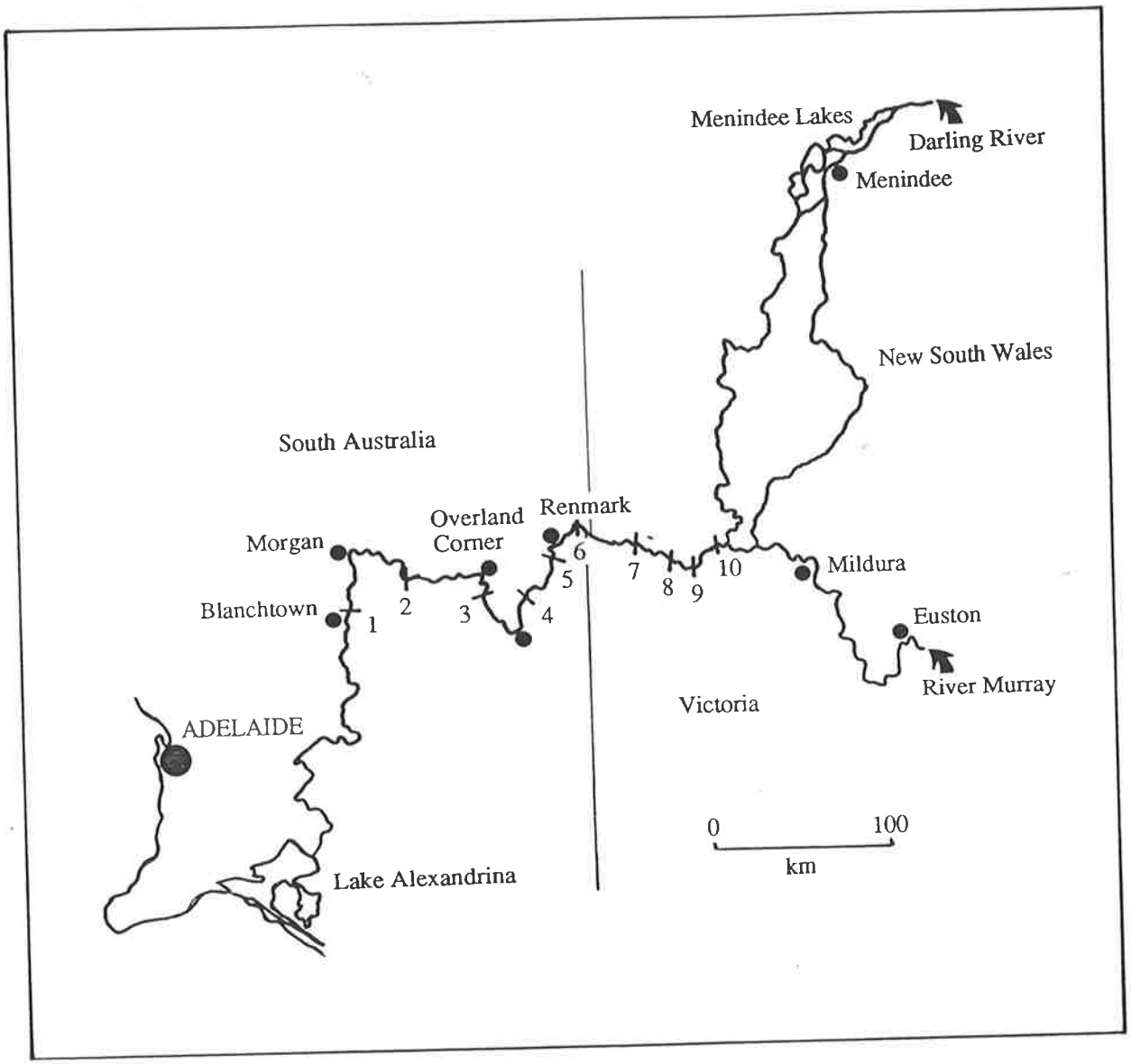
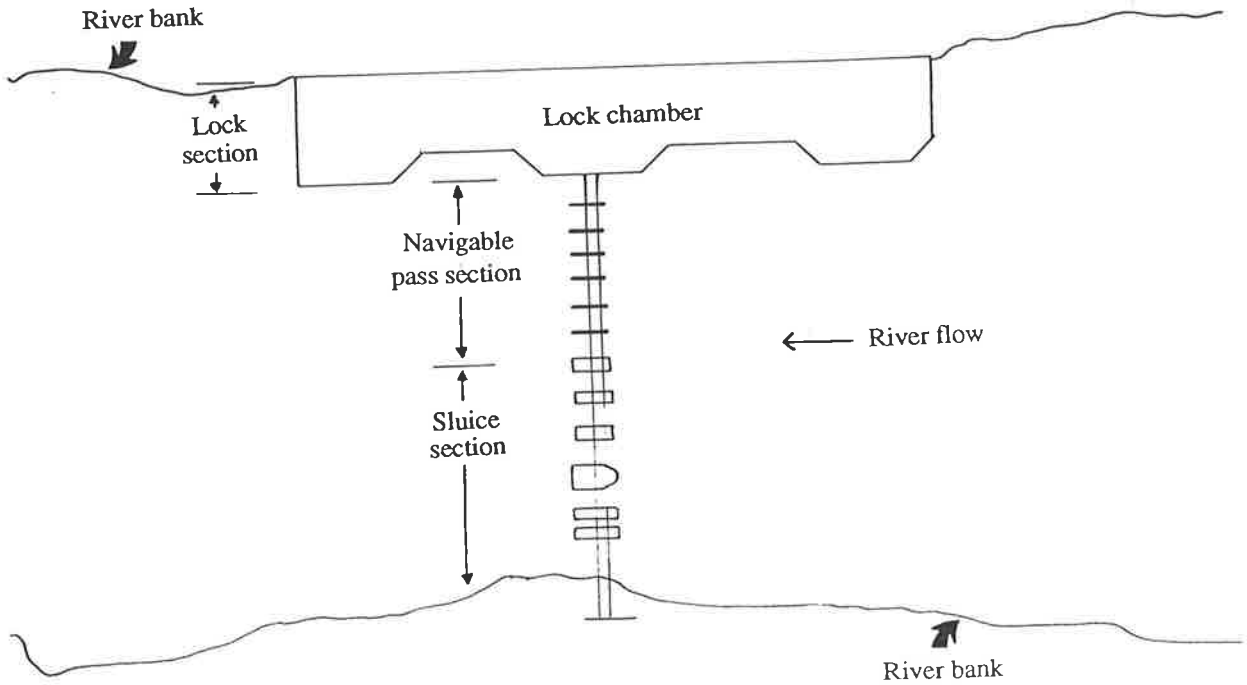


Figure 1.4 Position of Locks 1 to 10 on the lower River Murray.

Table 1.2 Some regulating structures in the Murray-Darling Basin in order of completion. Modified from Jacobs (1990)

Structure	Site	Year Completed	Storage Capacity (GL)	River
Lock & Weir 1	Blanchetown	1922	64	Murray
Lock & Weir 26	Torrumbarry	1924	38	Murray
Lock & Weir 3	Overland Corner	1925	52	Murray
Lock & Weir 9	Kulnine	1926	32	Murray
Lock & Weir 11	Mildura	1927	37	Murray
Lock & Weir 5	Renmark	1927	39	Murray
Lock & Weir 2	Waikerie	1928	43	Murray
Regulator	Lake Victoria	1928	680	Murray
Lock & Weir 4	Bookpurnong	1929	31	Murray
Lock & Weir 10	Wentworth	1929	47	Murray
Lock & Weir 6	Murtho	1930	35	Murray
Lock & Weir 7	Rufus River	1934	13	Murray
Lock & Weir 8	Wangumma	1935	24	Murray
Hume Dam	Albury	1936	1520	Murray
Lock & Weir 15	Euston	1937	38	Murray
Yarrawonga Weir	Yarrawonga	1940	120	Murray
Barrages	Murray Mouth	1940	2020	Murray
Eildon Dam	Goulburn River	1956	3390	Goulburn
Hume Dam (Extension)	Albury	1961	3040	Murray
Weir 32	Menindee Lakes	1968	1680	Darling
Dartmouth Dam	Mitta Mitta River	1979	4000	Mitta Mitta



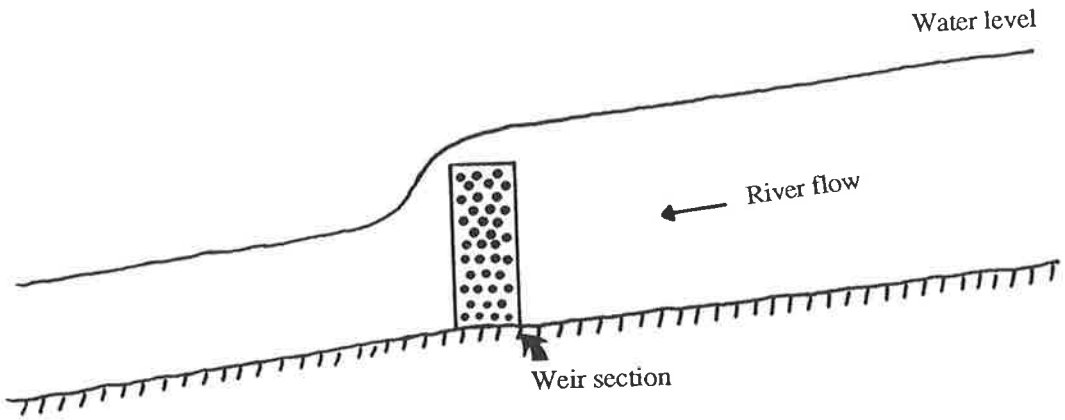


Figure 1.5 (a) Schematic representation of a Boulé weir-lock system on the lower River Murray. (b) Schematic representation of target water level and allowed tolerance upstream of a weir section, lower River Murray.
Modified from Maheshwari *et al.*, (1993).

Figure 1.6 shows water-level changes in the lower pool of Pool 2 (Overland Corner) during 1980-1989. In this period daily rises and falls of ±200 mm were commonplace and changes of more than ±500 mm occurred about once a year (Walker *et al.,* 1992). The extent and magnitude of these water-level changes decrease with the approach towards the next weir. This progression however, is not linear; magnitudes decline relatively rapidly immediately below the weir (10-15 km) and then remain static. This is partly demonstrated in Figure 1.7 via a sequence of river levels from the lower pool region of Pool 3 below Lock 4 (Bookpurnong) through the weir pool of Pool 3 to the lower pool of Pool 2 immediately below Lock 3, a distance of 85 river-km, in 1983-1986. The fluctuations apparent below Lock 4 are transferred downriver with diminishing amplitude in the approach to Lock 3. The sequence is then reset, beginning a new progression downriver towards Lock 2 (Waikerie). In this way the series of weirs on the lower River Murray creates a sequence of repeated flow gradients.

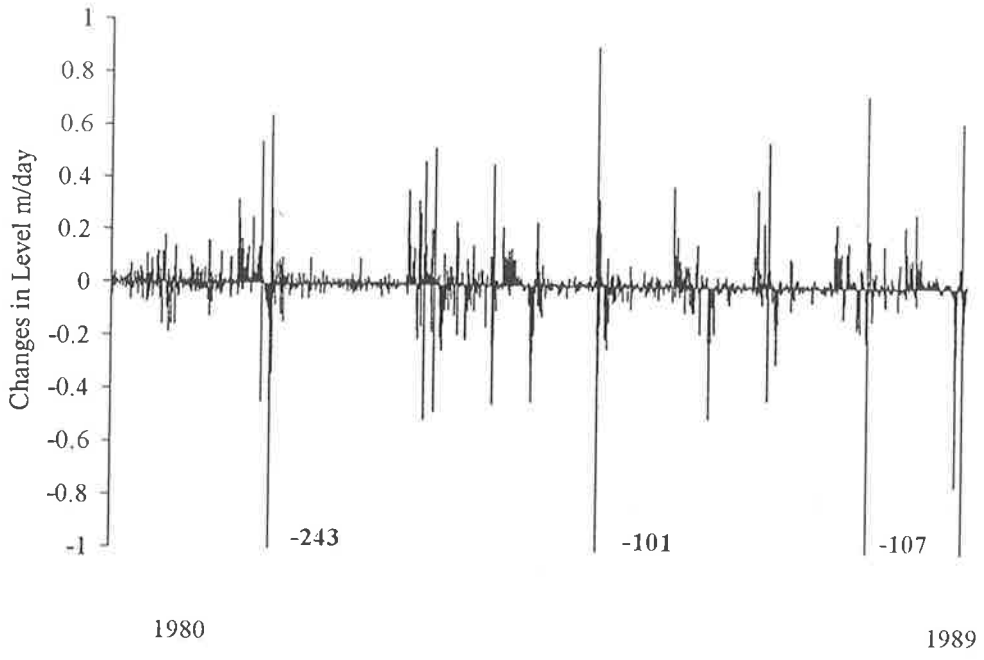


Figure 1.6 Changes in water level in the lower pool of the weir at Lock 3, Overland Corner, from January 1980 to December 1989. From Walker *et al.*, (1992).

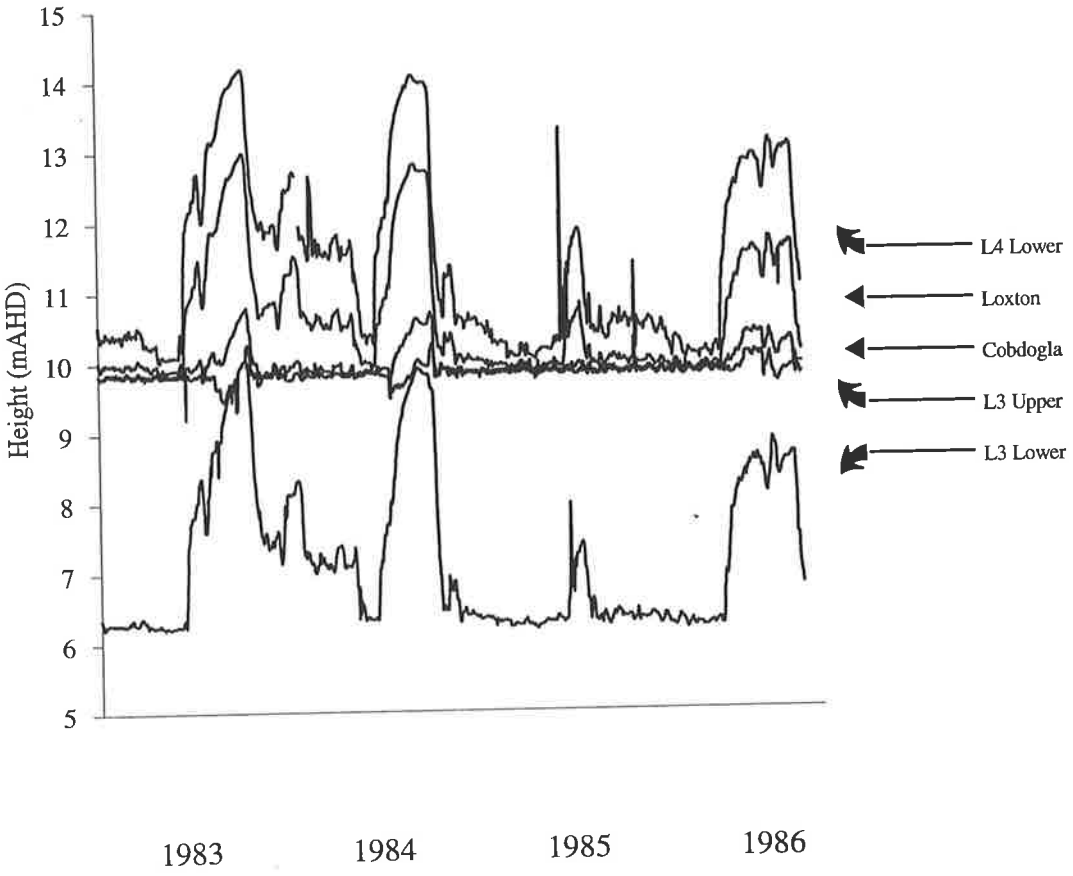


Figure 1.7 A progression along the lower River Murray showing water levels, 1983 to 1986, immediately below Lock 4 (Bookpurnong), 27km below Lock 4 (Loxton), 71 km below Lock 4 (Cobdogla) and at sites immediately above and below Lock 3, 85 km below Lock 4; modified from Walker *et al.* (1992). (AHD, Australian Height Datum)

The environmental impacts of these fluctuations are most apparent with regard to bank stability and the development of the littoral zone. Weir construction has caused the river to begin a sequence of channel adjustments, including changes in bed slope and localised erosion and deposition (Thoms and Walker, 1989; 1992). The water level fluctuations contribute incrementally to bank erosion, making some banks vulnerable to collapse following flood recession (Thoms and Walker, 1992). Fluctuations also have adverse impacts on the littoral zone, with the different regions of each weir pool (upper, middle and lower) supporting some different aquatic plants (cf. Walker *et al.*, 1994). The Secchi transparency of the lower Murray averages approximately 30 cm; thus, the river below a weir fluctuates through a depth range roughly equivalent to the photic zone (cf. Walker *et al.*, 1992).

As well as changes in short-term (daily and weekly) water level movements there have also been changes over a broader time scale, seasonally and annually. Daily river heights in the upper pool of Pool 3 and lower pool of Pool 2, Overland Corner, from 1921 until 1989, depict these changes (Figure 1.8). The completion of Lock 3 (1925) is indicated by the first temporary separation of upper and lower pool records. Prior to this, river flows display a sequence of seasonal floods followed by periods of low flow. After lock construction river levels in the upper pool do not fall below the structure height, 9 mAHD (Australian Height Datum). Levels in the lower pool are still variable, with seasonal rises and falls similar to the patterns in the unregulated river. After the completion of Lock 2 (1928) the minimum level of the lower pool of Pool 2 became constrained by Lock 2 and lower pool levels do not fall below 6 mAHD. The sequential nature of the weir construction has therefore created a minimum (base) pool level, extending from the barrages near the Murray mouth upstream to Lock 10.

The storages in the upper portion of the Murray catchment have also had an impact on water levels in the lower Murray. Hume Dam was completed in 1936 and in subsequent years there has been a decrease in the frequency of small seasonal floods in lower pool regions of the lower river (Figure 1.8). A series of droughts during the 1960's stabilised water levels in upper pool regions and further decreased the frequency of small floods in lower pool regions. The completion of Dartmouth Dam on the Mitta Mitta River in 1979 further stabilised river levels in upper and lower pools (Figure 1.8).

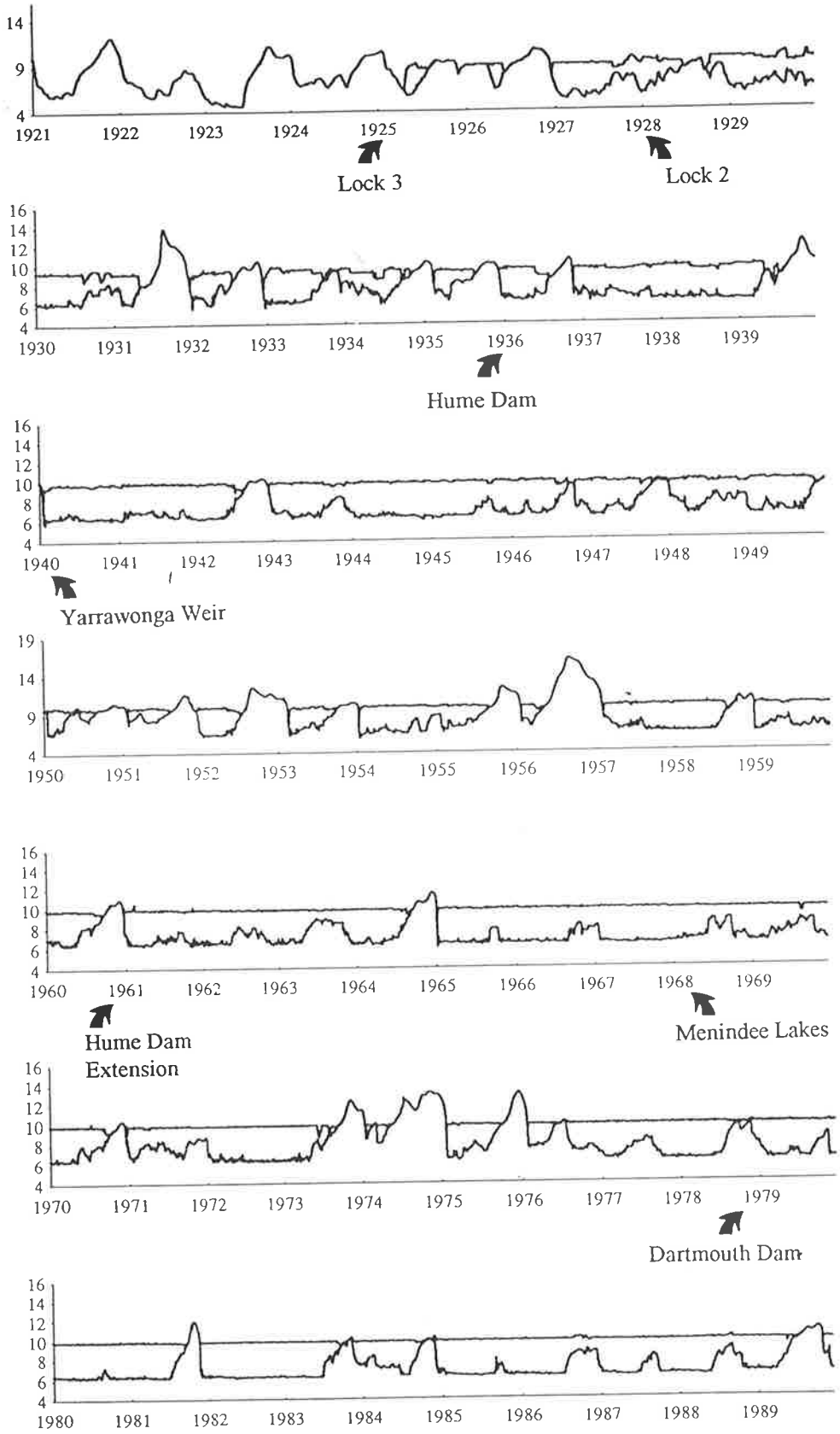


Figure 1.8 Daily river heights (mAHD) in the upper and lower pools of Lock 3, Overland Corner, from 1921 until 1989. Arrows indicate the construction of a number of storages and regulators.

Modified after Walker and Thoms (1993)

The changes between regulated and unregulated conditions have been demonstrated using simulated data from a computer model run by the MDBC (see Jacobs, 1989; Close, 1990). The comparison demonstrates the effect that levels of water use in 1988 would have had on historical flows (1892-1972) (cf. Walker and Thoms, 1993). In summary, regulation has markedly reduced the frequency of low flows up to 500 GL and increased the frequency of moderate flows (500-1500 GL). The river is now generally maintained at or near bankfull levels (Walker and Thoms, 1993).

The result of 60 years of increasing flow regulation in the lower Murray has been to rescale the frequency and amplitude of the water level changes in the littoral zone. There has been an increase in the frequency of small and erratic water level changes (±200 mm), particularly in the lower pools immediately downstream of weirs (Walker *et al.*, 1992). In contrast there has been a decrease in the frequency and amplitude of seasonal in-channel flood events (Walker and Thoms, 1993).

1.2.4 Impacts of Regulation on the Aquatic Fauna

Many of the native plants and animals of the Murray-Darling Basin have declined in both range and abundance since the commencement of flow regulation. The decline appears to have intensified with the rapid expansion of irrigated agriculture and the increase in storage capacity of dams since about 1950 (Walker and Thoms, 1993).

Prior to flow regulation at least 26 species of native fish occurred in the Murray-Darling Basin (cf. Lloyd and Walker 1986; Anderson, 1989; Cadwallader and Lawrence, 1990; Lloyd *et al.*, 1991). At the turn of the century two species, Murray cod and callop (*Macquaria ambigua*) supported a commercial fishery with catches comparable to similar fisheries on other major world rivers (cf. MDBC, 1991). Despite annual variation in commercial fish extraction, the decline in catch size of both Murray cod and callop corresponds with the rapid expansion of water storages and diversions after the 1950's (Figure 1.9; Walker and Thoms, 1993). The massive declines in fish populations initiated seasonal restrictions, catch limits and then, in 1990, a moratorium on the catching of Murray cod. Overall, catches of commercial species have dropped to the point where the Murray now has the lowest commercial fish yield per square kilometre of floodplain of any of the world's major rivers

(Walker and Thoms, 1993). A number of factors may be responsible for the decline in native fish populations, including increasing levels of pollution, interactions with exotic species (e.g. common carp) and overfishing (Cadwallader and Lawrence, 1990). However, the greatest impact appears to be related to flow regulation (Lloyd and Walker, 1986; Lloyd *et al.*, 1991).

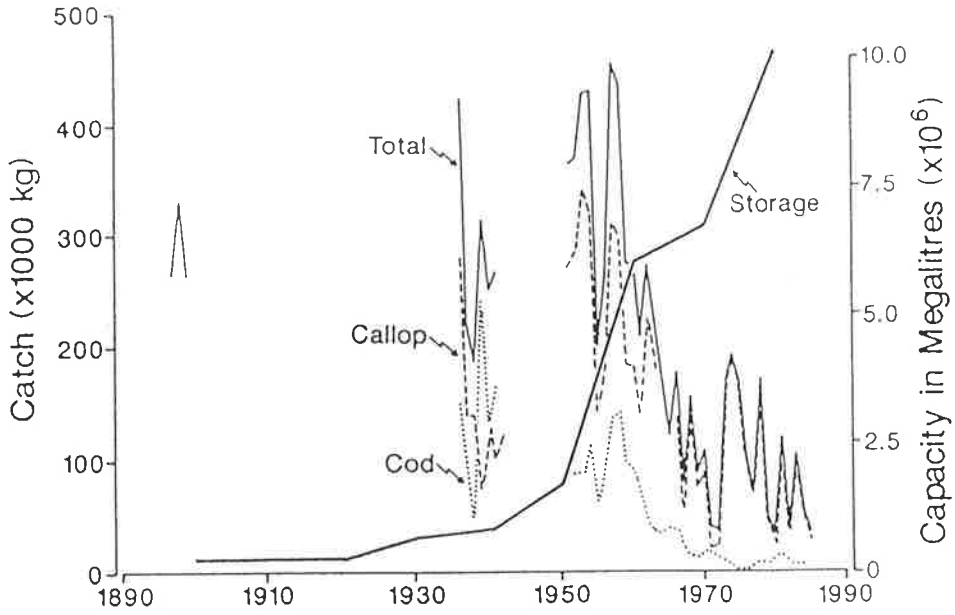


Figure 1.9 Historical catches of callop and Murray cod from the River Murray in South Australia. The expansion of flow regulation in the river system after 1950 is shown by the trend of water storage capacity.
From Walker and Thoms (1993)

Changes have been observed in the invertebrate fauna. Since flow regulation there have been shifts in the distribution and abundance of the two crayfish, the River Murray crayfish (*Euastacus armatus*) and the yabbie (*Cherax destructor*). These species differ in their habitat distribution and seasonal activity, with *E. armatus* preferentially inhabiting main channel habitats of the Murray and its major tributaries, the Murrumbidgee, Goulburn and Ovens Rivers, where water temperatures are lower and more stable and flow and oxygen levels are higher (Geddes, 1990). In comparison, *C. destructor* is a common inhabitant of billabongs and backwaters throughout the Murray-Darling Basin where environmental conditions are likely to be much less stable. Since the 1940's populations of *E. armatus* have declined to a level where the species has virtually disappeared in the South Australian section of the River Murray. The decline corresponds with habitat modification due to flow regulation (Geddes, 1990).

Flow regulation has also contributed to changes in distribution patterns of the freshwater molluscs inhabiting the Murray. The floodplain species of freshwater mussel, *Velesunio ambiguus,* has increased in abundance in the main channel of the lower river, particularly in the regions behind weirs where waters have become lentic. The river mussel (*Alathyria jacksoni*) is physiologically restricted to the deeper and faster flowing regions of the main channel (Sheldon and Walker, 1989). With the 'ponding' of the channel habitat the range of this species may have decreased (Walker, 1990). There have also been changes in the distribution and abundance of a number of freshwater gastropod taxa, including local extinction of some (Sheldon and Walker, 1993a) and a marked reduction in abundance of others (cf. Walker *et al.*, 1992). The association between flow regulation and the change in gastropod populations is discussed in more detail in Section 1.2.5.

The impact of flow regulation on other invertebrates is impossible to specify. The first surveys of freshwater invertebrates in the River Murray were not conducted until the 1970's (e.g. Walker and Hillman, 1976). Since this time there have been a number of invertebrate surveys covering particular sections of the river (e.g. Boulton and Lloyd, 1991; Goonan *et al.,* 1992), and a large survey covering the entire length of the Murray from Hume Dam to the Murray mouth (Bennison *et al.,* 1989). Each survey, however, used different collecting methods, making it difficult to compare between data sets.

A 5-year sampling program conducted by the Murray-Darling Basin Commission (Bennison *et al.*, 1989) suggests that a change has occurred in the invertebrate

assemblages of the lower Murray in association with flow regulation. The survey sampled 14 sites, covering the entire length of the River Murray, four times per year between 1980-85. The results show the macroinvertebrate fauna of the highly regulated lower Murray to be depauperate compared with the upper and middle river. This however, relates to numbers of organisms rather than taxa. The number of individuals per sample from the three sites on the lower Murray ranged from 60-207 compared with 1000-2000 in samples from upstream sites. With respect to the number of taxa, sites on the lower Murray yielded 85-104 compared with 87-139 at comparable stations upstream.

The results of this survey, however, should be treated with some caution as samples were collected using artificial substrata (plastic onion bags in plastic mesh 'boxes'). The dominant faunal group in the lower Murray is the Crustacea, including the highly mobile palaemonid and aytid shrimps. The mobility of these taxa suggests their abundance may be underestimated when sampling with artificial substrata. Despite these limitations, the survey results suggest a decrease in the abundance of invertebrates in the lower Murray, without a corresponding change in diversity. This indicates a community under stress from a physical factor rather than chemical pollution. In South Australia this factor may be related to the high levels of suspended solids in the water and the strictly regulated flow regime (Bennison *et al.*, 1989).

1.2.5 Regulation and Prosobranch Gastropods in the Murray-Darling Basin

Aquatic gastropods are abundant in rivers and small streams throughout the world (Aldridge, 1983). In large rivers they are commonly associated with littoral and floodplain habitats (Spence and Hynes, 1971). Limited historical evidence suggests freshwater gastropods were also once abundant throughout the Murray-Darling Basin. Smith (1978), Smith and Kershaw (1979) and Smith (1992) included the lower River Murray in the distributions of at least 18 species from eight families (Table 1.3), with some doubt over the precise number due to taxonomic confusion and the paucity of early collections.

Table 1.3 Gastropod species in the lower River Murray before about 1950. Based on Smith (1978), Smith and Kershaw (1979), Smith (1992) and Sheldon and Walker (1993b), with synonymies according to Smith (1992). All species except *Physa acuta* are natives.

Ancylidae	*Ferrissia petterdi* (Johnston, 1979)
	Ferrissia tasmanica (Tenison Woods, 1886)
Bithyniidae	*Gabbia australis* (Tryon, 1865)
Hydrobiidae	*Angrobia angasi* (Smith, 1882)
	Posticobia sp.
	Potamopyrgus niger (Quoy & Gaimard, 1835)
Lymnaeidae	*Austropeplea lessoni* (Deshayes, 1830)
	Austropeplea tomentosa (Pfeiffer, 1855)
	Lymnaea stagnalis (Linne, 1758)
Planorbidae	*Glyptophysa aliciae* (Reeve, 1862)
	Glyptophysa conica (Walker, 1988)
	Gyraulus meridionalis (Brazier, 1975)
	Isidorella hainesii (Tryon, 1866)
	Isidorella newcombi (Adams & Angus, 1864)
	Segnitila victoriae (Smith, 1882)
Physidae	*Physa acuta* (Draparnaud, 1805)
Thiaridae	*Thiara balonnensis* (Smith, 1991)
Viviparidae	*Notopala hanleyi* (Frauenfeld, 1864)
	Notopala sublineata (Conrad, 1850)

The families Viviparidae and Thiaridae are of most interest in the context of this study, as they were the largest of the gastropod fauna in the basin and reasonably reliable records exist for their historical distributions and abundances. Species of both families are a common component of the invertebrate fauna of large rivers throughout SE Asia, North America and Europe (cf. Stoddart, 1982; Richardson and Brown, 1989). Most are large, long-lived, and can reach high densities in some systems (Jokinen *et al.*, 1982; Richardson and Brown, 1989). Their feeding habits are variable but most are detritivores (Richardson and Brown, 1989). In both the Cooper Creek and the Diamantina River (Lake Eyre Basin, north east South Australia) taxa from both families form a dominant portion of the total invertebrate biomass (Sheldon, unpublished data).

An examination of shell morphometry in specimens of Australian Viviparidae held in the Australian Museum, Sydney, suggests that historically two species of *Notopala* (Gastropoda: Prosobranchia: Viviparidae) occurred in the Murray-Darling Basin.

Notopala sublineata was distributed throughout the western region of the Basin, including the Darling River and the lower River Murray below its confluence with the Murrumbidgee. This taxon is also common in the Lake Eyre Basin. The second species, *Notopala hanleyi*, appears to have been restricted to the lower River Murray being apparently absent from the Darling River and the Lake Eyre Basin (Sheldon and Walker, 1993b; Figure 1.10). *Thiara balonnensis* is a cosmopolitan species being distributed over a wide geographical range in Australia (Stoddart, 1985).

Historical Evidence

The contents of aboriginal shell middens (100 years to several thousand years of age), found along the banks of rivers in the Murray-Darling Basin, provide an indication of the historical presence, and possible distribution, of these gastropod taxa (Walker, 1981). These middens are formed from discarded occupational debris such as the remains of mollusc shells, crustacean exoskeletons, vertebrate bones and ash from camp fires (Barbetti and Allen, 1972; Parker, 1989 unpubl. Hons. Thesis). Although not an exact representation of faunal assemblages present in the ecosystem, as mainly the larger and more easily obtained edible species were collected (Barbetti and Allen, 1972), they do give an indication of the species present at the time the midden was formed. In the middens of the lower Murray the most common shells are of the freshwater mussels, *Alathyria jacksoni* and *Velesunio ambiguus*, and the shells of the prosobranch gastropods *N. hanleyi, N. sublineata* and *T. balonnensis* (Parker, 1989, unpubl. Hons Thesis).

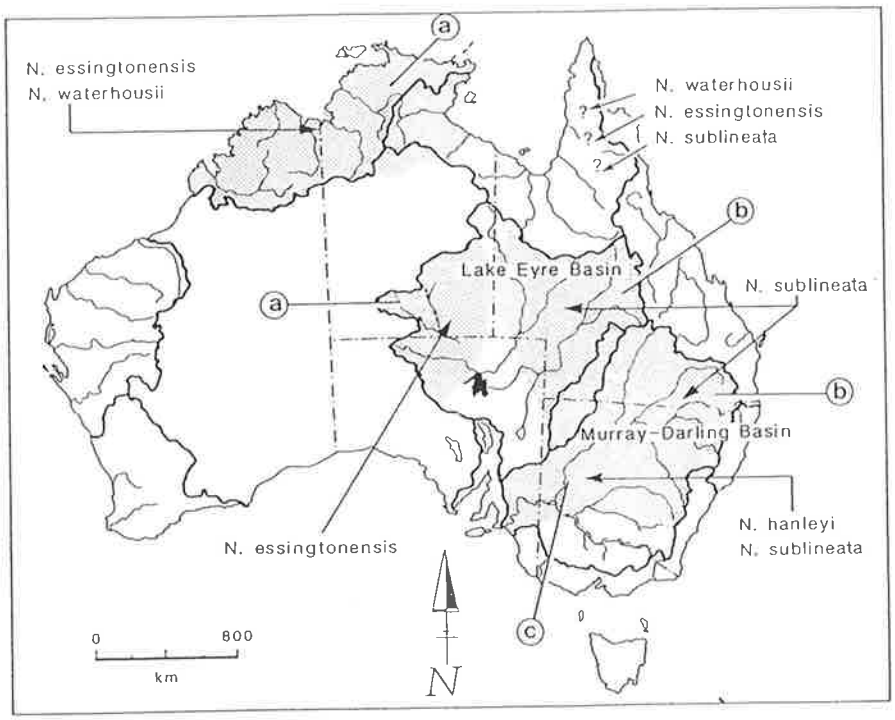


Figure 1.10 Geographical distribution of *Notopala* species in Australia; "a", *N. waterhousii* and *N. essingtonensis*; "b", *N. sublineata*; "c", *N. sublineata* and *N. hanleyi*. From Sheldon and Walker (1993)

Table 1.4 Published records of parasitologists in the *Transactions of the Royal Society of South Australia*, 1938-59 indicating the numbers of snails found at sites along the lower Murray during field visits between 1937 and 1958. Synonymies according to Smith (1992).

Reference	Location	Species	Synonymies
Johnston and Cleland (1938) **62**:127-131	Tailem Bend Swan Reach	*Ancylus australicus* 343 439	*Ferrissia petterdi* (Johnson 1879)
Johnston and Simpson (1939) **63**:63-68	Lower Murray Swan Reach	*Ancylus australicus* (large numbers) *Plotiopsis tatei* 899	*Ferrissia petterdi* (Johnson 1879) *Thiara balonnensis* (Smith 1991)
Johnston and Angel (1939) **63**:200-203	Tailem Bend	*Planorbis isingi* 2488	*Gyraulus isingi* (Cotton & Godfrey 1932)
Johnston and Angel (1941) **65**:140-144	Tailem Bend & Swan Reach	*Lymnaea lessoni* 680	*Austropeplea lessoni* (Deshayes 1830)
Johnston and Angel (1941) **65**:285-291	Tailem Bend	*Amerianna pyramidata* 3163	*Glyptophysa gibbosa* (Gould 1846)
Johnston and Angel (1941) **65**:317-322	Tailem Bend	*A. pyramidata* and *A. pectorosa* 4506	*G. gibbosa* and *G. pectorosa* (Gould 1850)
Johnston and Angel (1942) **66**:50-59	Tailem Bend	*Plotiopsis tatei* 954	*Thiara balonnensis* (Smith 1991)
Johnston and Angel (1942) **66**:119-123	Tailem Bend	*Amerianna* spp. 12482	*Glyptophysa* spp.
Johnston and Simpson (1944) **68**:125-132	Tailem Bend	*Lymnaea lessoni* 3030	*Austropeplea lessoni* (Deshayes 1830)
Johnston and Beckwith (1956) **69**:222-242	Tailem Bend to Morgan	*Plotiopsis tatei* 7592	*Thiara balonnensis* (Smith 1991)

Due to their conspicuous size, both *Notopala* species and *T. balonnensis* were frequently collected by early natural historians. The South Australian malacologist, Bernard Cotton, described *Notopala* as occurring "commonly in the marginal mud of slow rivers and in lakes" (Cotton 1935: page 96). Published records of South Australian parasitologists (T.H. Johnson and colleagues) between 1930-1960 refer to the collection of thousands of specimens of gastropods from the families Ancylidae, Planorbidae, Lymnaeidae, Thiaridae and Viviparidae (Table 1.4) from riparian swamplands along the lower River Murray (e.g. Johnston and Cleland, 1938; Johnston and Angel, 1939, 1941, 1942, 1951, Johnston and Beckwith, 1945, 1947;

Johnston and Muirhead, 1949; Angel, 1959). There are specific references to *Notopala* spp. and *T. balonnensis* in the *Transactions of the Royal Society of South Australia* (see Johnston and Beckwith, 1945, page 229; and Johnston and Beckwith, 1947, page 328) with mention of the collection of 4,677 specimens of *Notopala* and 7,592 specimens of *T. balonnensis* from the Murray between Renmark and Tailem Bend between 1937 and 1947. There is evidence to suggest, therefore, that both taxa were abundant and easily collected from the littoral zone of the lower River Murray at least until the late 1940's.

Recent Collections

In comparison with the above records recent invertebrate collections from both riverine and floodplain environments of the lower Murray suggest that most gastropod species have either declined sharply in range and abundance or disappeared completely (Thompson, 1986; Bennison *et al.*, 1989; Lloyd *et al.*, 1990; Boulton and Lloyd, 1991). Since the 1980s there have been occasional records of *Glyptophysa conica*, *Gyraulus meridionalis*, *Posticobia* sp., *T. balonnensis* and *Notopala* spp. (Walker *et al.*, 1992), but only *Ferrissia petterdi* and the introduced *Physa acuta* have been collected regularly.

The extent of gastropod population decline in the lower river is evident in the results of the Murray-Darling Basin Commission survey (1980-85) (Bennison *et al.*, 1989). During this period only two specimens of *Notopala* spp. were collected, one from Murray Bridge in September 1982 and the other from Merbein in November 1982. Five specimens of *T. balonnensis* were collected from Morgan in November 1982. In a survey of the macroinvertebrates from aquatic habitats on the Chowilla floodplain, lower Murray, Boulton and Lloyd (1991) collected seven species (Table 1.5), with no records of *Notopala* spp. or *T. balonnensis*. A survey of the floodplain wetlands between Chowilla and Morgan (Goonan *et al.*, 1992) listed five of the taxa previously recorded at Chowilla, again specimens of *Notopala* spp. or *T. balonnensis* were not collected (Table 1.5).

Table 1.5 Gastropod taxa collected in three recent surveys of habitats on the lower River Murray floodplain.

Species	Bennison *et al.* (1989)	Boulton and Lloyd (1991)	Goonan *et al.* (1993)
Ferrissia petterdi	*	*	*
Ferrissia tasmanica	*	*	
Gabbia australis			
Angrobia angasi			
Posticobia sp.			
Potamopyrgus niger	*	*	*
Austropeplea lessoni		*	
Austropeplea tomentosa			
Lymnaea stagnalis			
Glyptophysa aliciae	*	*	
Glyptophysa conica			
Gyraulus meridionalis	*		
Isidorella hainesii	*		*
Isidorella newcombi	*	*	
Segnitila victoriae		*	
Physa acuta	*	*	*
Thiara balonnensis	*		
Notopala hanleyi			
Notopala sublineata	?		

These recent collections suggest that *Notopala* spp. and *T. balonnensis* are rare and perhaps extinct in the littoral zone of the lower Murray. One population of *N. hanleyi* was recently discovered in an irrigation pipeline from the Murray in the South Australian Riverland (Sheldon and Walker, 1993a). This population, along with the reports of other gastropods *G. conica* and *T. balonnensis* and the bivalve *Corbiculina australis* (Deshayes) in other pipelines (Woolford, 1984, unpubl. Hons. Thesis), shows that the irrigation pipelines are a refuge for "endangered" taxa. Although little is known of the biology of the pipeline gastropods, it is likely that the wetted inner surfaces of the pipes provide an extensive area for microbial production and organic accumulations that are potentially food (cf. Aldridge, 1983; Dudgeon and Yipp, 1983; Thomas, 1990).

Reasons for the Decline

It is interesting to speculate over why gastropods are able to survive in the pipelines and not in the river. Snails other than *Notopala* spp., including *T. balonnensis*, still occur in the Murray above its junction with the Darling (Bennison *et al.*, 1989). This suggests that the decline in the lower river is due to local factors, or to factors intensified by accumulation from upstream. Increasing agricultural and urban influences in the Murray-Darling Basin have caused a decline in water quality

(Mackay *et al.*, 1988) that may have affected gastropod populations. Salinity increases downstream in the Murray, partly as a byproduct of irrigation, but mean levels are still well below the peaks recorded before regulation (Mackay *et al.*, 1988). Adult *G. conica* and *T. balonnensis* tolerate salinities well above those prevailing in the river (Evans, 1981 unpubl. Hons. Thesis), although juveniles may be less tolerant. Water quality is therefore unlikely to be a major cause of gastropod decline, particularly as the populations surviving in the pipelines are generally exposed to water drawn from the river at times of lowest flow (summer-autumn) and therefore poorest water quality. The abundant pipeline populations are exposed to virtually the entire range of agricultural and urban effluent in the river water.

Turbidities in the Murray may have increased, although there are few supporting data (Mackay *et al.*, 1988). The practice of artificially increasing the proportion of Darling flows in the lower Murray commenced in 1968 and must have contributed to a change in the overall turbidity regime of the lower river, as the Darling is strikingly more turbid than the Murray (Bennison *et al.*, 1989; Walker *et al.*, 1992). Further, cores demonstrate marked changes in the character of the river-bed sediment with the advent of regulation, including a 30% decrease in median grain size (Thoms and Walker, 1992). Increased levels of turbidity would have reduced light penetration in the littoral zone, restricting plant growth and hence food resources and habitat for snails. Silt accumulation may also decrease the nutritive value of periphyton, the main food for gastropods. It is unlikely that turbidity has caused extinction of the gastropods, however, as photic depths in both Cooper Creek and the Daimantina River, where both taxa are abundant, are less than the average levels in the Murray.

Common carp *(Cyprinus carpio* L.) became widespread in the Murray in the early 1970s and probably have had adverse affects on many aquatic plant and animal species, including the gastropods (cf. Fletcher *et al.*, 1985). It seems unlikely that they are a sole factor in gastropod decline, as they cohabit with snail populations in the middle reaches of the Murray. Nevertheless, carp are implicated in the degradation of wetlands and must have contributed significantly to the destruction of snail habitats.

Flow regulation has had a catastrophic impact on the native fauna and flora (e.g. Walker and Thoms, 1992), and is undoubtedly a factor in the decline of the snails. Perhaps the large prosobranch gastropods were unable to respond to the erratic short-term (daily-weekly) water-level variations associated with weir operations in the lower Murray (cf. Section 1.2.3). Littoral regions subjected to artificial water level

changes in other regulated rivers support lower numbers of invertebrate taxa and individuals than corresponding unregulated areas (cf. Fisher and LaVoy, 1972; Hunt and Jones, 1972; Brusven *et al.* 1974, Kaster and Jacobi, 1978), with slow moving species becoming stranded and unable to survive the sudden fluctuations (cf. Corrarino and Brusven, 1983).

Alternatively, changes in the movement of the littoral zone may have modified or eliminated gastropod habitats or resources. In the regulated lower Murray seasonal floods have been limited by changes in the magnitude and frequency of monthly and annual flows, wetland areas are either permanently flooded or isolated from the river for abnormally long periods, and stable water levels occur along the entire length of the lower Murray. In rivers where stable depths are maintained for extended periods, benthic algae are known to dominate the periphytic community (cf. Lowe, 1979; Petts, 1984; Biggs and Price, 1987) compared with a heterotrophic microbial film in systems where light penetration may be limited due to moving water levels (cf. Edwards and Meyer, 1987; Couch and Meyer, 1992).

1.3 THESIS PLAN

This thesis examines the ecology of the littoral zone of the lower River Murray with reference to the impacts of flow regulation. It has the following aims:

- To define the spatial and temporal dimensions of the lotic littoral zone in large rivers, review the ecological features of the littoral zone and predict changes in structure and function associated with flow regulation (Chapter 2).

- To examine the spatial patterns in the littoral zone using macroinvertebrate assemblages from habitats on the lower Murray and the Darling River (Chapter 3).

- To explore the predictions concerning changes associated with flow regulation using macroinvertebrate assemblages in the lower Murray and the two gastropod taxa once common in the lower Murray, *Notopala* spp. and *Thiara balonnensis*. This will be achieved by addressing the following specific questions:
    i. Do low-level weirs modify the spatial patterns of macroinvertebrate assemblages in the main channel habitat of the lower Murray? (Chapter 4)
    ii. Are the gastropods, *Notopala* spp. and *Thiara balonnensis* able to respond to sudden water level changes with magnitudes comparable to those common below the low-level weirs on the lower Murray? (Chapter 5)
    iii. What is the diet of natural populations of *Notopala* spp. and *T. balonnensis* and could this be affected by flow regulation? (Chapter 6)
    iv. How has flow regulation changed the nature of food resources in the lower Murray? (Chapter 7)

- To utilise the information on responses of macroinvertebrate assemblages and aquatic gastropods to flow regulation in the lower Murray to predict the impacts of flow regulation on littoral processes in large rivers (Chapter 8).

- To provide recommendations for the management of water levels in the lower River Murray and broad strategies for dryland rivers in general (Chapter 9).

1.4 Papers Bound in Support

A number of papers is bound in support of this thesis:

- Walker, K.F., M.C. Thoms and F. Sheldon (1992) Effects of weirs on the littoral environment of the River Murray, South Australia, In *River Conservation and Management* (Eds: P.J. Boon, P. Calow and G.E. Petts), pp. 271-292, John Wiley and Sons.

- Sheldon, F. and K.F. Walker (1993) Pipelines as a refuge for freshwater snails, *Regulated Rivers: Research and Management* **8:**295-299.

- Sheldon, F. and K.F. Walker (1993) Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae), *Journal of the Malacological Society of Australia* **14:** 59-71

- Walker, K.F. and F. Sheldon (1994) The ecological importance of floodplains, In *Ecotones at the river basin scale-global land/water interactions*: proceedings of Ecotones Regional Workshop, Barmera, South Australia, 12-15 October 1992. (Ed: A. Jensen), pp. 21-27, UNESCO Ecotones Research Project, 'Role of land/inland water ecotones in landscape management and restoration'.

- Walker, K.F., A.J. Boulton, M.C. Thoms and F. Sheldon (1994) Effects of water-level changes induced by weirs on the distribution of littoral plants along the River Murray, South Australia, *Australian Journal of Marine and Freshwater Research*. Submitted.

- Puckridge, J.T., F. Sheldon, A.J. Boulton and K.F. Walker (1994) Flow variability and the Flood Pulse Concept, Unpublished MS.

Lower River Murray, South Australia

Chapter 2

Impacts of Flow Regulation on the Littoral: A Review

2.1. INTRODUCTION

Lotic systems range from small streams in headwater catchments to the largest expanses of tropical rivers such as the Amazon. One way of categorising rivers according to size is *stream order* (Horton, 1947). Thus, first-order streams are the terminal "twigs" of drainage systems and have no tributaries; they combine to form second order streams, which, when joined with either first or second-order tributaries, form third-order systems, and so on. In this thesis, references to "large rivers" apply to systems of fifth-order or more, with fringing floodplains. Examples of large rivers include the Mississippi and Colorado rivers in the USA, the Rhine, Rhône and Danube in Europe, the Zaïre and Orange-Vaal in Africa and the Murray and Darling in Australia.

Rivers are often depicted as corridors with distinct lateral boundaries meandering through a terrestrial landscape; this highlights longitudinal linkages but conceals lateral, vertical and temporal linkages (Mulholland, 1981; Ward, 1989a; Boon, 1992; Walker *et al.,* 1992). Rivers normally flow in well-defined channels, but during periods of high discharge wide floodplain areas may be inundated (Junk *et al.,* 1989). A large river is therefore a network of more-or-less interconnected water bodies existing at various spatial (lateral, longitudinal, vertical) and temporal scales (cf. Amoros and Roux, 1988; Puckridge *et al.,* unpublished MS). The resulting patchwork, or mosaic, influences the distributions, interactions and adaptations of riverine organisms (Scarsbrook and Townsend, 1993).

Within a river are habitats, like the main-channel and floodplain, characterised by features such as substratum type, vegetation and hydrology (Palmer *et al.,* 1993a, 1993b). The floodplain has been described as the *"area of low lying land that is subject to inundation by the lateral overflow of waters from the river or lake with which it is associated"* (Junk *et al.,* 1989, page 112). This reflects a geomorphic distinction between the main-channel and the floodplain. Floodplain rivers are composed of different geomorphic surfaces, including *active channels* carrying channelised streamflow, and *floodplains* created from fluvial deposition of mainstem sediments (Gregory *et al.,* 1991). From an ecological perspective, however, the

critical distinction between the floodplain and other river habitats should be related to patterns of inundation.

Unlike small rivers and streams, where *longitudinal* linkages dominate nutrient and organic matter exchange (cf. Vannote *et al.,* 1980; Newbold *et al.,* 1982), in the lower reaches of large rivers *lateral* (e.g. main-channel - floodplain) and *temporal* (e.g. season-season or pulse-pulse) linkages are significant (MacArthur, 1988; Junk *et al.,* 1989). This difference may reflect the low gradients of lowland rivers, where longitudinal changes in abiotic factors such as temperature, conductivity, substrate type and oxygen concentration are relatively minor. Major changes in these factors occur laterally, between floodplain and channel, and temporally, between periods of flood and drought. In pristine rivers of temperate and tropical regions, the bulk of riverine biomass is derived from production within the floodplain (Junk *et al.,* 1989). The organic matter that accumulates in the main channel, and provides food and habitat for many lotic animals, is also derived from the floodplain (cf. Cuffney, 1988). The periodic flooding of large rivers connects main channel and floodplain habitats.

The floodplain may be viewed as the edge or boundary of the river, extending from the permanent aquatic region of the channel to the permanent terrestrial region of the surrounding landscape. The riverine littoral zone (cf. Fisher and LaVoy, 1972; Nilsson, 1984; Walker *et al.,* 1992) is essentially the edge of the aquatic phase that periodically moves across this floodplain, and is an example of an ecological boundary. Compared with the open waters of the main channel, the riverine littoral zone provides a region of decreased water velocity, comparatively stable sediments and increased microhabitat complexity in the form of rocks, snags, vegetation and different substrata (cf. Walker *et al.,* 1992). The littoral boundary is likely to be the most productive and diverse region of the river system (cf. Naiman *et al.,* 1988; Pinay *et al.,* 1990).

The littoral zone of large rivers is not static; rather, it changes over various scales in space and time (Décamps and Naiman, 1990). In response to a flood pulse it becomes the "edge of the aquatic environment that traverses the floodplain", or the *moving* littoral (cf. Junk *et al.,* 1989). This review examines the lotic littoral zone in large dryland rivers. It asks:

- what are the spatial and temporal dimensions of the littoral zone in large rivers?
- what features of dryland rivers make the littoral zone a key habitat?
- what roles does the littoral zone play in ecological processes?

- are present concepts in lotic ecology adequate for explaining littoral processes in large rivers?
- how is the littoral zone likely to be affected by flow regulation?

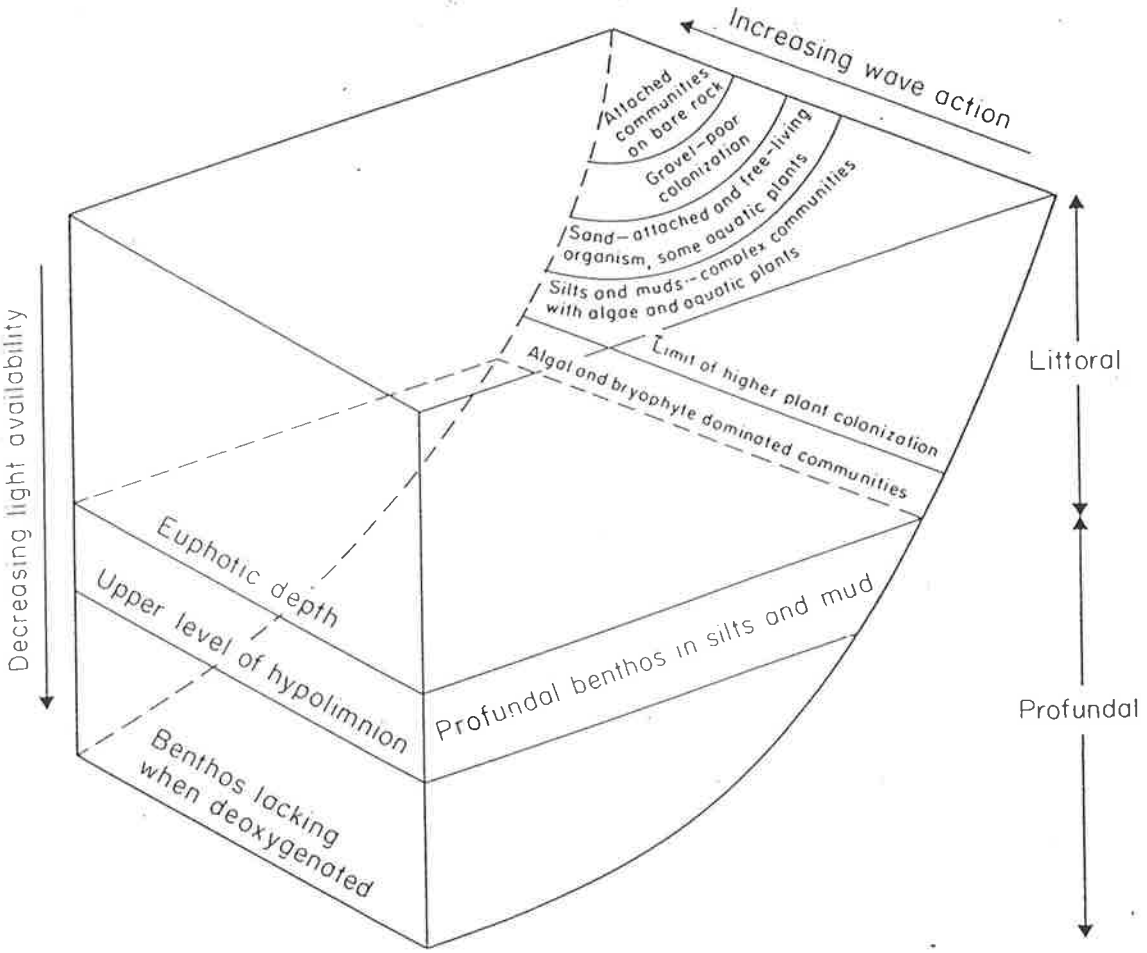


Figure 2.1 A typical pictorial representation of the position of the littoral zone in a freshwater system. From Moss (1988).

2.2 Ecological Aspects of The Riverine Littoral Zone

2.2.1 The Littoral Zone of a Floodplain River System

The term *littoral* usually is associated with lakes or coastal marine environments, being the band of water that extends from the shoreline to the depth where aquatic plants disappear (Figure 2.1) (Cole, 1983; Moss, 1988). The extent of the littoral zone depends on the flooding and drying regime as well as on the configurations of shore terrace and adjacent terrestrial areas, on water level fluctuations and on depositional and erosional processes (Pieczynska, 1990). In marine systems the littoral zone is essentially equivalent to the intertidal region, with its spatial (lateral) extent dependent upon the physical structure of the shoreline. Temporal movements of the water's edge across the marine littoral are regular, due to tides, and many organisms show specific adaptations to this periodic movement.

Lakes also have a distinct littoral zone that provides diverse habitats for animals and plants and acts as a trap for allochthonous and autochthonous organic matter (Howard-Williams and Lenton, 1975). In these systems the complexity of the littoral zone, or shoreline, may be described mathematically by an index of shoreline development (e.g. Hutchinson, 1957). This relates lake shoreline length to the circumference of a circle with the same area as the lake. An irregular shoreline, with a high development index, is conducive to increased diversity and trophic status (Cole, 1983; Ryder and Pesendorfer, 1989). The spatial dimension of the lentic littoral depends on the configuration of the shoreline as well as on seasonal water level movements (Pieczynska, 1990). In lakes, such as Lake Windermere (UK), where seasonal floods cause changes in the level of the littoral zone, littoral communities have been shown to follow the rise and fall of the water level (Moon, 1935).

The index of shoreline development essentially describes the "wetted perimeter" of a lake. These ideas can be extended to lotic systems: the littoral zone of a floodplain river is the wetted perimeter, or edge of the aquatic environment, that traverses the channel and floodplain in response to a flood-pulse (Figure 2.2). Depending upon the water level, the wetted perimeter will include habitats within the channel and on the floodplain (cf. Sedell *et al.,* 1990). The physical complexity of the littoral zone will also reflect the spatial scale at which it is examined.

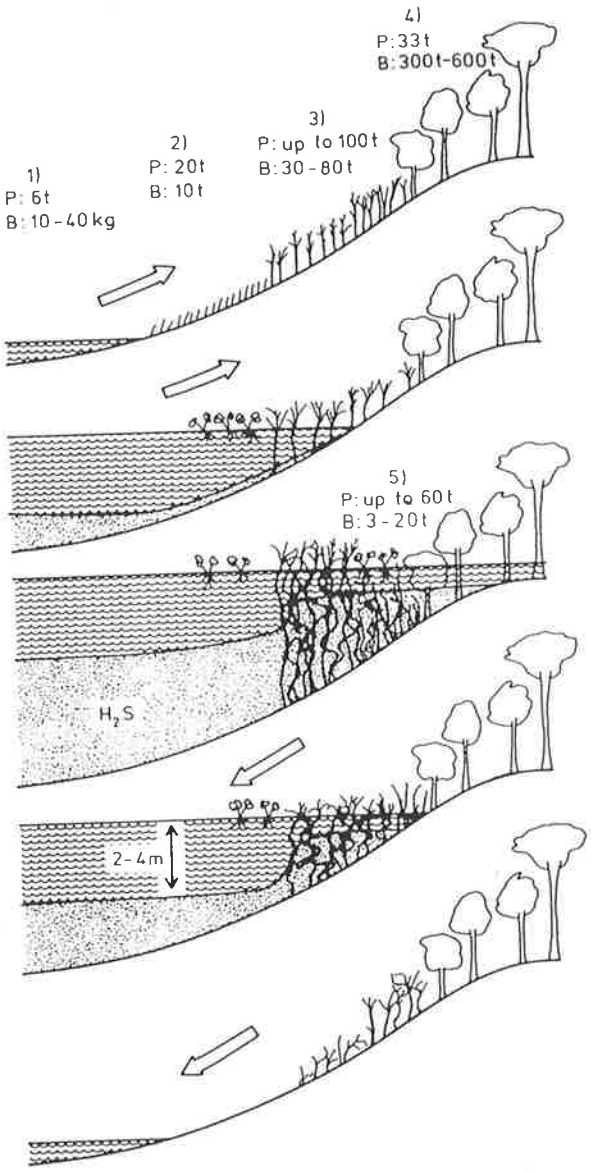


Figure 2.2 The moving phase of the riverine littoral zone. From Junk *et al.* (1989).

Biggs and Gerbeaux (1993) highlight the need to take scale into account when viewing lotic ecosystem processes. They suggest that the macro-scale is fundamental to long-term community structure, and micro-scale features provide the local conditions under which communities develop. The main processes creating spatial heterogeneity in riverine littoral zones are related to the erosion, accumulation and reworking of sediment along the fluvial corridor (Salo, 1990).

If the littoral zone of a floodplain river includes the "edge" of all habitats then its complexity, structure and function may be described by hierarchical classification (cf. Naiman *et al.,* 1988; Kotliar and Weins, 1990; Gosz, 1993). Using a hierarchical approach (Urban *et al.,* 1987; Kotliar and Weins, 1990), the spatial structure of the littoral zone can be defined for a snapshot in time (Figure 2.3). *Macrohabitats* reflect morphodynamic zones (*sensu* Zwolinski, 1992) on the floodplain; these are determined by flow energy and patterns of sedimentation, or macroprocesses (Salo, 1990). The littoral zone also exists at the *mesohabitat* level as the edge region of backwaters, billabongs, anabranches and the main channel or as inundated low-lying land during overbank flows (*sensu* macrohabitats: Lloyd and Walker, 1986; Boulton and Lloyd, 1991; mesohabitats: Puckridge *et al.,* unpublished MS). Mesohabitats are created by geomorphic mesoform processes (Salo, 1990) and correspond to "segment systems" (Poff and Ward, 1990) and "channel units" (Sedell *et al.,* 1990).

Within mesohabitats the littoral zone is composed of *microhabitats* (*sensu* Lloyd and Walker, 1986; Boulton and Lloyd, 1991; Puckridge *et al.,* unpublished MS) such as snags (fallen timber), emergent vegetation, submerged vegetation and substrata. Microhabitats are created by geomorphic microprocesses (Salo, 1990), and correspond to "microhabitat systems" (Poff and Ward, 1990) and "particles" (Sedell *et al.,* 1990). Although microform processes are the smallest geomorphic process identified by Salo (1990), the ecological hierarchy of the littoral zone will continue. Within each microhabitat smaller patches relate to refuges and food resources and, within these, patches reflect nutrient release, and so on.

The recognition of these habitats describes the physical character of the littoral zone at only one point in time and relies on geomorphic features. The littoral zone also has a hydrological aspect, the flood pulse, which gives it a temporal dimension. The complexity and structure of the littoral zone changes in response to a flood pulse. As the littoral edge rises within the channel microhabitat features will change, new patches of vegetation appear, snags become inundated while others become increasingly submerged within the channel.

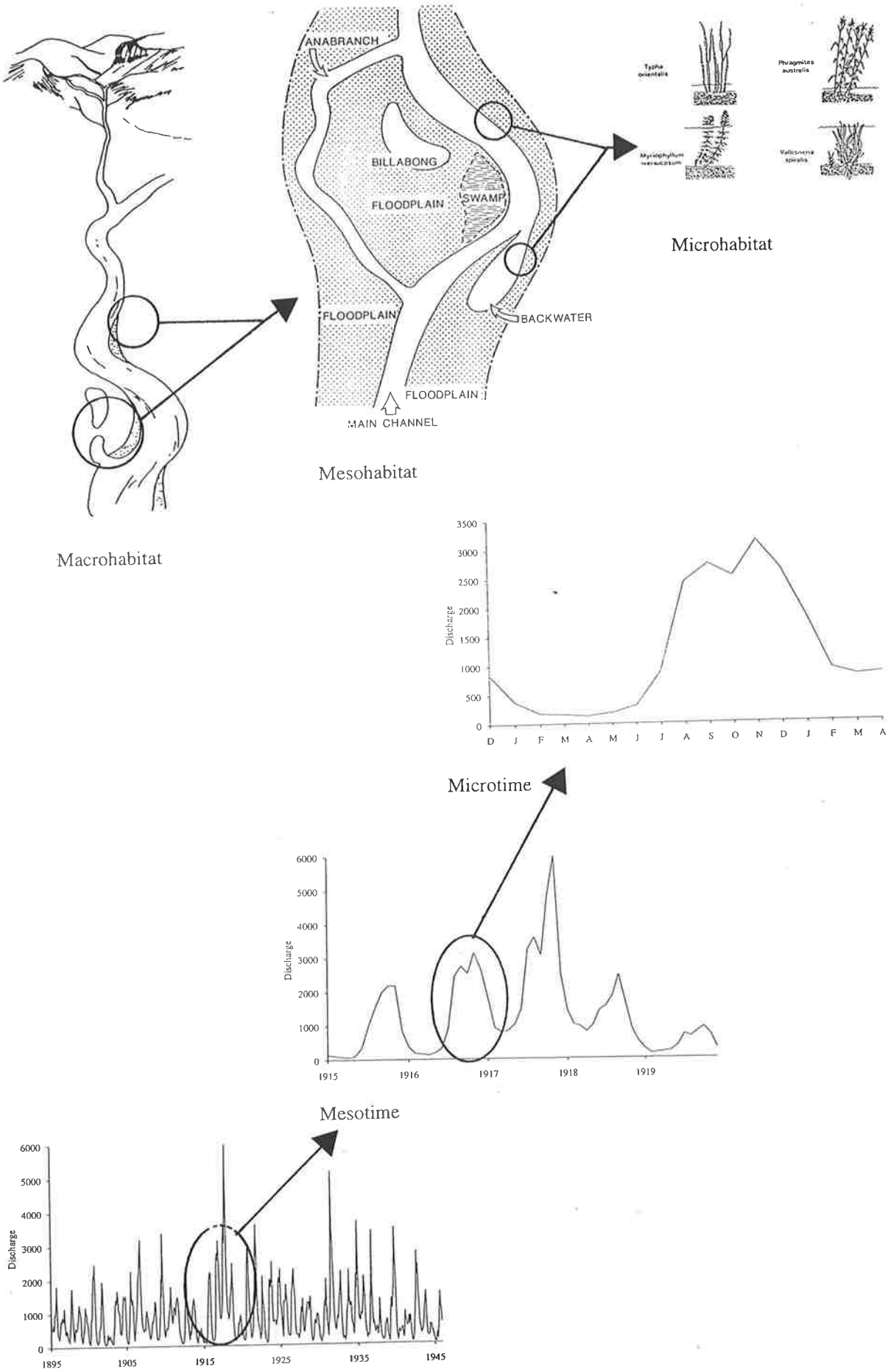


Figure 2.3 Spatial and temporal scales for a large floodplain river.

At various stages within a flood-pulse mesohabitat features will also take on different forms. During periods of low flow the littoral zone is confined to the permanent aquatic habitats of the channel and permanent floodplain lakes with the floodplain essentially dry. As water levels rise in response to flooding the littoral zone is most complex, including the wetted perimeter of different mesohabitats and their respective microhabitats. As water levels continue to rise there is increased inundation of the floodplain and the littoral may lose some mesohabitat complexity, retaining microhabitat structure through the inundation of floodplain vegetation.

In the same way littoral zone structure is developed in space it may also be developed through time by focussing on the flow regime (cf. Pinay *et al.,* 1990; Puckridge *et al.,* unpublished MS). Littoral zone processes may be affected through time at a number of scales (Figure 2.3). A *macrotime* scale refers to the long-term flood/drought cycles controlled by climatic fluctuations and common to many large river systems (cf. Molles *et al.,* 1992). A *mesotime* scale covers periods of both moderate floods and droughts (in dryland rivers this would be in the range of 5 to 10 years). *Microtime* scales refer to the annual or seasonal flow events that are necessary for maintaining ecological processes such as nutrient cycling, providing breeding cues and enhancing juvenile recruitment (Lloyd *et al.,* 1991). In many temperate rivers this time scale would refer to the annual overbank flood, whereas in dryland rivers it may refer to any flood pulse, within channel as well as overbank flow events. In some cases it may be appropriate to consider time scales at finer resolutions, such as weeks or even days, particularly if the river system has been subject to anthropogenic disturbances.

The spatial and temporal habitat patches, however, do not exist in isolation; they exhibit strong linkages both within a scale (e.g. mesohabitat) and between subsequent scales (e.g. mesohabitat-microhabitat) (Kotliar and Weins, 1990). Thus, although the littoral is patchy at any point in time, and recognition of this allows its instantaneous structure to be described, the patches form part of a spatial and temporal continuum. For reasons explained above, flow is a vital factor that maintains patchiness in the littoral zone of large rivers (Welcomme, 1977; Junk *et al.,* 1989; MacArthur, 1989; Poff and Ward, 1990).

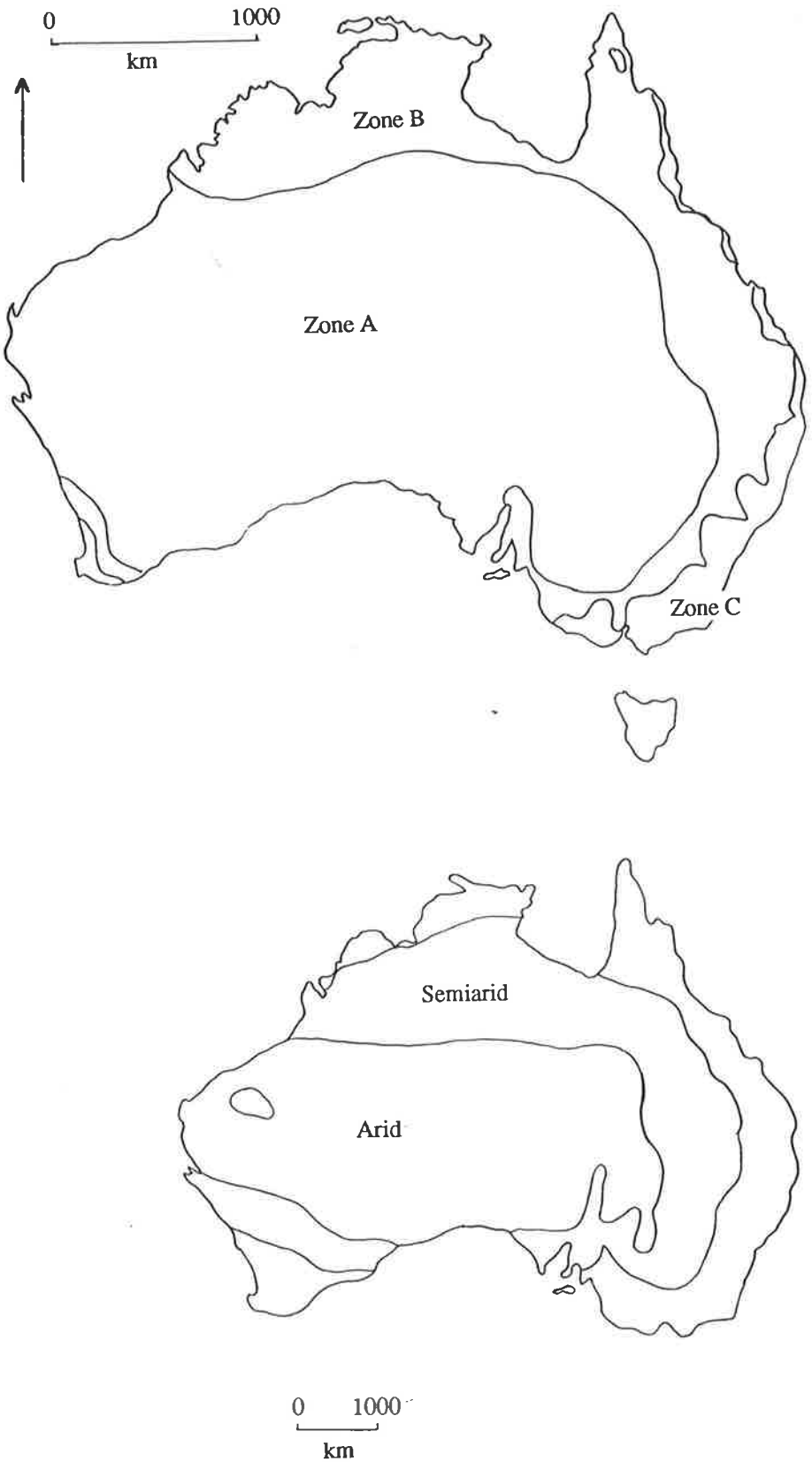


Figure 2.4 (a) Zones depicting median annual rainfall in Australia, Zone A <400 mm, Zone B 600-800 mm, Zone C >800 mm. From Finlayson and McMahon (1988).
(b) The drylands of Australia, from Graf (1988).

2.2.2 The Littoral Zone of Dryland Rivers

Arid and semi-arid regions occupy approximately one-third of the world's land mass (Thomas, 1989) and, despite low rainfall, their land surfaces are mostly the products of water and wind action (Graf, 1988). Most of the continental landmass of Australia is arid or semi-arid (cf. Figure 2.4) and the two largest drainage basins, the Murray-Darling Basin and the Lake Eyre Basin, lie within this region. Climatic variability is promoted by the El Niño-Southern Oscillation or ENSO (see Nicholls, 1988; Ropelewski and Halpert, 1987). Much of Australia is subject to ENSO climatic patterns and Australian rivers therefore exhibit flow variability 2-3 times greater than those of Europe and North America (Ropelewski and Halpert, 1987). This makes them, with many southern African rivers, among the most variable in the world (McMahon and Finlayson, 1992).

Dryland rivers oscillate between periods of flood and drought (Kotwicki, 1986; Molles *et al.,* 1992), evident in the hydrographs of four Australian dryland rivers (Figure 2.5). Flow variability in these and 11 other large rivers were subjected to Principal Components Analysis by Puckridge *et al.* (unpublished MS), who suggested that two of the Australian dryland rivers, Cooper Creek and the Diamantina River, were more variable in their flood amplitude than rivers from tropical and temperate regions. This may reflect the geographic position of their headwaters in the semi-arid zone; such regions are subject to highly variable rainfall which is reflected in river discharge variability. All the rivers examined had distinctive and complex patterns of hydrological variability. The dryland rivers in particular, displayed a high degree of variability in flood-pulse timing, duration and amplitude. These factors are likely to be significant in influencing ecological processes and life history strategies in dryland rivers (Puckridge *et al.,* unpublished MS).

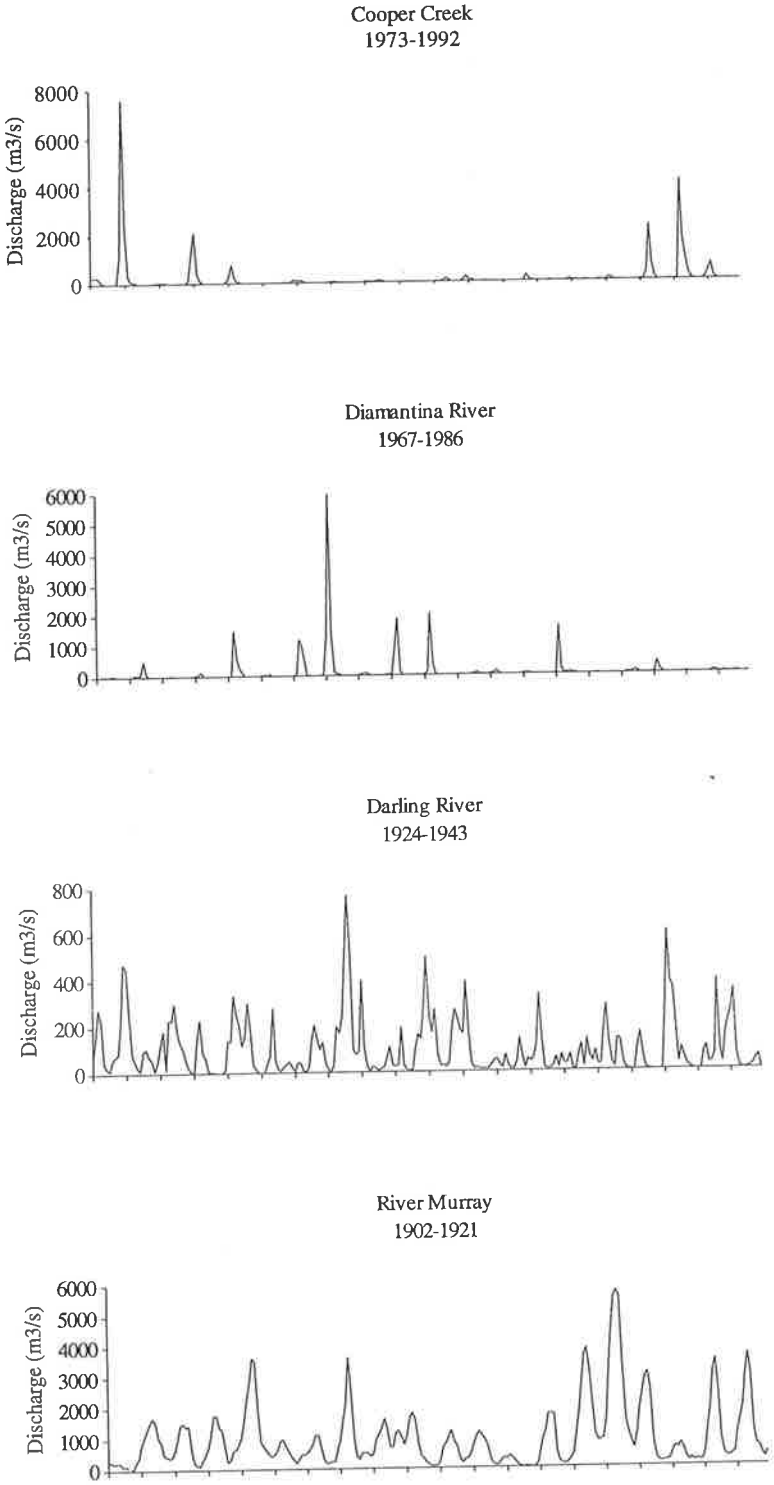


Figure 2.5 Twenty-year hydrographs of mean monthly discharge for some Australian dryland rivers: Cooper Creek and Diamantina River from the Lake Eyre Basin, north eastern South Australia and the Darling River and River Murray from the Murray-Darling Basin in south eastern Australia.

The ecology of many southern hemisphere dryland rivers is poorly understood, as lotic research has tended to concentrate on the rivers of temperate North America and Europe (e.g. Gray *et al.,* 1983; Castella *et al.,* 1984; Rader and Ward, 1988; Castella *et al.,* 1991; Munn and Brusven, 1991; Obrdlik and Fuchs, 1991) and rivers of the tropics, such as the Amazon (e.g. Junk, 1984, 1986, 1989; Junk *et al.,* 1989). In the dryland rivers of southern Africa, the biota face the difficulty of matching life histories with unpredictable environments (Allanson *et al.,* 1990). The fish fauna of the Orange-Vaal system in arid southern Africa is depauperate and exhibits life histories adapted to the unpredictable flow regime (Skelton, 1990). The fish also tend to be generalist feeders able to take full advantage of the periodic floods. The fish fauna of the Murray-Darling Basin in semi-arid Australia is similar, with only 26 native species recorded (compared with over 1300 for the Amazon basin) and is dominated by generalist feeders (Cadwallader and Lawrence, 1990).

Biological processes in dryland rivers are strongly influenced by flood and drought. Flow variability in these rivers suggests that the extent of flooding or drying will rarely be the same for any two flood pulses. Successive pulses may have amplitudes that differ by several orders of magnitude. The biota of dryland rivers, therefore, must contend with the asynchrony of hydrological and seasonal cues, as well as variations in the degree of floodplain inundation. This will range from small flood pulses that are contained within the channel, allowing limited recruitment, to large extended pulses that inundate most of the surrounding floodplain and allow mass recruitment. The littoral zone therefore, may be a key region in dryland rivers; regardless of the extent of flooding, the movement of the littoral zone with every flood pulse will stimulate processes such as nutrient release, organic matter cycling and autotrophic and heterotrophic production.

2.2.3 The Role of the Littoral in Riverine Processes

The complexity and extent of the spatial and temporal linkages influence the nature and intensity of ecological processes in the littoral zone. Junk *et al.* (1989) recognised that the moving phase of the littoral zone, during a flood-pulse, plays a role in nutrient release and primary production. This is similar to the processes initiated on the inundated floodplain by a seasonal flood (Figure 2.6) (Ward, 1989b). Initially, there is a burst of nutrients from newly inundated soils; this stimulates the breeding and growth of many aquatic organisms. During the pulse peak there is a period of maximum production, growth and detrital processing on the floodplain. As flood waters recede, freed nutrients are carried into the channel.

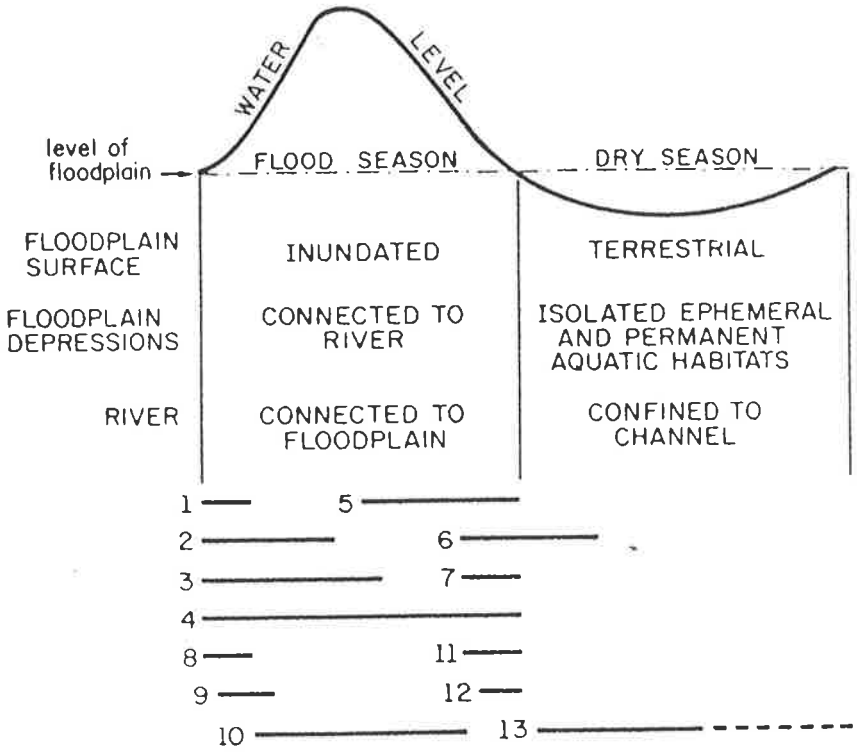


Figure 2.6 Idealised changes in water level over an annual cycle for a fringing floodplain. Numbered horizontal bars indicate characteristic annual periodicity patterns for some major interactions as follows: (1) nutrients released as floodplain surface is flooded; (2) nutrient subsidy from river; (3) rapid growth of aquatic plants and invertebrates on floodplain; (4) major period of detrital processing on floodplain; (5) DOM and FPOM exported to the river; (6) maximum plankton production in floodplain depressions; (7) drift of plankton, benthos, and macrophytes to river; (8) fishes enter floodplain from river and fishes that survived dry season in floodplain depressions move to floodplain surface; (9) major period of fish spawning on floodplain; (10) period of maximum fish growth; (11) fishes move from floodplain to river; (12) heavy fish predation; (13) high mortality of fishes stranded in floodplain depressions. From Ward (1989).

In dryland rivers the processes associated with flooding are essentially the same as described above, but the floods may not occur seasonally or annually, and are not always large enough to overflow the banks. The floodplain processes described by Ward (1989b) may occur at a smaller scale, in the leading edge of the littoral zone as it moves within the channel and occasionally across the surrounding floodplain. Junk *et al.* (1989) suggest that pristine rivers are highly productive systems, kept in a state of early succession by the movement of the littoral zone. As the edge moves up the channel banks and traverses the floodplain there is increased growth of vegetation and associated food and habitat for animals. The recession of the flood pulse triggers aquatic production via an increase in nutrient input and an increase in aerobic decomposition of organic matter (Odum, 1969; Junk *et al.,* 1989).

Many dryland rivers may experience periods where reaches cease flow or dry completely. In these systems, the beginning or end of a flood pulse and the stimulation of nutrient release, may be as significant as the topping of the banks, especially after periods of drought. The notion of system productivity being maintained by the continual pulsing of floods, the movement of the littoral zone, is in keeping with ideas relating to *pulse stability,* suggested by Odum (1969). Fluctuating environments are maintained at an early successional stage by natural cyclic fluctuations. The continual movement of the water level may be akin to a continual and repeated disturbance event, and is therefore likely to enhance productivity (cf. Lamberti *et al.,* 1991). The increased productivity associated with fluctuating environments, however, will work only if the community is adapted to the particular frequency and intensity of the perturbation (Odum, 1969).

The relationship between productivity and flooding is reflected in the variation in composition and biomass of microinvertebrates emerging from soils at different elevations on the Chowilla floodplain, lower River Murray, Australia (Boulton and Lloyd, 1992). Soils close to the channel and inundated annually produced the greatest biomass and diversity of invertebrates, whereas soils on the outer margins of the floodplain yielded a small biomass, dominated by protozoans. This suggests that floodplain areas inundated frequently are most productive.

The riverine littoral zone also functions in the dissipation of flood peaks. When physically complex littoral areas are destroyed through dyking, impoundment and levying the amplitude of the flood wave is increased and its downstream transfer accelerated (cf. Pinay *et al.,* 1990; Sparks *et al.,* 1990). Riparian zones act as natural

filters, absorbing nutrient inputs (Peterjohn and Correl, 1984), and aquatic littoral regions along river margins may also function in this way.

The destruction of littoral complexity can cause marked changes in physical habitat structure, organic matter cycling and flora and fauna composition. Sedell and Froggatt (1984) document the change in shoreline length of the Willamette River, USA, where a 25 km section surveyed in 1854 had over 250 km of complex shoreline. Over the next 100 years an active process of desnagging and engineering works confined the river to a single channel and reduced the shoreline length to 64 km, a four-fold decrease. This isolated the floodplain from the main channel and decreased the biomass of organic carbon accumulating in the channel. There was elimination of the complex aquatic habitats created by snags and dominance of a less patchy habitat structure, combined with the removal of fringing vegetation and a decrease in littoral shading. Benthic algal production also increased (Sedell and Froggatt, 1984).

The littoral zone is perhaps the most dynamic habitat within a large river. The cyclic fluctuations of water levels create physically complex habitats which contribute to biotic diversity and enhance the fluxes of organic matter and nutrients between the main-channel and the floodplain (cf. Gregory *et al.*, 1991). Concepts for large rivers that ignore the littoral zone, therefore, may have limited application for understanding the changes observed in such systems when they are subjected to human disturbances such as flow regulation.

2.3 PERSPECTIVES IN THE ECOLOGY OF LARGE RIVERS

Rivers can be viewed in four dimensions (cf. Ward, 1989a); three spatial dimensions (lateral, longitudinal and vertical) and one temporal dimension. The dominance of any dimension, however, is likely to change along the course of the river as well as between different systems. Explanations for the functioning of riverine ecosystems (Table 2.1) tend to focus on only one of the spatial dimensions.

Table 2.1 Some perspectives in lotic ecology.

Concept	Emphasis	Authors
River Continuum	longitudinal	Vannote *et al.* (1980)
Nutrient Spiralling	longitudinal	Newbold *et al.* (1982)
Serial Discontinuity	longitudinal	Ward and Stanford (1983)
Flood Pulse	lateral	Junk *et al.* (1989)
Patch Mosaic	patches	Frissell *et al.* (1986)

Both the River Continuum Concept (RCC) and ideas regarding nutrient spiralling (Vannote *et al.,* 1980; Newbold *et al.,* 1982; Elwood *et al.,* 1983; Minshall *et al.,* 1985) treat the stream-river profile as a continuum of physical gradients and associated biotic adjustments with emphasis on the longitudinal dimension. The processes occurring in downstream reaches are connected to those in upstream reaches by the flow of water and materials.

The RCC and Nutrient Spiralling Concept were initially developed for streams and small rivers, with their generalisations later extrapolated to large rivers (e.g. Minshall *et al.,* 1985). They are of limited value, however, in understanding the structure and function of large river systems as they tend to ignore lateral and temporal perspectives (MacArthur, 1988; Junk *et al.,* 1989; Sedell *et al.,* 1989). This is especially the case when they are applied to dryland rivers, as longitudinal continuity may be disrupted by drought.

Junk *et al.* (1989) proposed an alternative concept for large rivers, the Flood-Pulse Concept (FPC), which focuses on the lateral dimension. The FPC, based on studies of rivers in the tropics and temperate regions, proposes that the pulsing of river discharge, the *flood pulse*, controls biota in floodplain river systems. A similar perspective for large rivers, with an emphasis on the relative role of lateral linkages in organic matter cycling, was proposed by MacArthur (1988).

The FPC suggests that the flood pulse facilitates the lateral exchange of nutrients and biota between floodplain and main-channel habitats, and creates conditions for nutrient cycling from allochthonous sources within the floodplain. This differs from the suggestions of the RCC where the lower reaches of large rivers are regarded as autotrophic, minimally influenced by fringing vegetation and dominated by algal and macrophyte growth (Vannote *et al.,* 1980). In many large rivers, however, the

movement of organic material from the floodplain, or main channel border regions, into the channel itself often exceeds material imported from upstream (Cuffney, 1988; MacArthur, 1988). When lateral linkages between channel and floodplain habitats are incorporated into concepts concerning the ecology of large rivers the importance of *in situ* autotrophic production decreases and the role of diverse allochthonous inputs from the floodplain is recognised (MacArthur, 1988). These lateral and *within-floodplain* processes may have a greater impact on biota than the nutrient cycling processes and downstream linkages described in the RCC (Vannote *et al.,* 1980, Newbold *et al.,* 1982).

Vertical links between hyporheic and surface water influence the ecology of small stream systems (Boulton, 1993). The hyporheos is involved in nutrient cycling, invertebrate migration and refuge during scouring spates, and is the sole habitat for many species (Cooling and Boulton, 1993). In large rivers the importance of the hyporheic habitat will depend upon the degree and nature of substrate siltation. In channels that are aggrading vertical exchanges will be reduced as the substrate will trap fine sediment within the gravel, whereas in degrading channels vertical linkages may be enhanced as fine sediments are flushed from the system (Amoros *et al.,* 1987). Dryland rivers exist in a state of dynamic equilibrium, aggrading during periods of low flow with periods of degradation during large floods (Graf, 1988). In the lowland sections of dryland rivers fine sediment is most likely to dominate the substratum; these rivers are therefore unlikely to have a well developed hyporheic habitat.

The consideration of longitudinal, lateral and vertical linkages in large rivers accentuates their spatial form. Main-channel - floodplain complexes, however, evolved in response to periodic flooding (Ward, 1989b). Thus, large rivers also exhibit temporal variability, or linkages through time (cf. Wiens *et al.,* 1985), with floodplain communities completely reliant on periodic flooding. The wetland forests and macrophytes on the Amazonian floodplain rely on seasonal flooding for survival (cf. Junk and Howard-Williams, 1984; Klinge *et al.,* 1990; Junk and Welcomme, 1990). In Australia the large river red gum (*Eucalyptus camaldulensis*) forests that occur along the banks of rivers in the Murray-Darling Basin require inundation for vigorous growth (Bren, 1988). Many fish species in the world's large floodplain rivers require periodic flooding for successful breeding and juvenile recruitment (Welcomme, 1970). Successive floods and differing flood magnitudes also influence the spatial nature of the river habitats (Pinay *et al.,* 1990).

Lotic systems may also be viewed as mosaics of habitat *patches* (cf. Frissell *et al.*, 1986; Pringle *et al.*, 1988), encompassing ideas from "landscape ecology" (Forman and Godron, 1986). The concept of a "patch" implies a unit with a spatial pattern, without the constraints of size, degree of internal homogeneity or discreteness (see Pickett and White, 1985). Small patches tend to occur within large patches which form the entities of even larger patches, or units often termed "biomes" (cf. Gosz, 1993). Such hierarchical perspectives, encompassing a number of cascading levels of patches within the landscape (cf. Allen and Starr, 1982; Allen *et al.*, 1984; Urban *et al.*, 1987; Kotliar and Weins, 1990), apply to the structure of lowland river systems.

Table 2.2 Habitat spatial boundaries for small stream systems. From Frissell *et al.* (1986).

System Level	Capacity time scale[a] (years)	Vertical boundaries[b]	Longitudinal boundaries[c]	Lateral boundaries[d]	Linear spatial scale[a] (m)
Stream	10^6-10^5	Total initial basin relief; sea level or other base level	Drainage divides and seacoast, or chosen catchment area	Drainage divides: bedrock faults, joints controlling ridge valley development	10^3
Segment	10^4-10^3	Bedrock elevation; tributary junction or falls elevation	Tributary junctions; major falls, bedrock lithologic or structural discontinuities	Valley sideslopes or bedrock outcrops controlling lateral migration	10^2
Reach	10^2-10^1	Bedrock surface; relief of major sediment-storing structures	Slope breaks; structures capable of withstanding <50-year flood	Local sideslopes or erosion-resistant banks: 50-year floodplain margins	10^1
Pool/riffle	10^1-10^0	Depth of bedload subject to transport in <10 year flood: top of water surface	Water surface and bed profile slope breaks; location of genetic structures	Mean annual flood channel: midchannel bars; other flow-splitting obstructions	10^0
Microhabitat	10^0-10^{-1}	Depth to particles immovable in mean annual flood: water surface	Zones of differing substrate type, size, arrangement: water depth, velocity	Same as longitudinal	10^{-1}

[a] Scaled to a second or third order mountain stream
[b] Vertical dimension refers to upper and lower surfaces
[c] Longitudinal dimension refers to upstream-downstream extent
[d] Lateral dimension refers to cross-channel or equivalent horizontal extent.

Patch mosaic concepts have been used extensively to describe the structure of small stream systems (cf. Frissell *et al.*, 1986; Minshall, 1988; Pringle *et al.*, 1988; Poff and Ward 1990; Sedell *et al.*, 1990; Gregory *et al.*, 1991). In these models hierarchically arranged patches are described for various scales in space and time. For example, Frissell *et al.* (1986) started at the spatial scale of a stream system (10^3 m) and extended downwards to a microhabitat system with a linear spatial scale of 10^{-1} m (Table 2.2). On a temporal scale the hierarchy extends from 10^6 years to 10^{-1} years. Minshall (1988) further extended this notion into 16 orders of magnitude in both space and time. This analogy began at a spatial scale of less than 0.1 mm, in the range of dissolved organic matter, moving upwards to include the largest drainage basins and the globe. In a temporal dimension the scale began in the range of 1 second, insect movement dimensions, and extended to the time-frame of tectonic events (100 million years). These perspectives have been modified for large rivers by Pinay *et al.* (1990), such that the hierarchy extends over a useful range and includes the floodplain and complex microhabitats (Figure 2.7).

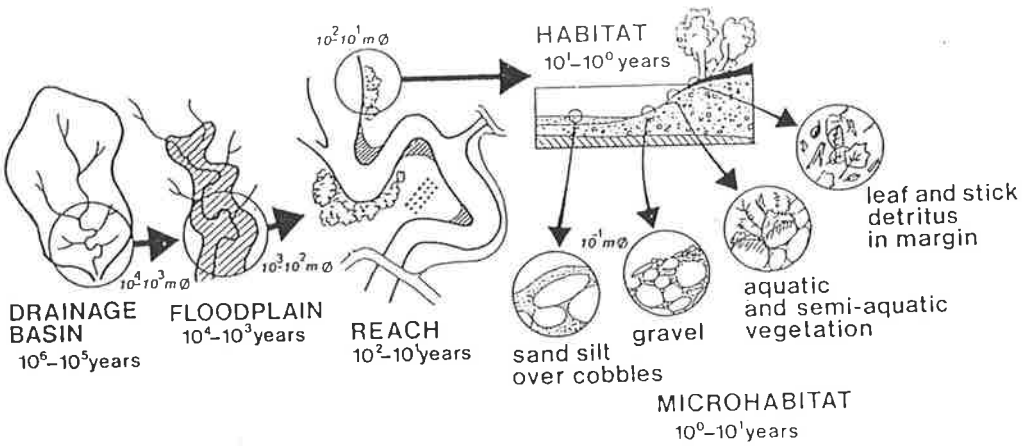


Figure 2.7 An example of the spatial scales of complexity in a river system. From Pinay *et al.* (1990).

Viewing rivers as cascading patches highlights their spatial structure and provides a useful approach for sampling, as stratified random techniques (cf. Elliott, 1977) are most often employed. The approach is limited for understanding broad system processes, however, as it neglects linkages of the habitat patches in space and time. A combination of the above concepts, particularly the RCC and FPC, provides a more realistic insight into river system function; lotic patches will be linked in space and time by the actions of the flood-pulse and the flow of water (cf. Naiman *et al.,* 1988). The relative significance of the spatial linkages (longitudinal, lateral, vertical) will vary with river distance, from the headwaters to the mouth, depending on stream gradient and degree of floodplain development (cf. Sedell *et al.,* 1990) (Figure 2.8). This will have implications for organic matter transport, nutrient cycling and invertebrate migration pathways, as outlined below.

Headwater streams are usually small with steep gradients and small or non-existent floodplains. Pools and riffles dominate the patch types, often differing in abiotic variables, habitat structure and invertebrate assemblage composition (Boulton and Lake, 1992a). Over short distances small streams can display rapid downstream changes in physical and chemical variables including temperature, conductivity, substratum type and microhabitat composition. These characteristics suggest longitudinal linkages between pools and riffles will dominate both abiotic and biotic processes. Nutrients may be cycled and transported downstream with the flow of water (cf. Elwood *et al.,* 1983). Organic matter is derived from allochthonous sources through either patchy or continuous riparian litter fall (cf. Vannote *et al.,* 1980; Winterbourn, 1981; Lake *et al.,* 1984). In systems where the influence of the riparian zone is reduced, considerable instream autochthonous production may occur (Lake *et al.,* 1984). From either source, however, coarse organic matter tends to dominate the detritus in headwater streams. The downstream movement of water displaces invertebrates, many of which have evolved life cycles requiring upstream migration before reproduction (cf. Brittain and Eikeland, 1988; Williams and Williams, 1993).

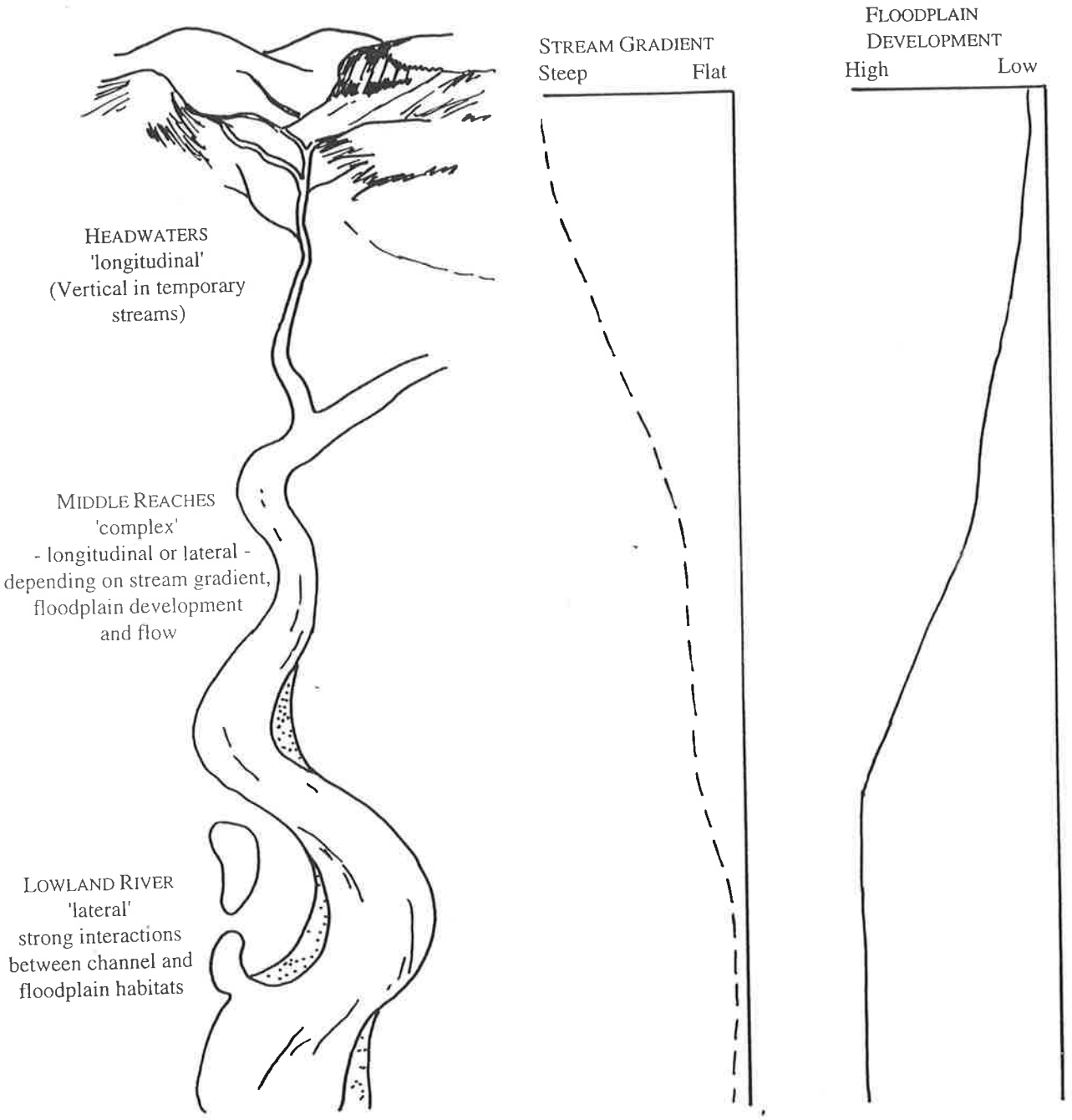


Figure 2.8 Spatial dimensions in a river system, and their relationship with stream gradient and floodplain development

In many temporary headwater streams, particularly in arid and semi-arid climates, the above generalisations may not apply as surface waters will often dry completely. In such systems, a combination of vertical (surface-hyporheic) and longitudinal dimensions will dominate processes. Riparian vegetation is often limited and organic matter is derived from instream autochthonous production, with nutrients upwelling from hyporheic waters (Boulton, 1993). Invertebrates may migrate between surface and hyporheic waters to avoid downstream displacement during floods or desiccation when surface waters dry (Boulton, 1989; Cooling and Boulton, 1993).

In the lower reaches of large rivers, gradients are minimal and the floodplain is often well developed. Although downstream changes in physical parameters exist, over short distances the greatest changes occur laterally, between channel and floodplain habitats. Backwaters and billabongs on large river floodplains can differ markedly in temperature, conductivity and oxygen saturation, even within 100 m of the main-channel (cf. Sheldon and Lloyd, 1990). Main-channel and floodplain habitats also contain distinct invertebrate assemblages (cf. Boulton and Lloyd, 1991). Lateral linkages, between the channel and the floodplain through flooding, will dominate processes in the lower reaches of large rivers. Nutrients will be cycled between channel and floodplain habitats, with pulses of nutrient released from dry floodplain soils on inundation and exported back to the channel as flood waters recede (Junk *et al.,* 1989; Ward, 1989b). Likewise, coarse, fine and dissolved organic matter derived from within-floodplain processes and allochthonous accumulations will be transported to the channel via lateral water movement during floods (Cuffney, 1988; Grubaugh and Anderson, 1989). Different fish species in large rivers show strong lateral movements from the channel onto the floodplain during floods; enhancing reproduction, as well as feeding and recruitment in juveniles (Welcomme, 1979; Cadwallader and Lawrence, 1990; Lloyd *et al.,* 1991).

The situation in the middle sections of rivers will be complex, differing between systems depending on stream gradient and floodplain development. Where gradients remain relatively steep and floodplain development is restricted, longitudinal linkages will be significant. The other extreme is reflected in the River Murray, Australia, where lateral linkages dominate processes in the middle river. In the 350 km headwater region stream gradient drops from an elevation of 1500 m to 300 m (Eastburn, 1990). In the middle reaches below Hume Dam (cf. Figure 1.1), changes in elevation are less, approximately 16 cm km^{-1} (Walker, 1992), and extensive lateral floodplain forests develop (Bren, 1990). This highlights the significance of lateral water movement.

Thus, concepts focussing on only one spatial dimension may not adequately explain biological processes occurring in the littoral zone of large rivers. One criticism of these concepts, particularly the RCC and the FPC, is they lack a predictive framework for exploring the biological changes observed in large rivers in response to flow regulation. The alternative approach, where rivers are regarded as a series of patches with the direction of the links between patches determined by a combination of stream gradient and floodplain development, may be more conducive for predicting changes in response to flow regulation.

2.4 The Environmental Impacts of River Regulation

All large rivers in the temperate zone, and an increasing number in tropical and arid regions, are regulated to some degree (Petts, 1989). The benefits include enhancing water quality, guaranteeing water quantity, hydropower, maintaining navigation, enhancing fish production and for recreation (Sparks *et al.,* 1990). Flow regulation may be accomplished by constructing dams, weirs, levees or barrages, by changing the physical nature of the channel and by abstracting or adding water through interbasin transfers or offstream storage (Petts, 1984). All forms of regulation change the characteristics of the river in particular, its hydrology, thermal regime, sediment regime, water quality and the nature of the biota (Ward, 1976a, 1976b; Rader and Ward, 1988; Mûnoz and Prat, 1989; Palmer and O'Keefe, 1990, Maheshwari *et al.,* 1994). Although all may cause changes (e.g. Swales, 1982), this review is restricted to the impacts of dams and weirs as these are the dominant structures modifying the flow regime of the regulated lower Murray.

2.4.1 Types of Regulation and Regulatory Structures

The type of regulatory structure built at a particular site and its mode of operation depends on factors such as its intended use (water storage, flood mitigation, power generation) and the nature of the site. The two most common types of regulatory structures are dams and weirs.

Dams

Dams (>10 m) are usually constructed in the upper reaches of river systems. Owing to their size and location, they have the potential to affect the entire river below. Dams modify the immediate upstream and downstream sections, creating two distinct environments. Upstream a reservoir forms in which the limnology more closely resembles a lake rather than a river. Downstream the river remains, however, its flow patterns are modified by the regulated releases of the dam. Dams allow water to be stored during periods of high natural flow and released when natural flows are low. The physical conditions in the reservoir can also influence the physical and chemical nature of the river below. In this way the water discharged from a dam can be of a different chemical composition and follow a different seasonal pattern to that of the natural river (Petts, 1984).

A number of factors affect the quality of the water discharged from reservoirs. These are discussed in detail by Petts (1984) and include climate (precipitation and temperature), catchment characteristics (geology, soil character, vegetation), reservoir morphology, inflow of tributary or human effluent, operational procedures and type and location of outflow structure.

The physical and chemical nature (e.g. temperature and oxygen saturation) of the water released can modify invertebrate assemblage composition and standing crop in the downstream river (e.g. Ward, 1976a, 1976b; Walker *et al.,* 1978, plus many others). These changes diminish with increasing distance downstream, as was observed below Hume Dam on the River Murray (Walker *et al.,* 1978). The oxygen sag in the downstream river, resulting from the release of hypolimnetic oxygen-depleted water, changed from 50% saturation near the dam wall to normal levels 100 km further downstream. Changes in water quality below dams tend to be concentrated locally, compared with the wider impacts that changes in the flow regime inflict. This review is concerned with the latter in more detail below.

Dams may be operated for water storage, hydro-electric power and flood control and the manner in which water is released from these dams will modify the original flow regime in a specific way. Four broad regimes can be recognised for most regulated rivers (cf. Ward, 1976a):

- *Reduced flow* occurs downstream of dams from which water is diverted for domestic or irrigation supply, or off-stream power generation. These

operations cause local decreases in the extent of the littoral zone (wetted perimeter), changes in depth, surface area and current velocity of the receiving river. Reduced flows can shift natural perennial rivers towards intermittency (Bruwer and Ashton, 1989).

- *Seasonal flow changes* are common in rivers downstream of dams utilised for water storage to supply irrigation, agriculture or domestic needs. Water is stored during peak run-off periods and released during periods of normally low flow. Such operations may completely reverse the seasonality of flow in the immediate downstream river, with winter floods being held back and subsequently released in summer (Jacobs, 1990). In the lower reaches of such rivers changes in flood seasonality may not be as apparent due to the influence of tributary inflows (Close, 1990). Total flow, however, will be reduced and overall variation in flow decreased, being replaced by extensive periods of constant flow (Petts, 1984; Hellawell, 1988). Constant flow increases bank stability, can decrease turbidity and dampen the effects of floods and spates, both locally around the dam and for extended distances downstream.

- *Increased flow* may result from any alteration of the natural flow pattern or the addition of water diverted from another drainage area. Additional flow will increase local flow variability and create permanent habitats from temporary ones. It will have variable effects on seasonality depending on the timing of flow increases.

- *Short-term flow fluctuations* may occur below dams utilised for water storage, especially when water is released in pulses to meet irregular irrigation demands (Petts, 1984). They are, however, most common below dams used for the generation of hydropower. Flow usually exhibits various diurnal patterns with typical maximum discharge occurring during the day, with reduced flows at night and on weekends. The greatest impact of these reservoirs will occur locally, related to erratic fluctuations in water level, often many metres in a day, immediately downstream of the dam. The biotic impacts of short term flow fluctuations are determined by the timing and the quantity and quality of water discharged (Petts, 1984).

These four flow regimes are not mutually exclusive: a regulated river may be characterised by more than one. This is demonstrated in the context of the regulated River Murray. Overall, flows at Albury, immediately below Hume Dam (Figure 1.1), have increased as a result of interbasin transfers through the Snowy River Scheme (Close, 1990). Although total flows have increased, they have also been seasonally redistributed. Compared with the natural regime, periods of reduced flow below the dam now occur during winter and spring as high flows are stored in Hume Dam. Increased flow occurs during summer and autumn when the stored flows are released to supplement naturally low flows (Close, 1990; Chapter 1)

In the lower Murray, below the Darling junction (cf. Figure 1.1), total flows have been reduced as water is diverted for irrigation. Compared with the natural flow regime, the regulated flows are more stable (seasonal flow constancy) owing to "entitlement" releases from the upstream storages (Close, 1990). Thus, different regions of the regulated Murray are affected by reduced flows, increased flows and seasonal flow constancy.

Weirs

Weirs are generally small structures with heights of less than 10 metres, giving them a relatively small storage capacity. They are usually constructed to maintain a minimum area of shallow water and thereby facilitate navigation and water abstraction by canals or pumps for irrigation (Bruwer and Ashton, 1989; Jacobs, 1990). Water is usually discharged over the top of the weir, via the manipulation of metal gates and panels (cf. Jacobs, 1990). The weirs across the main-channel of the River Murray are partly dismantled, or in some cases entirely withdrawn, during high flows (Jacobs, 1990).

A weir creates a barrier across the channel. The influence of an individual weir on the flow regime may be negligible during periods of high flow, but this is seldom the case during the dry season (Bruwer and Ashton, 1989). In some rivers weirs create permanent aquatic habitats from previously temporary ones. They are usually built in series and in this way their impacts are compounded; a series of weirs can modify a river for hundreds of kilometres (Bruwer and Ashton, 1989; Thoms and Walker, 1993). In the lower Murray the positioning of the sequential weirs, combined with upstream water releases, contribute to the maintenance of bankfull water levels for approximately 800 km.

As with dams, the river downstream of a weir can experience a combination of any of the four broad flow regimes outlined above (cf. Ward, 1976a). For example, in the lower Murray, short-term flow fluctuations are common downstream of weirs as a result of water level manipulations in the upstream weir pool (cf. Chapter 1).

2.4.2 Impacts on the Littoral Zone

By definition, river regulation imposes an unnatural flow regime on a natural system (Boon, 1988). Native riverine biota are adapted to the natural regime, depending on high flows and periods of low or even zero flow to satisfy the requirements of their life cycles (Petts, 1984). Regulation can change the pattern and timing of discharge, the chemical, physical and biological quality of water released, channel morphology, substrate composition and stability, and the distribution of macrophytes, microbiota, invertebrates and vertebrates (Petts, 1984).

Through modifications to the natural flow regime (flood frequency, amplitude and duration) regulation can disrupt longitudinal linkages in small streams and rivers and restrict lateral water movements in large rivers. This changes:

- the source and composition of organic matter and nutrients entering the littoral zone,
- channel morphology and, therefore, meso and micro-habitat structure,
- the rate of water level movement in the littoral zone,
- littoral zone flora and fauna assemblage composition.

These points are elaborated below.

Most secondary production in large rivers is detritus based with organisms utilising coarse, fine and dissolved organic matter (Grubaugh and Anderson, 1989; Corkum, 1992). Backwater and floodplain habitats trap and process coarse material, releasing fine particles to the main channel during floods (cf. Lieberman and Burke, 1993). As the nutritive quality of detritus changes with particle size and degree of conditioning (Angradi, 1993), changes to flooding frequency or duration can affect the quality of the organic detritus accumulating in the river channel.

Flow regulation in rivers or streams where longitudinal gradients are significant (cf. Vannote *et al.*, 1980) modifies the source of the detritus entering the channel (Perry and Perry, 1991; Angradi, 1993). Immediately downstream of dams autochthonous detritus from the upstream reservoir, or immediate river bed, is a more abundant food source for invertebrates than is allochthonous material derived from upstream

terrestrial sources. In large rivers, floodplain forests influence the quantity of organic detritus transported to the channel, through lateral water movement (Grubaugh and Anderson, 1989). Disruptions to these lateral exchanges through flow regulation, therefore, will modify the source of the detritus entering the river. There will be a decrease in laterally derived allochthonous material and an increase in the significance of instream autochthonous production. This has obvious implications for biotic processes, particularly in those groups utilising detritus as a food source (cf. Corkum, 1992).

Nutrients released from newly inundated soils stimulate the breeding and production of many organisms (cf. Crome and Carpenter, 1988). These processes have been described for temperate river floodplains during seasonal flood events (cf. Ward, 1989b; Figure 2.6). In hydrologically variable dryland rivers similar processes may occur in the littoral zone as it traverses the channel banks and occasionally the floodplain (Section 2.2.2). Flow regulation can reduce the magnitude of the water level movements in the littoral zone, thereby disrupting processes of nutrient release and production.

Flow regulation also changes channel morphology, modifying the spatial complexity of littoral zone habitats. Increased erosion (degradation) may be common immediately downstream of weirs, with cross-sectional channel areas increasing; whereas, depositional regions (aggradation) occur upstream, with cross-sectional areas decreasing (Thoms and Walker, 1993). This pattern is reflected in the littoral zone microhabitat composition of the lower River Murray (Walker *et al.,* 1994). Stands of submerged macrophytes (e.g. *Vallisneria spiralis*) are common in the depositional zone above the weir, whereas the region immediately downstream is characterised by semi-aquatic species (e.g. the spiny sedge, *Cyperus gymnocaulos*).

Most forms of flow regulation change the rate or amplitude of water level movements in the littoral zone. These changes are particularly apparent below reservoirs subjected to short-term (daily-weekly) flow fluctuations. Downstream of the deep-release dams on the Gunnison River, Colorado, the diversity and richness of trichopteran (Hauer *et al.,* 1989) and plecopteran (Stanford and Ward, 1989) larval assemblages was reduced. Likewise, after regulation in the Clearwater River, Idaho, diversity decreased and the community became dominated by orthoclad chironomids and the mayfly *Ephemerella infrequens* (Munn and Brusven, 1991). These changes were attributed to the increased fluctuations in littoral water levels as well as reduced habitat diversity and altered food resources.

Unpredictable and sometimes harsh conditions are common in the littoral region below hydropower reservoirs, where extreme water level fluctuations are common. Downstream of the Turner's Falls dam on the Connecticut River (Massachusetts), such fluctuations may be responsible for the periodic exposure of most of the littoral area (Fisher and LaVoy, 1972). The exposure was irregular but usually diel with the extent related to season; in the periodically exposed areas benthic invertebrate communities were lower in density and diversity than those in continually flooded areas. Conditions below hydro-electric dams tend to favour opportunistic species with either flexible, asynchronous life cycles or a short active nymphal stage, able to take advantage of favourable conditions of short duration (Brittain and Saltveit, 1989). Such conditions may be in contrast to those characteristic of the unregulated river.

Not all regulated systems show a lower diversity. Ward and Short (1978) found relatively high invertebrate diversity at Joe Wright Creek, below an irrigation reservoir in northern Colorado. They suggested the specific fluctuating conditions below the dam were a primary cause for increased diversity. Within limits these conditions create an environment alternately favouring different species, thus allowing some niche overlap not available under stable conditions.

Other forms of regulation, particularly when flows are kept constant, may lead to increased water-level stability in the littoral zone. This permits enhanced benthic algal growth, potentially modifying assemblage composition through changed food resources or trophic status (Ward, 1976; Petts, 1984). Elimination of high seasonal discharge on the Strawberry River (Utah) resulted in massive increases in attached algal growth and in those invertebrates, such as *Baetis* sp., associated with algal mats (Williams and Winget, 1979). Although not dryland rivers, the same was observed below Cow Green Reservoir in the United Kingdom (Armitage, 1976) and on rivers in Scandinavia (Brittain and Saltveit, 1989).

Regulation may also introduce gradients in food resources for macroinvertebrates, from predominantly filamentous chlorophytes close to the dam to diatoms further downstream in less impacted regions. This was observed below a hypolimnetic-release reservoir on the Blue-River (Colorado) (Voelz and Ward, 1990). The qualitative nature of the detritus also changed with increasing distance from the dam; initially decaying algal material and planktonic organisms dominate, shifting to a diverse detritus, containing leaf and wood fragments with little algal material further

downstream. These longitudinal changes in food resources were reflected in the types of functional feeding groups (cf. Cummins and Klug, 1979) represented in the invertebrate assemblages. Filter feeders dominated close to the dam, utilising the fine organic matter released from the reservoir. Further downstream collectors, gatherers and scrapers became more abundant in association with increased levels of coarse organic matter.

As demonstrated above, most flow regulation studies focus on a particular reservoir or river system. Overall, the study of regulated rivers lacks an adequate perspective that is conducive to predicting the impacts of river regulation. Despite some criticism (cf. Junk *et al.,* 1989; Sedell *et al.,* 1989) the RCC (Vannote *et al.,* 1980) gave lotic ecology a perspective with which to critically examine processes operating in river systems. Likewise, the FPC (Junk *et al.,* 1989) followed the same role for the ecology of large rivers in tropical and temperate regions. Neither concept, however, provides predictions relating to how rivers may change in response to flow regulation. A combination of these concepts is perhaps a better explanation of river system function (Section 2.3), and may allow predictions to be made regarding the changes induced by various forms of flow regulation.

The Serial Discontinuity Concept (SDC) (Ward and Stanford, 1983) is specific in its application to regulated rivers. Where the regulated river is disrupted by sequential structures, such as dams or weirs, it predicts there will be longitudinal shifts in abiotic (e.g. temperature) and biotic parameters (e.g. abundance and diversity), in relation to the position of the structure along the stream profile (Ward and Stanford, 1983). The regulated river becomes an alternating series of lentic and lotic environments. The SDC, however, presupposes that the RCC and concepts concerning nutrient spiralling (cf. Vannote *et al.,* 1980; Elwood *et al.,* 1983) are conceptually sound and their underlying assumptions valid (Ward and Stanford, 1983). As outlined in Section 2.3, the RCC is an inappropriate framework for large rivers (see also MacArthur, 1988; Junk *et al.,* 1989; Sedell *et al.,* 1989). This would indicate that the SDC is also inappropriate for understanding the changes induced by flow regulation in large rivers. If the perspective for river system function outlined in Section 2.3 is applied to regulated systems, the advantages and limitations of the SDC become apparent.

Serial discontinuities in plecopteran (Stanford and Ward, 1989) and trichopteran (Hauer *et al.,* 1989) assemblages have been measured in association with flow regulation below a hypolimnial-release reservoir on the Gunnison River (Colorado).

The stream gradient over which sampling occurred in this river was steep; thus, longitudinal linkages are likely to be significant and the SDC appropriate for explaining observed patterns. In large rivers where flow regulation reduces lateral flooding, a strong longitudinal gradient is imposed, shifting processes from lateral-linked towards longitudinal-linked. The regulated river may be further disrupted by the presence of sequential regulatory structures, such as dams or weirs, further accentuating longitudinal dimensions. In these situations the SDC may be adequate in predicting some of the changes induced by regulation.

The SDC, however, with an emphasis on longitudinal linkages, may not adequately explain lateral changes in abiotic and biotic parameters associated with flow regulation. Sequential weirs in the upper Mississippi River are operated to maintain a constant water level for navigation during low to moderate flows, reducing the amplitude of the flood-pulse, and decreasing the mean annual flood period (Sparks *et al.,* 1990). These changes affect lateral processes. Juvenile fish at the water margins are stranded as water levels drop rapidly, the volume of allochthonous terrestrial litter entering the river is reduced and the area of floodplain habitat for fish spawning and feeding is decreased (Sparks *et al.,* 1990). In these situations the SDC should be extended so that predictions regarding changes in floodplain-channel processes, and the littoral zone, can be made.

2.5 Predicting the Impacts of Flow Regulation in Large Rivers

The riverine littoral zone can be described over a number of spatial (macro, meso and microhabitat) and temporal (macro, meso and microtime) scales. If rivers are viewed as systems of hierarchical patches where spatial linkages between patches vary from the headwater to the mouth, it may be possible to predict how flow regulation modifies littoral processes. In large rivers regulation reduces the lateral linkages between the main-channel and the floodplain and accentuates upstream-downstream longitudinal links. This shifts the source of organic detritus from lateral, derived from floodplain processes, to longitudinal where downstream transport is significant. These changes will also be reflected in the physical nature of the detritus. That derived from the floodplain is diverse (coarse to dissolved) and likely to support assemblages comprising a number of different functional feeding groups (scrapers, shredders and collectors: cf. Cummins and Klug, 1979). Organic matter imported from upstream will be fine or dissolved (RCC: Vannote *et al.,* 1980) and result in assemblages dominated by filterers (cf. Cummins and Klug, 1979).

Flow regulation modifies the extent, frequency and rate of littoral zone water level movements (cf. Maheshwari *et al.,* 1993). Given the suggested importance of the littoral zone in dryland rivers, the impacts of regulation in these systems, and the consequent modification of the littoral zone, will be extreme. As the exact changes associated with regulation will depend on the resulting flow regime, we can use the broad patterns suggested by Ward (1976a), and outlined in Section 2.4, to predict changes in littoral processes in large rivers in both space and time.

Reduced flows will confine water in channel habitats and isolate many floodplain mesohabitats. This will reduce lateral linkages between the main channel and the floodplain. Reduced flows will decrease the magnitude and amplitude of flood pulses at both meso and microtime scales. This will impede those faunal groups requiring pulses of certain magnitudes for successful breeding and juvenile recruitment. Nutrient release from flooded soils and organic matter cycling on the floodplain will also be reduced, with consequences for the overall nutrient budget of the river. If the floodplain is isolated the source of the organic matter entering the channel will shift to within-channel production or downstream export.

Seasonal flow changes eliminate low flows and reduce the frequency of high flows. Some previously temporary habitats will become permanent and others will be isolated from periodic flooding. This will change the composition of the invertebrate assemblages of these habitats; assemblages of temporary water bodies are often different to those in permanent ones. A constant flow will eliminate most pulses at the microtime scale and modify the flow regime at a mesotime scale. This decreases the movement of nutrients and organic matter from the floodplain to the channel. The overall result of seasonal flow constancy is stability of the littoral zone. The creation of a uniform habitat (in terms of temporal variability) has been suggested as a primary cause of communities in many regulated rivers having a reduced diversity and increased biomass (Petts, 1984).

Increased flow, as well as impacts caused by a change in current velocity, will increase in number of permanent mesohabitats in the river. Increased flow may eliminate those microhabitats with particular flow requirements, such as particular vegetation types. In large rivers, increased flows may change the balance between lateral and longitudinal linkages, enhancing the importance of the longitudinal dimension. This may enhance the export of nutrients and detritus downstream.

Flood pulses will tend to be modified at a microtime scale through the reduction in low flows which will lead to changes in the flow regime at a mesotime scale.

Short term flow fluctuations will affect the microhabitat structure of the river below the regulator through changes in the extent of erosion and deposition. The major change in the flood pulse will be a shift from amplitude changes at a microtime scale to a smaller (e.g. nanotime) scale such as days or weeks. This may impact fauna through stranding. Flood pulses at these time scales will be too small to initiate many littoral zone processes, particularly faunal breeding responses or organic matter cycling.

The regulated lower River Murray is an ideal region in which to examine the impacts of regulated flows on the littoral zone. The lower river is subjected to a modified flow regime that includes an increase in summer-autumn flows, an increase in flow constancy caused by regulated releases from upstream dams and storages, and short term flow fluctuations resulting from the management of water levels in association with the low-level weirs (Chapter 1). We may predict, therefore, that this form of regulation will change mesohabitat structure of the littoral zone, some previously temporary habitats will become permanent and others will be isolated from flooding for extended periods. These changes will also affect the microhabitat composition of the mesohabitats. The short-term flow fluctuations below weirs may be expected to modify the microhabitat composition of these regions through changes in erosion and deposition and modify invertebrate assemblage composition by selecting for those taxa able to tolerate regulated conditions. There will be changes in the flood pulse at a microtime scale through a reduction in the frequency of both low flows and moderate floods. The hydrograph and consequently the movement of the littoral zone will be stabilised, minimum flows are eliminated and floods reduced. The isolation of the floodplain from the channel will lead to decreased organic matter input, while a stabilised littoral zone will favour increased autochthonous production.

Thus, the ecological impacts of flow regulation tend to be concentrated at the meso and micro scales in both space and time. The aim now is to understand how the summation of these changes affect the overall ecology of the regulated river.

Chapter 3

Spatial Patterns in the Murray-Darling Littoral

3.1 Introduction

Rivers and streams exist as patchworks of habitats that may be described by their physical environmental conditions (cf. Pringle *et al.,* 1988). For large rivers, the spatial complexity in littoral zone habitats occurs over a range of scales (macro, meso and microhabitats) (Chapter 2). The particular characteristics of each habitat will influence the distribution of macroinvertebrates, such that subjectively defined habitats may be occupied by distinct assemblages (Downes *et al.,* 1993; Palmer *et al.,* 1993a, 1993b).

A large number of studies have demonstrated the significance of spatial complexity in structuring invertebrate assemblages in small streams, particularly with respect to the number of taxa (richness) and the abundance of individuals. Examples from southern hemisphere streams suggest differences occur across all habitat scales. Distinct assemblages exist within macrohabitats (stream or reach) (e.g. Marchant *et al.,* 1985; Scarsbrook and Townsend, 1993), between some mesohabitats (pools and riffles) (e.g. King *et al.,* 1988; Boulton and Lake, 1992a, 1992b; Downes *et al.,* 1993; Scarsbrook and Townsend, 1993), as well as microhabitats (particle size, vegetation type) (e.g. Marchant *et al.,* 1985; Downes *et al.,* 1993). Combined, these studies indicate that spatial complexity is a significant feature in small stream systems. The same is likely to apply to large rivers.

Most studies concerning invertebrate distribution patterns in large rivers compare regulated and unregulated conditions (e.g. Ward and Short, 1978; Rader and Ward, 1988; Fruget, 1991; Munn and Brusven, 1991; Adamek and Sukop, 1992), with few focussing on the significance of spatial complexity. Adjacent hydrogeomorphic floodplain sectors (macrohabitats), such as the Rhône and Ain Rivers (France) (Castella *et al.,* 1991), can differ in invertebrate composition and diversity, indicating the significance of geomorphological determinants on floodplain communities. In the middle and lower reaches of the Buffalo River, southern Africa, distinct invertebrate assemblages occur across a number of spatial scales: macrohabitat (reach type), mesohabitat (pool and riffle) and microhabitat (Palmer *et al.,* 1991). Likewise,

Boulton and Lloyd (1991) describe similar patterns in meso and microhabitats on the Chowilla floodplain, River Murray (Australia). A similar range of spatial scales (macro- meso- and micro-) as observed in small stream systems, therefore, is likely to influence assemblages in large rivers.

Another way of exploring assemblage differences between habitats is via functional feeding groups (FFG's) (cf. Cummins and Klug, 1979). FFG's may include predator, grazer, collector (gatherer or filterer) or shredder. Intuitively, the proportions of FFG's in an assemblage should reflect the environmental conditions of the habitat, particularly the source of organic energy (cf. King *et al.,* 1988). This formed the focus of many generalisations in the RCC (cf. Vannote *et al.,* 1980). In the upper reaches of rivers where coarse organic matter (CPOM) is an abundant food resource, shredders and collectors would dominate assemblages. In the lower reaches where fine, ultrafine and dissolved organic matter (FPOM, UPOM and DOC) are suggested to dominate, filters would be more abundant (Vannote *et al.,* 1980).

Criticism of this portion of the RCC, with respect to southern hemisphere streams, has been strong (e.g. Winterbourn *et al.,* 1981; Lake *et al.,* 1984), owing to the difficulty of assigning southern hemisphere invertebrates to the FFG's erected from northern hemisphere studies (King *et al.,* 1988). Marchant *et al.* (1984) found the abundance of different FFG's along the course of the La Trobe River, Victoria, did not reflect the suggestions of the RCC. They attributed this to a greater abundance of CPOM in the lower reaches of the La Trobe River, owing to bark and twig fall from riparian vegetation, mostly *Eucalyptus* spp. The representation of different FFG's in an assemblage may therefore be a useful indicator of the dominant food sources for invertebrates in river systems.

This chapter examines the spatial patterns in littoral zone macroinvertebrate assemblages at three habitat scales: macro, meso, and micro. The macro scale focuses on differences between two river reaches, the lower River Murray and the lower Darling River (cf. Figure 3.1), these differ in geomorphology and floodplain development. The River Murray has a broad floodplain (1-20 km) with extensive forests and wetlands, whereas the Darling River flows in a 10 m deep channel with a discharge too low and irregular to sustain substantial fringing floodplain communities (Jacobs, 1990; Walker *et al.,* 1992).

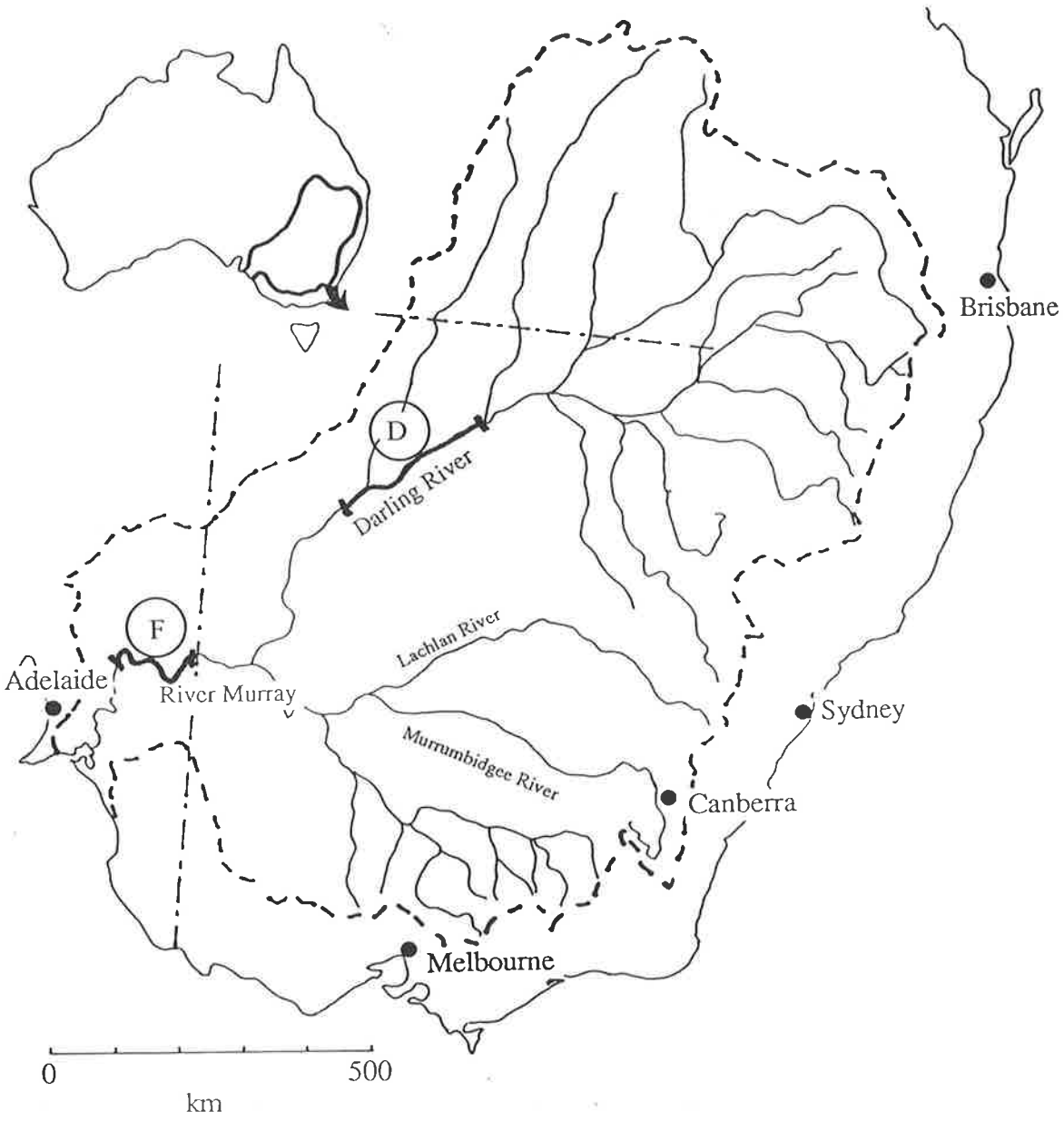


Figure 3.1 Position of the two study regions, 'D' Darling River and 'F' lower River Murray, in the Murray-Darling Basin, Australia.

On both the lower Murray and the lower Darling sampling sites were chosen to represent the following mesohabitats (Figure 3.2).

- **Main channel:** the main channel carrying most of the flow
- **Anabranches:** much narrower channels with a variety of flow regimes. They usually remain connected to the main channel but leave and rejoin the river at separate points
- **Backwaters:** water-bodies connected at one point to the main channel at normal pool level, having little or no flow.
- **Billabongs:** water-bodies that are isolated from the river at normal pool level and connected to the main channel only during overbank flow events. Two types of billabongs are recognised "temporary" and "permanent".

Within these mesohabitats the following eight microhabitats were identified (cf. Boulton and Lloyd, 1991):

- **Emergent vegetation** such as reeds (*Phragmites australis*), bulrushes (*Typha domingensis*), rush (*Juncus* sp.) and the sedge (*Cyperus gymnocaulos*), forming sometimes dense stands along the edges of the main channel and in the upper pools behind weirs,
- **Submerged vegetation** (e.g. *Vallisneria spiralis*),
- **Attached floating vegetation** (e.g. *Ludwigia peploides* and *Myriophyllum* spp.),
- **Submerged woody debris** ('snags'), represented by the roots or fallen limbs of river red gums (*Eucalyptus camaldulensis*),
- **Coarse organic matter,** leaf litter and twigs,
- **Unvegetated littoral** areas either with a silt and clay substratum or a sandy substratum, free of vegetation, woody detritus or other cover.

Multivariate analyses were used to identify the environmental variables structuring the assemblages within, and between, the macrohabitats. Functional feeding group composition of assemblages in different habitats was used to explore the significance of organic matter as a food source for invertebrates. We may expect all habitat scales to influence invertebrate assemblage structure and composition, however, given the significance of lateral linkages in large rivers the greatest differences should lie between mesohabitats. Lateral water movements also contribute to an increased diversity of organic matter in all habitats (Chapter 2). Thus, the FFG composition of assemblages should be diverse and not restricted to 'filterers', as suggested for large rivers in the RCC.

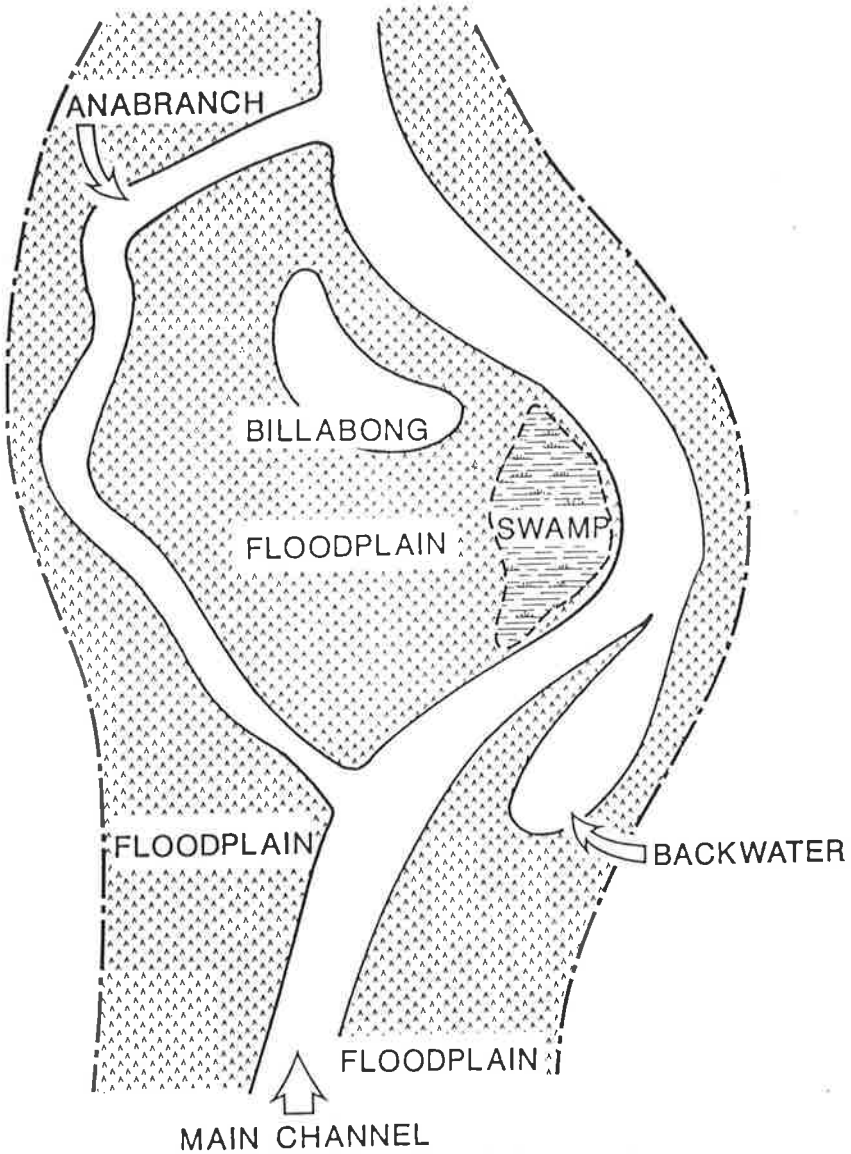


Figure 3.2 Graphical representation of the different mesohabitats found on the floodplain of rivers within the Murray-Darling Basin.

3.2 Study Sites

On the lower Darling River (NSW) samples were from 14 sites between Bourke and Wilcannia (Figure 3.3, Table 3.1). This section of the river traverses flat, low-gradient plains formed primarily of very fine-grained cohesive sediments (Woodyer, 1978). The mesohabitats sampled included temporary and permanent billabongs and the main channel. The temporary billabongs, Site 7 (WBBB) and Site 14 (CPBB), are shallow depressions in the "high-level" floodplain (cf. Woodyer, 1979), filled during overbank flows. In January 1990 when the samples were collected, water-levels in the main channel and billabongs were receding, with the last overbank flows occurring during 1989 (Figure 3.4). Neither temporary billabong supported aquatic vegetation; the dominant microhabitat was fallen wood (snags).

Table 3.1 Number and abbreviation of sites sampled on the Darling River floodplain in January 1990.

No	Abbreviation	Site
1	BKBB	Big Billabong, North Bourke
2	BWUP	Weir pool above Bourke Weir
3	OTBB	Orange Tree Billabong
4	GWUP	Weir pool above Glen Villa Weir
5	GWLP	Region immediately below Glen Villa Weir
6	WBMC	Main channel at Winbar Station
7	WBBB	Billabong on Winbar Station
8	TWUP	Weir pool above Tilpa Weir
9	TWLP	Region immediately below Tilpa Weir
10	WYMC	Main channel at Wygilla Station
11	NBMC	Main channel at Nelyambo Station
12	WWUP	Weir pool above Wilcannia Weir
13	CPMC	Main channel at Culpaulin Station
14	CPBB	Billabong on Culpaulin Station

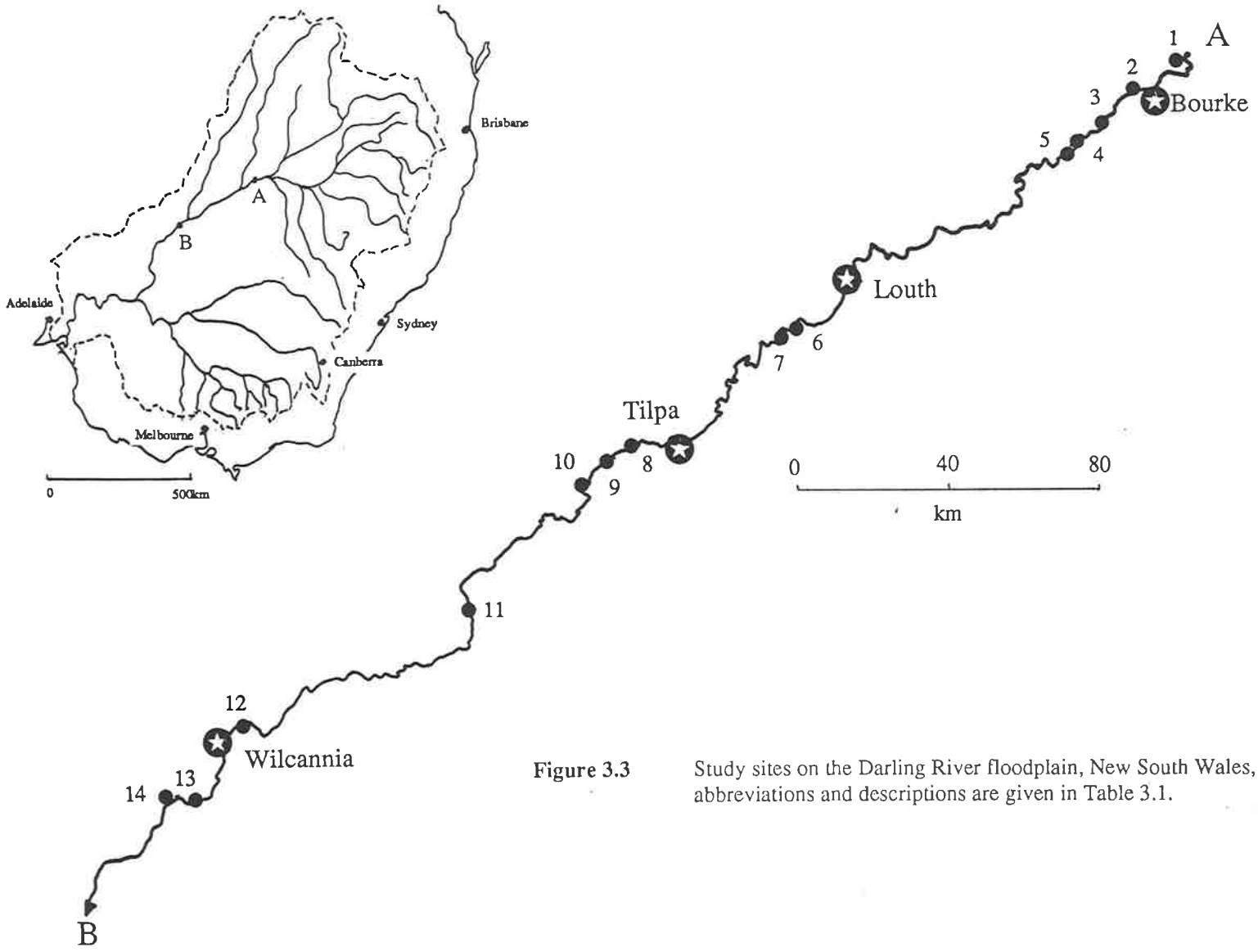


Figure 3.3 Study sites on the Darling River floodplain, New South Wales, January 1990. Site abbreviations and descriptions are given in Table 3.1.

The permanent billabongs, Site 1 (BKBB) and Site 3 (OTBB), are typical ox-bow lakes; they are deep and support a number of aquatic macrophyte species. At the time of sampling Bourke billabong (BKBB) supported areas of the "water primrose" *L. peploides* and stands of the sedge *Cyperus gymnocaulos*. In OTBB the water level is kept raised due to an artificial levee and large numbers of black box (*Eucalyptus largiflorens)* are inundated by shallow water, wood and leaf litter therefore form the dominant microhabitats. *Cyperus gymnocaulos* is also abundant.

Although flows in the Darling River are essentially unregulated, a number of 'fixed-crest' weirs (cf. Mallen-Cooper and Edwards, 1990) have been constructed across the main channel. Their design does not allow water-level manipulation so they have minimal influence over flow. The main function of these structures is to maintain a stable base level during periods of low flow for local water supply. However, due to the extremely low gradient of the Darling (cf. Woodyer *et al.,* 1979) the weirs potentially modify main channel habitats, with sections immediately above the weirs being deeper and more stable than sections of the river immediately below (cf. Walker *et al.,* 1992).

Samples were therefore collected from three regions of the main channel: immediately above weirs (upper pool), Site 2 (BWUP), Site 4 (GWUP), Site 8 (TWUP) and Site 12 (WWUP), immediately below weirs (lower pool) Site 5 (GWLP), and Site 9 (TWLP) and from regions of the main channel that were unaffected by weirs Site 6 (WBMC), Site 10 (WYMC), Site 11 (NBMC) and Site 13 (CPMC). The upper pool sites supported large stands of *L. peploides.* Lower pool sites were characterised by few microhabitats, with open littoral areas of clay and sand substrata dominating the channel. Main channel sites (unaffected by weirs) contained a higher diversity of microhabitats, including snags and leaf litter.

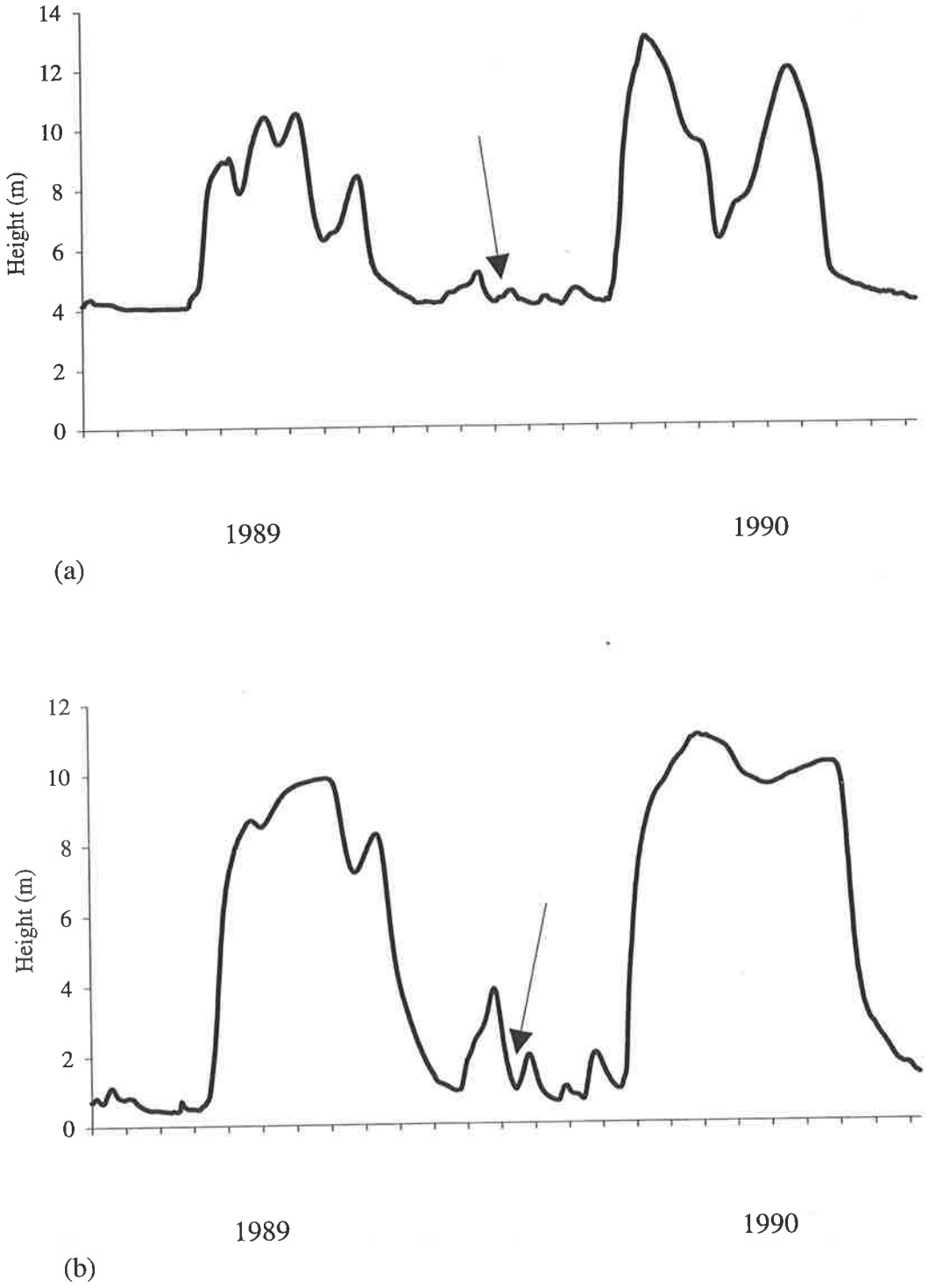


Figure 3.4 Hydrographs for the Darling River at (a) Bourke and (b) Wilcannia for the period January 1989 until December 1990. Arrows indicate the time of sampling.

Samples from the lower River Murray were from 12 sites between Renmark and Morgan (Table 3.2). The sites covered three floodplain areas: Chowilla (Figure 3.5a), Pike River (Figure 3.5b) and Scott Creek (Figure 3.5c), chosen due to their relatively pristine condition. The Chowilla floodplain (Wetland M207; Thompson, 1986) is the largest remaining region of floodplain habitat in the lower Murray, occupying an area of 1650 km^2 upstream from Renmark. This was the location of the 1988 Nature Conservation Society of South Australia Biological Survey (cf. O'Malley and Sheldon, 1990). Descriptions of the geography, physical habitats, aquatic macroinvertebrates and aquatic/riparian vegetation of the floodplain are given elsewhere (cf. NEC, 1988; Roberts and Ludwig, 1990; Sheldon and Lloyd, 1990; Boulton and Lloyd, 1991; Roberts and Ludwig, 1991).

The Pike River floodplain (Wetland M193; Thompson, 1986) lies on the eastern side of the River Murray and south of Renmark and Lock 5. The area comprises a complex system of creeks, backwaters, lagoons and billabongs with approximately 410 ha of permanent water. A description of the geography, vegetation and land management within the region is provided in the *Pike River Land Management Project* (DEP, 1983). The Scotts Creek floodplain (Wetland M089; Thompson, 1986) lies within the Gorge section of the lower River Murray (Chapter 1 and Chapter 4) on the western side of the main channel downstream from Morgan. It is a small area of floodplain habitat covering only 23 ha. Most of the waterbodies in the wetland are directly connected to the main channel of the Murray at normal pool level.

The mesohabitats sampled on the lower Murray floodplain include permanent billabongs, backwaters, fast and slow flowing anabranches and the main channel. The billabongs, Site 2 (SLBB) and Site 10 (CGBB), are shallow depressions in the floodplain replenished during overbank flows. The backwaters, Site 4 (IMBW), Site 8 (PRBW) and Site 12 (SCBW) are large, deep water bodies connected to the main channel at normal pool level. At the time of sampling they contained diverse microhabitats including submerged and emergent vegetation, snags and unvegetated littoral areas. Slow anabranches, Site 6 (MNAB) and Site 7 (PRAB), are the dominant anabranch type on the lower Murray floodplain and are characteristically wide and deep. MNAB contains few microhabitats dominated by unvegetated open littoral areas and snags whereas PRAB, perhaps due to a more stable water-level, supports large stands of *V. spiralis*.

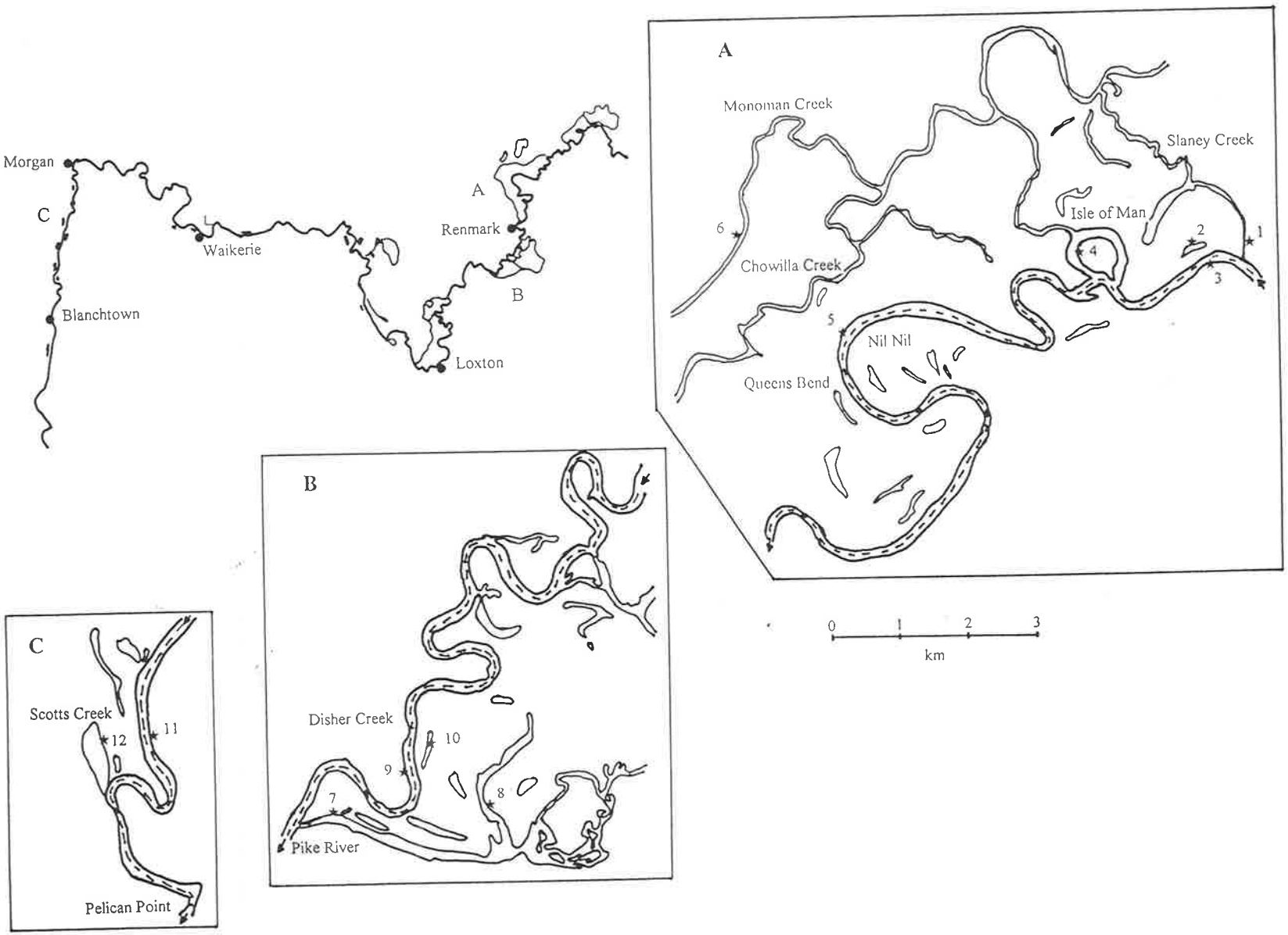


Figure 3.5 Study sites on the lower River Murray floodplain, South Australia, January 1990. Site abbreviations and descriptions are given in Table 3.2.

Table 3.2 Number and abbreviation of sites sampled on the lower River Murray floodplain in January 1990.

No	Abbreviation	Site
1	SLAB	Slaney Creek, fast anabranch, Chowilla
2	SLBB	Billabong near Slaney Creek, Chowilla
3	SIMC	Main channel near Slaney Island, Chowilla
4	IMBW	Isle of Man Backwater, Chowilla
5	QBMC	Main channel near Queens Bend, Chowilla
6	MNAB	Monoman Creek, slow-flowing anabranch, Chowilla
7	PRAB	Pike River, slow-flowing anabranch
8	PRBW	Pike River Backwater
9	PRMC	Main channel near Pike River
10	CGBB	Coongaleena Billabong
11	MGMC	Main channel downstream of Morgan
12	SCBW	Backwater at Scott Creek

Fast flowing anabranches are rare on the lower Murray floodplain at normal pool level. In this study they were represented by one site, Site 1 (SLAB), which has a relatively narrow and deep channel. The main channel of the lower Murray, Site 5 (QBMC), Site 9 (PRMC) and Site 11 (MGMC), is both wide and deep containing a range of microhabitats. Samples were collected in summer 1990; river levels were typical of summer, high flows having occurred the previous spring (cf. Figure 3.6).

The specific mesohabitats sampled on the floodplain of the Darling and the Murray are summarised in Table 3.3.

Table 3.3 Distribution of sites among mesohabitats sampled on both the Darling River and River Murray floodplain.

Mesohabitat	Darling River	River Murray
Temporary Billabong	WBBB, CPBB	
Permanent Billabong	BKBB, OTBB	SLBB, CGBB
Backwater		IMBW, PRBW, SCBW
Slow Anabranch		MNAB, PRAB
Fast Anabranch		SLAB
Main Channel	WBMC, WYMC, NBMC, CPMC	SIMC, QBMC, PRMC, MGMC
Upper Pool, Main Channel	BWUP, GWUP, TWUP, WWUP	
Lower Pool, Main Channel	GWLP, TWLP	

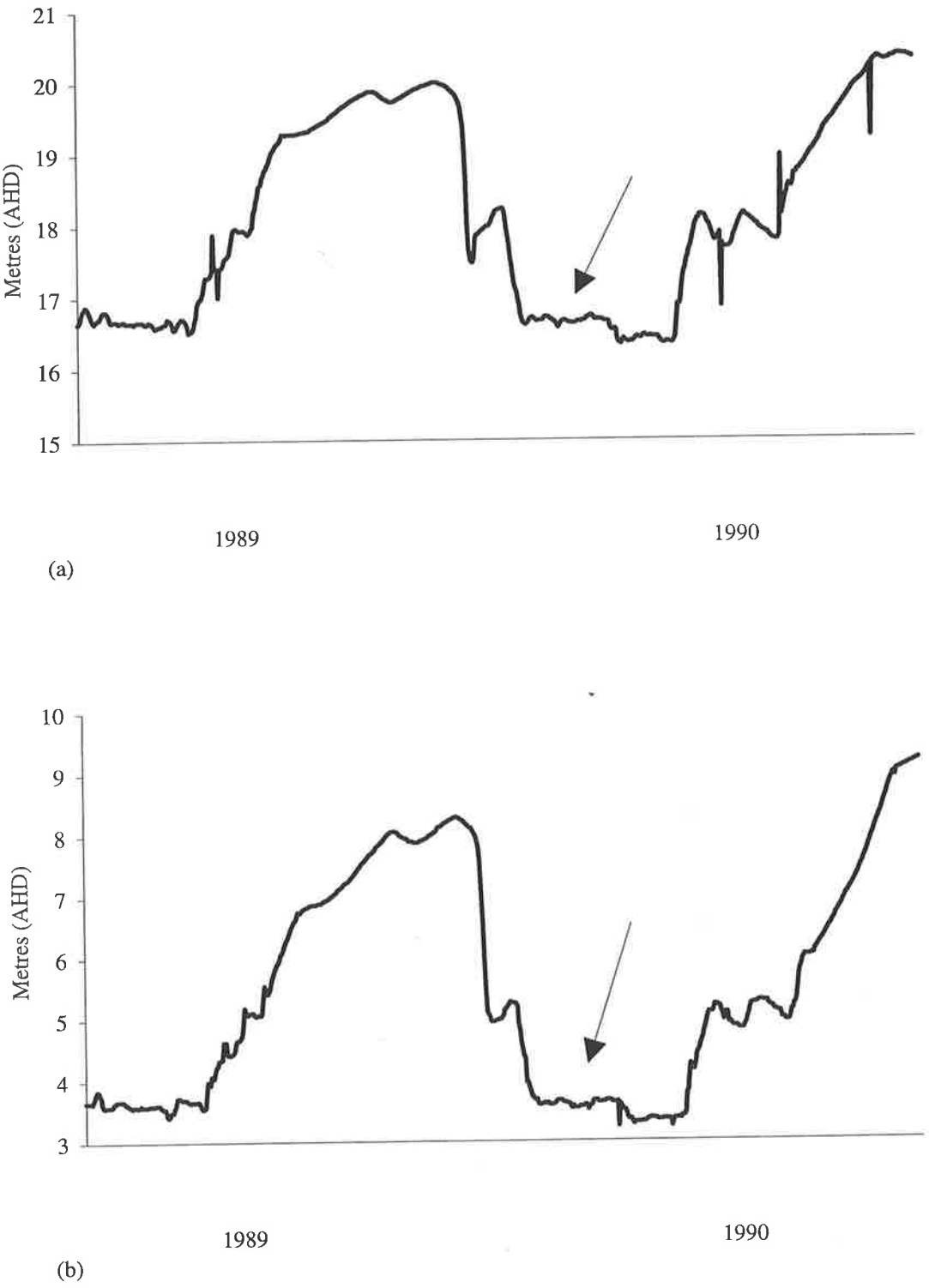


Figure 3.6 Hydrographs for the lower River Murray at (a) lower pool of Lock 6 and (b) lower pool of Lock 2 for the period January 1989 until October 1990. Arrows indicate the time of sampling.

3.3 METHODS

3.3.1 Field Methods

When an area containing a diversity of habitats is to be sampled stratified techniques (e.g. stratified random sampling) are of the greatest value (Southwood, 1966). Stratifying increases sampling efficiency as the population is divided into sub-populations or strata (cf. Elliott, 1977). These strata tend to be more homogeneous in character than the whole population. The littoral zone of a river can be described across a number of spatial scales (Chapter 2); thus, sites in the littoral zone of both rivers (macrohabitats) were chosen to represent the major mesohabitats present. Each mesohabitat was subsequently stratified into the microhabitats defined above; the most abundant of these were then sampled randomly.

Benthic, nektonic and epiphytic invertebrates were collected in three replicate samples from each microhabitat by sweeping a pond net (500 µm mesh) for 20 seconds while moving over the microhabitat. Samples were preserved in 70 percent ethanol and returned to the laboratory. At each site instantaneous values for water temperature, dissolved oxygen, conductivity, turbidity and water depth were measured. Substratum type was recorded as clay, sand or silt. The amount of fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) in each sample was ranked from 0 (absent) to 5 (very abundant). Conductivity values (K), at 18 °C, were converted to salinity (mg/L) using the following formulae:

$K_t \rightarrow K_{18}$ $\quad K_{18} = \dfrac{K_t}{1+0.025(t-18)}$ $\quad K$ = conductivity (μScm^{-1}); t = temperature (°C)

K18 → Salinity $\quad$ Salinity (mg/L) = $K_{18}(0.666+0.0034K_{18})$; regression due to Williams (1966)

3.3.2 Laboratory Processing

Preserved samples were washed through a nest of sieves with mesh sizes of 4000, 2000, 1000 and 250 µm. Taxa retained on each mesh were hand-sorted by eye. Macroinvertebrates were enumerated, and identified as far as practicable using keys (Table 3.4). Tiny specimens too small to classify beyond family were placed into artificial categories (e.g. 'Tiny Zygoptera') and included in the analysis as separate taxa.

Table 3.4 List of keys used for invertebrate identification.

Group	Reference
General	Williams, W.D. (1980) *Australian Freshwater Life,* MacMillan, Australia.
Mollusca	Smith, B.J. and R.C. Kershaw (1979) *Field Guide to the Non-Marine Molluscs of South-eastern Australia*, Australian National University Press.
Insecta: Ephemeroptera	Suter, P.J. (1986) The Ephemeroptera (Mayflies) of South Australia. *Records of the South Australian Museum* **19**:339-397.
Insecta: Odonata	Hawking, J.H. (1986) *Dragonfly larvae of the River Murray System,* Murray-Darling Freshwater Centre (MDFRC) Technical Report 6.
	Watson, J.A.L. (1991) The Australian Gomphidae. *Invertebrate Taxonomy* **5**:289-441.
Insecta: Hemiptera	Anderson, N.M. (1969) A new Microvelia from Australia with a check-list of Australian species (Hemiptera, Veliidae), *Entomologiske Meddelelser* **37**:253-261
	Lansbury, I. (1969) The genus *Anisops* in Australia (Hemiptera-Heteroptera, Notonectidae. *Journal of Natural History* **3**:433-458.
Insecta: Coleoptera	Watts, C.H.S. (1963) The larvae of Australian Dytiscidae (Coleoptera) *Transactions of the Royal Society of South Australia* 87:23-40.
	Mathews, E. *Beetles of South Australia, Parts 1-5*, Museum of South Australia
Insecta: Chironomidae	Martin, J. Various unpublished keys to the Australian Chironomidae.
	Cranston, P.S. Unpublished key to the Australian Chironomidae
Insecta: Trichoptera	Cartwright, D.I. and J.C. Dean (1982) A key to the Victorian genera of free-living and retreat-making caddis-fly larvae (Insecta: Trichoptera). *Memoirs of the National Museum*, Victoria 43:1-13.
	Cartwright, D. (1991) Key to mature larvae of the families Ecnomidae, Philopotamidae and Polycentropodidae of Australia. Unpublished Key from Trichoptera Workshop, MDFRC, February 1991.
	Cartwright, D. and J.C. Dean (1991) Key to genera of selected families of Australian Trichoptera larvae. Unpublished Key from Trichoptera Workshop, MDFRC, February 1991

Each taxon was assigned to one of three broad functional feeding groups (FFGs): collectors, predators and scrapers (cf. Cummins and Klug, 1979), with collectors incorporating shredders, filterers and gatherers. The assigned FFGs, particularly "collectors", are tentative as the diets of most taxa are little known. The use of broad FFG's for classifying the taxa from large rivers may be more appropriate than the narrower groups applied to the taxa from small streams (e.g. Boulton and Lake, 1992a, 1992b), as Palmer *et al.* (1993a) found the gut contents of a majority of the mayfly and caddis-fly taxa from the Buffalo River, South Africa, consisted of fine amorphous organic matter. Classification of these taxa beyond general "collector" was difficult and relied heavily on behavioural and morphological details (Palmer *et al.,* 1993b). The use of behaviour and morphology for determining diet may be misleading as many taxa have generalised mouthparts capable of scraping, brushing and collecting. Species with similar mouthparts may use different strategies for food collection and behaviour can change through development (Boulton, 1988). Despite

the limitations, FFG's are used in this study to suggest the significance of different food resources in the habitats.

In this study classification of taxa into functional feeding groups followed Cummins and Klug (1979), Boulton (1988) and Boulton and Lloyd (1991).

3.2.3 Data Analysis

Kruskal-Wallis non-parametric one-way ANOVAs (SYSTAT v. 5.0; Wilkinson, 1990) were used to compare richness, total abundance and the three broad FFG's (predator, collector and scraper) between sites, mesohabitats and microhabitats in the Darling and Murray, separately. Within each river these tests are not independent. Thus, to decrease the chance of Type I errors, the nominated significance level (0.05) was adjusted by dividing with the number of non-independent tests (the Bonferroni procedure: Neter *et al.,* 1985). Differences were located using Tukey's Honestly Significant Difference (HSD) test (Zar, 1984) for unplanned multiple comparisons. The Tukey's test is a parametric method. As the data were not normal, non-parametric multiple comparisons would have been more appropriate for locating differences, however, their computations are complex, particularly when this number of samples is considered. As nearly all the differences located using Kruskal-Wallis ANOVAs were highly significant, Tukey's tests were used. All univariate statistics were computed using SYSTAT (Wilkinson, 1990).

Abundances of benthic invertebrates, even in replicate samples, are variable and can span several orders of magnitude. If this is the case, and untransformed data are used in multivariate analyses, then only the few dominant species, rather than the entire species composition, will control the results (Elliott, 1977; Gauch, 1982). Appropriate transformation of abundance data into an intermediate range, approximately 0 to 10, allows both quantitative and qualitative information to be expressed without one dominating the other (Gauch, 1982). Before analysis abundances of macroinvertebrates were transformed by $\log_{10}$ (x+1) (see Elliott, 1977).

The polythetic divisive classification TWINSPAN (Two-Way INdicator SPecies ANalysis: Hill *et al.,* 1975; Hill, 1979), recommended for hierarchical classification of ecological data (Gauch, 1982), in the DECODA (Database for Ecological COmmunity DAta; Belbin, 1991) computer package, was used to summarise the data and identify assemblages characteristic of the meso- and microhabitats. TWINSPAN

uses reciprocal averaging to initially order the samples, then breaks the ordination near its middle to produce a crude dichotomy of the samples. TWINSPAN not only classifies sites but constructs an ordered two-way table from a sites-by-species matrix. It deals with quantitative data by converting species abundances into categories known as *pseudospecies* (Hill *et al.,* 1975) which are determined by 'pseudospecies cut levels' (Hill, 1979). The construction of the two-way table in TWINSPAN is explained step by step in Jongman *et al.* (1987). Based on the range of species abundances in the dataset pseudospecies cut levels equivalent to 0, 2, 5, 10, 20, 50, 100, 200 and 750 were used, along with the default values for all other settings.

The two-way tables produced by TWINSPAN summarise species co-occurrences across the samples and group samples with similar species compositions (Boulton, 1988). The large two-way tables may be further summarised by calculating a "fidelity index" for each species and sample group (see Boesch, 1977 cited in Boulton, 1988 and Boulton and Lake 1992a, 1992b). This index measures sample group 'preference' or 'avoidance' by a species group by estimating the relative representations of species groups in various sample groups. The fidelity index (F_{ij}) is expressed as:

$$F_{ij} = \frac{(a_{ij} \sum_j n_j)}{(n_j \sum_j a_{ij})}$$

where a_{ij} is the number of occurrences of members of species group i in sample group j, and n_j is the number of entities in sample group j. Values greater than one demonstrate 'preference' by a species group for a sample group; values less than one indicate avoidance.

The way in which TWINSPAN classifies groups was recently criticised by Belbin and McDonald (1993). In a comparison of generated data sets of known characteristics TWINSPAN apparently misclassified 36 percent of the sites. One main reason for this misclassification is the use of the divisive clustering method. When one cluster is split the divisive nature of TWINSPAN precludes reconnection, an early error can have significant implications. Therefore, data for samples from both the Darling River and the lower River Murray were also examined using flexible-UPGMA in the PATN software package (Belbin, 1988). Flexible-UPGMA

is an agglomerative hierarchical method of classification which has been suggested to provide a better recovery of true clusters than TWINSPAN (Belbin and McDonald, 1993). The Kulczynski coefficient was used as the measure of dissimilarity between samples as it is one of the most robust and effective measures available (Faith *et al.*, 1987). Default options were chosen with a β value of 0, as suggested by Belbin (1993). In the present analyses flexible-UPGMA was only used to support the cluster output from TWINSPAN which provides a larger amount of useful ecological information, in the provision of indicator species and two-way tables.

Ordination of the macroinvertebrate data was conducted using Semi-Strong Hybrid multidimensional scaling (SSH) in the PATN software package (Belbin, 1988). The Kulczynski coefficient was again used as the measure of dissimilarity between samples. Solutions were calculated in both four and two dimensions. Where the 'stress' (badness of fit measure; Kruskal and Wish, 1978) was similar for both, the solution in two dimensions is presented. Fifty iterations and a ratio-ordinal cut value of 0.8 were used over 50 random starts. Sample group relationships were further illustrated by mapping the groups derived from TWINSPAN onto the SSH ordination.

Relationships between environmental and community data are usually many, complex and nonlinear (see Gauch, 1982). The aim of conducting multivariate analyses is to detect major differences in species composition for sample groups which are potentially related to environmental differences (Boulton, 1988). Spearman Rank correlations (Zar, 1984) between the physicochemical variables measured in the field and the ordination scores on the SSH axes were calculated to examine relationships between environmental factors and macroinvertebrate assemblage composition.

When the spatial patterns in both rivers were considered three measures of diversity were used to provide a reflection of differences in richness and evenness of the assemblages. The Margalef Index (D_{Mg}) and the Menhinick Index (D_{Mn}) are relatively simple indices that use a combination of S (the number of species recorded) and N (the total number of individuals summed over all S species) (Magurran, 1988).

$$D_{Mg} = (S-1)/\ln N$$

$$D_{Mn} = S/\sqrt{N}$$

The Berger-Parker Index (d) is also mathematically simple, expressing the proportional importance of the most abundant species, using N_{max} (the number of individuals in the most abundant species). The reciprocal form of the Berger-Parker index is usually adopted ($1/d$) such that an increase in the value of the index accompanies an increase in diversity and decrease in dominance (Magurran, 1988).

$$d = N_{max}/N$$

Margalef's index emphasises the richness component of the assemblage whereas the Berger-Parker index stresses the evenness component. The calculation of these indices was recommended by Magurran (1988) as a quick measure of the species abundance and dominance components of diversity.

3.4 Results

3.4.1 Darling River Floodplain

Environmental Conditions

The environmental conditions for all sites at the time of sampling are given in Table 3.5. The Darling River carries a high load of very fine suspended sediment, with particle diameters mostly less than 40 µm (Woodyer, 1978). Consequently, Secchi depths measured at each site were below or around 20 cm. Salinities at all sites, except CPBB, were low when compared with similar sites on the lower River Murray (cf. Section 3.3.2; Boulton and Lloyd, 1991), mostly near 200 mg/L. The temporary billabong (CPBB) differed from all other sites in having a high salinity (719 mg/L), due to receding water levels. All sites were well oxygenated, near saturation, with instantaneous water temperatures ranging from 20-31 °C.

Table 3.5 Environmental conditions measured in the littoral zone of each site on the Darling River, NSW in January 1990.

	Site	Salinity (mg/L)	Oxygen (% saturation)	Secchi depth (cm)	Temperature °C
1	BKBB	175.2	82	6	24
2	BWUP	183.1	74	8	28
3	OTBB	253.7	87	24	26
4	GWUP	173.8	98	9	30
5	GWLP	171.8	90	8	30
6	WBMC	184.1	79	11	27
7	WBBB	266.4	100	13	24
8	TWUP	196.2	96	12	29
9	TWLP	265.7	84	14	27
10	WYMC	201.8	85	11	27
11	NBMC	191.1	78	11	28
12	WWUP	203.1	76	11	28
13	CPMC	207.1	85	12	28
14	CPBB	719.3	88	7	20

Community Composition

A total of 18,303 individuals from 72 taxa (Appendix B) was collected in 111 samples. Insects were the dominant group, comprising 85 percent of taxa and 81 percent of individuals (Figure 3.7). Of the Insecta, the Diptera and Coleoptera comprised most taxa (26 and 15 respectively), with Hemiptera (7), Odonata (5), Trichoptera (5) and Ephemeroptera (3). With regard to the distribution of individuals amongst taxa the Hemiptera (47%) and Diptera (35%) were the most common (Figure 3.8). Overall, corixids (*Micronecta* spp.) were the most abundant taxon, with the freshwater prawn *Macrobrachium australiense* comprising the greatest biomass. Other abundant taxa included the mayflies (*Tasmanocoenis arcuata* and *Cloeon* sp.), gastropods *Ferrissia* spp., chironomids (*Coelopynia* sp. and *Dicrotendipes* sp.) and the trichopteran *Oecetis* sp. Eight taxa occurred only once.

Table 3.6 gives the mean (SE) number of taxa and individuals for each site. Both median number of taxa and number of individuals varied significantly between sites (Kruskal-Wallis H = 55.74, 58.87, respectively, $p<0.001$). When sites were grouped into mesohabitats differences remained (H = 49.25, 45.23, respectively, $p<0.001$).

Overall, billabongs had a greater number of taxa and individuals than channel habitats. The temporary billabongs (WBBB and CPBB) characteristically had more individuals than permanent billabongs (BKBB and OTBB) but contained similar numbers of taxa. An examination of the channel habitats showed upper pool sites (BWUP, GWUP, TWUP AND WWUP) to have more taxa than either lower pool sites (GWLP, TWLP) or sites unaffected by weirs (WBMC, WYMC, NBMC, CPMC). The abundance of individuals, however, was similar for all channel sites.

Significant differences also existed between mesohabitats for the three functional feeding groups (Table 3.7). Collectors comprised the greatest number of taxa across all habitats but were not always the most abundant (Table 3.8; Figure 3.9). More collectors occurred in the channel sites than in either the permanent or temporary billabong. The greatest abundance of collectors, mostly *Micronecta* spp., were found in the temporary billabongs. Although having a similar number of taxa, upper pool samples had comparatively few collectors with the assemblage dominated by predators. The highest number of predatory taxa occurred in the temporary billabongs. Scrapers comprised only a minor portion of the invertebrate community, both in number of taxa and overall abundance. Most scrapers were found in permanent billabongs and lower pool sites. The dominant scrapers were the ancylid gastropods *Ferrissia* spp.

Both, number of taxa and number of individuals, also differed between the microhabitats ($H = 44.92$, 42.36, respectively, $p<0.001$). More taxa were collected from vegetation and snags than from unvegetated littoral regions, however, the abundance of individuals was similar for all microhabitats (Table 3.9; Figure 3.10). Significant differences also existed between microhabitats for all functional feeding groups (cf. Table 3.7).

Table 3.6 The mean number *(SE)* of (a) taxa and (b) individuals in total and for three functional feeding groups at each site from the Darling River collected in January 1990. (n) = number of samples

(a)

	(n)	Total	Predators	Collectors	Scrapers
BKBB 1	3	21.3 *(0.30)*	9.3 *(0.66)*	10.0 *(0.57)*	2.0 *(0.57)*
BWUP 2	6	17.5 *(1.76)*	6.0 *(1.26)*	10.5 *(0.53)*	1.0 *(0.36)*
OTBB 3	9	20.5 *(1.77)*	5.7 *(0.85)*	12.4 *(0.91)*	2.3 *(0.41)*
GWUP 4	6	11.7 *(1.68)*	2.5 *(0.76)*	8.5 *(0.99)*	0.6 *(0.33)*
GWLP 5	6	4.7 *(3.48)*	1.3 *(0.56)*	2.8 *(0.95)*	0
WBMC 6	10	8.2 *(0.66)*	2.1 *(0.31)*	6.1 *(0.5)*	0
WBBB 7	5	18.6 *(2.29)*	7.0 *(0.71)*	10.6 *(1.32)*	1.0 *(0.40)*
TWUP 8	9	11.8 *(1.79)*	4.0 *(0.74)*	7.0 *(0.86)*	0.8 *(0.43)*
TWLP 9	6	9.6 *(1.56)*	2.3 *(0.61)*	7.3 *(0.98)*	0
WYMC 10	14	9.4 *(1.05)*	2.5 *(0.37)*	6.8 *(0.73)*	0.1 *(0.07)*
NBMC 11	9	9.8 *(1.44)*	2.2 *(0.36)*	7.2 *(1.05)*	0.3 *(0.16)*
WWUP 12	9	9.8 *(1.66)*	3.1 *(0.45)*	6.3 *(1.23)*	0.3 *(0.23)*
CPMC 13	16	8.1 *(0.81)*	2.4 *(0.33)*	5.6 *(0.55)*	0.1 *(0.06)*
CPBB 14	3	14.0 *(0.57)*	8.0 *(0.00)*	6.0 *(0.57)*	0

(b)

	(n)	Total	Predators	Collectors	Scrapers
BKBB 1	3	476.3 *(116.7)*	927.6 *(146.5)*	362.6 *(91.8)*	3.6 *(1.4)*
BWUP 2	6	126.3 *(23.9)*	35.8 *(12.8)*	87.8 *(10.9)*	2.6 *(1.2)*
OTBB 3	9	259.7 *(52.9)*	33.2 *(8.4)*	155.4 *(26.5)*	71.1 *(20.3)*
GWUP 4	6	49.6 *(10.5)*	5.0 *(2.2)*	44.0 *(9.6)*	0.6 *(0.3)*
GWLP 5	6	14.8 *(9.8)*	2.5 *(1.5)*	12.3 *(3.2)*	0
WBMC 6	10	41.6 *(5.9)*	4.4 *(0.9)*	37.2 *(5.3)*	0
WBBB 7	5	1149.4 *(81.5)*	194.0 *(45.6)*	948.2 *(82.9)*	7.2 *(5.6)*
TWUP 8	9	67.2 *(18.4)*	468.9 *(26.2)*	47.4 *(13.8)*	2.8 *(2.0)*
TWLP 9	6	42.3 *(6.6)*	7.2 *(2.6)*	35.2 *(4.4)*	7.2 *(2.6)*
WYMC 10	14	48.2 *(9.1)*	10.6 *(2.7)*	37.5 *(6.8)*	0.1 *(0.1)*
NBMC 11	9	61.6 *(13.4)*	9.3 *(2.5)*	51.9 *(11.2)*	0.4 *(0.2)*
WWUP 12	9	60.3 *(17.5)*	9.2 *(2.2)*	50.2 *(16.4)*	0.9 *(0.8)*
CPMC 13	16	36.7 *(6.1)*	10.8 *(2.3)*	25.8 *(5.3)*	0.1 *(0.1)*
CPBB 14	3	1336.3 *(303.8)*	198.6 *(29.4)*	1137.6 *(285.8)*	0

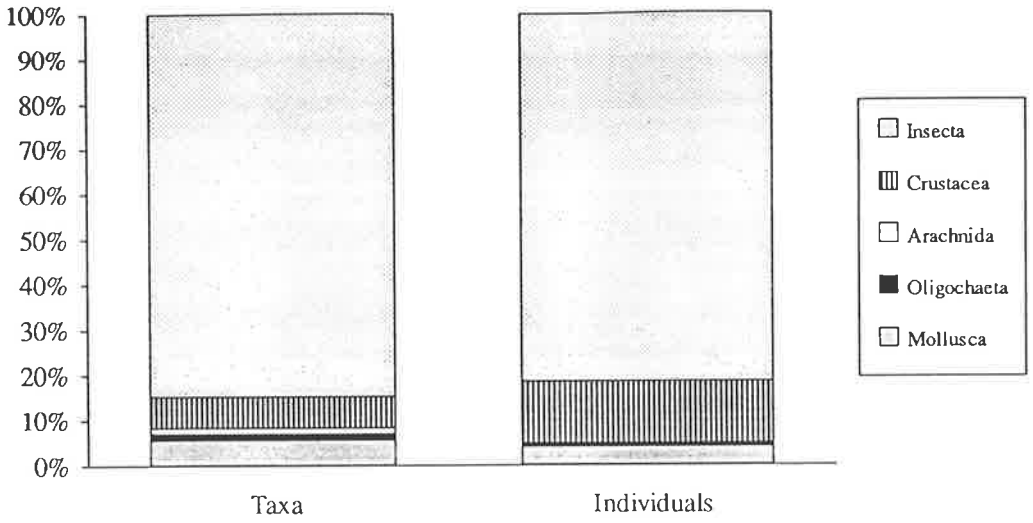


Figure 3.7 Percent representation of the major invertebrate groups in the Darling River, in terms of the number of taxa of each group and the abundance of individuals.

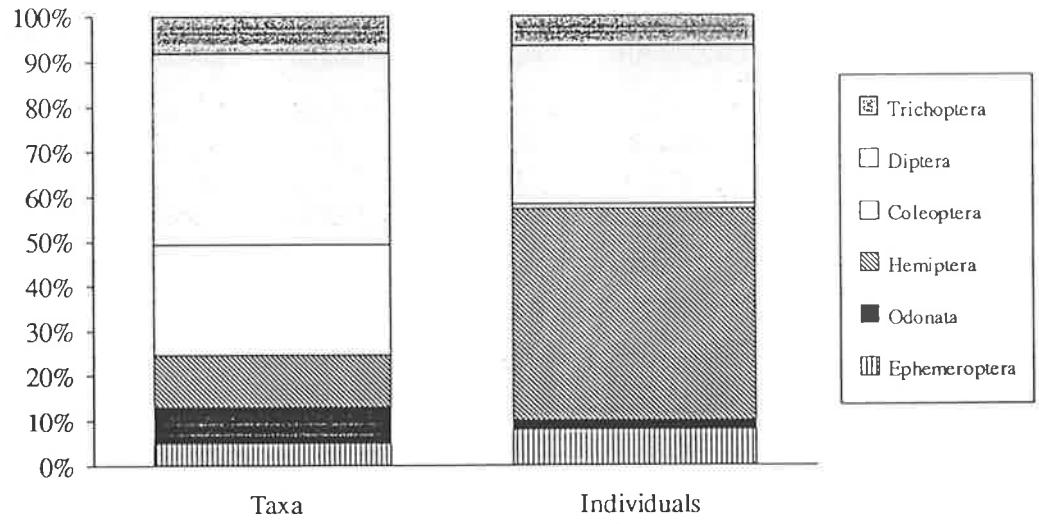


Figure 3.8 Percent representation of the major Insect orders from the Darling River, in terms of the number of taxa within each order and the abundance of individuals.

Table 3.7 Values for Kruskal-Wallis H for differences in the number of taxa and number of individuals in each FFG for mesohabitats and microhabitats.

	Number of Taxa	Number of Individuals
Mesohabitat		
Collector	H=31.32, p<0.001	H=47.37, p<0.001
Predator	H=44.64, p<0.001	H=37.56, p<0.001
Scraper	H=48.72, p<0.001	H=41.37, p<0.001
Microhabitat		
Collector	H=35.04, p<0.001	H=41.04, p<0.001
Predator	H=41.32, p<0.001	H=32.72, p<0.001
Scraper	H=47.89, p<0.001	H=40.28, p<0.001

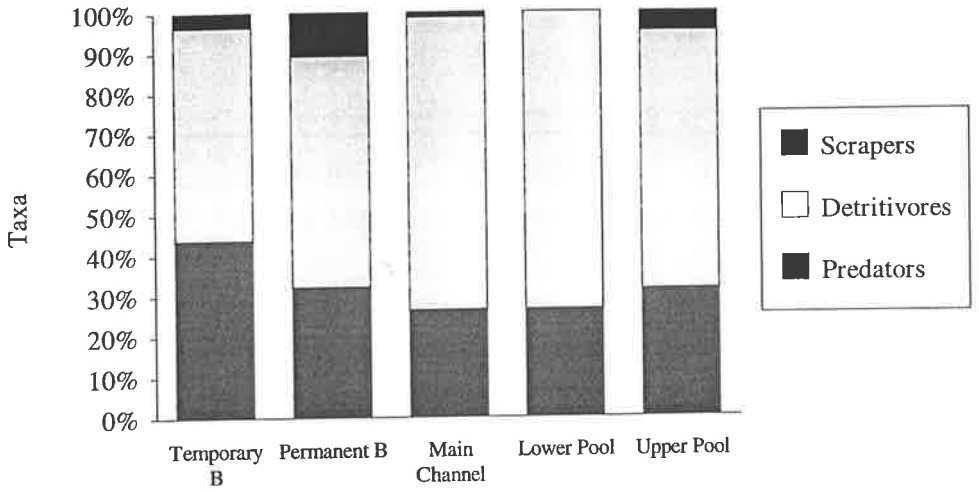
Table 3.8 The mean number *(SE)* of (a) taxa and (b) individuals in total and for three functional feeding groups for each mesohabitat sampled from the Darling River in January 1990. (n) = number of samples

(a)

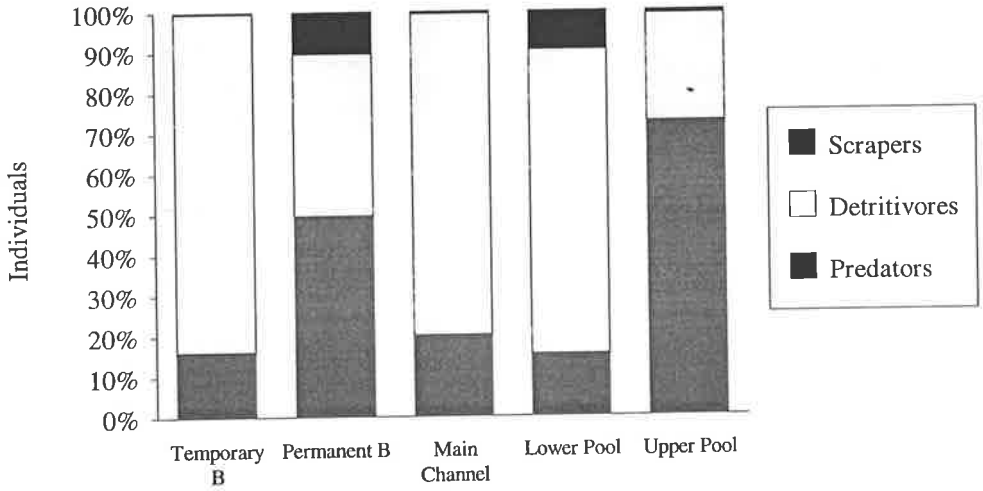
	(n)	Total	Predators	Collectors	Scrapers
Temporary Billabong	8	16.87 *(1.62)*	7.37 *(0.46)*	8.87 *(1.17)*	0.62 *(0.17)*
Permanent Billabong	12	20.75 *(1.31)*	6.67 *(0.79)*	11.83 *(0.76)*	2.25 *(0.33)*
Main Channel	49	8.77 *(0.49)*	2.33 *(0.17)*	6.35 *(0.35)*	0.12 *(0.05)*
Lower Pool	12	6.92 *(1.03)*	1.83 *(0.42)*	5.08 *(0.94)*	0
Upper Pool	30	12.3 *(0.98)*	3.83 *(0.43)*	7.80 *(0.56)*	0.67 *(0.17)*

(b)

	(n)	Total	Predators	Collectors	Scrapers
Temporary Billabong	8	1219.5 *(115.9)*	195.7 *(28.9)*	1019.2 *(111.4)*	4.5 *(3.6)*
Permanent Billabong	12	313.9 *(54.2)*	256.8 *(121.1)*	207.2 *(38.7)*	54.2 *(17.4)*
Main Channel	49	45.6 *(4.3)*	9.2 *(1.2)*	36.2 *(3.6)*	0.3 *(0.1)*
Lower Pool	12	28.6 *(5.5)*	4.8 *(1.5)*	23.7 *(4.3)*	3.1 *(1.6)*
Upper Pool	30	73.5 *(10.1)*	151.6 *(39.4)*	55.7 *(7.4)*	1.9 *(0.7)*



(a)



(b)

Figure 3.9 Proportion of each functional feeding group in the mesohabitats sampled on the Darling floodplain, January 1990, (a) taxa and (b) individuals.

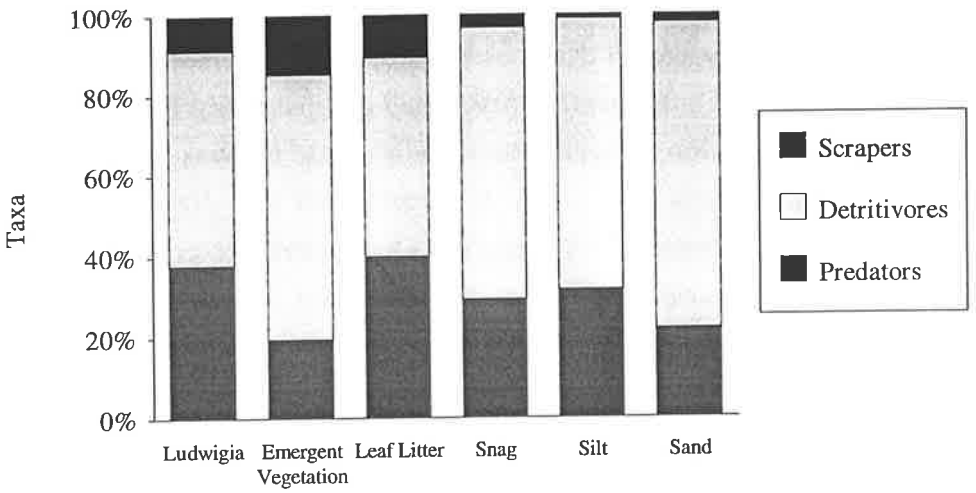
Table 3.9 The mean number *(SE)* of (a) taxa and (b) individuals in total and for three functional feeding groups for each microhabitat sampled from the Darling River in January 1990. (n) = number of samples

(a)

	(n)	Total	Predators	Collectors	Scrapers
Ludwigia	9	17.55 *(1.3)*	233.21 *(104.1)*	9.44 *(0.6)*	1.55 *(0.4)*
Emergent Vegetation	5	23.80 *(1.5)*	415.21 *(235.1)*	12.41 *(1.3)*	2.81 *(0.6)*
Leaf Litter	3	16.67 *(3.4)*	27.30 *(18.5)*	10.67 *(1.8)*	2.31 *(0.3)*
Snag	42	12.07 *(0.7)*	68.97 *(23.3)*	8.09 *(0.4)*	0.41 *(0.1)*
Sand	15	5.87 *(0.6)*	2.80 *(0.6)*	4.53 *(0.5)*	0.13 *(0.1)*
Silt	37	9.29 *(0.7)*	67.76 *(20.8)*	6.27 *(0.5)*	0.11 *(0.1)*

(b)

	(n)	Total	Predators	Collectors	Scrapers
Ludwigia	9	164.8 *(32.7)*	233.2 *(104.1)*	117.9 *(20.7)*	5.2 *(1.8)*
Emergent Vegetation	3	458.4 *(69.1)*	415.2 *(235.1)*	306.8 *(61.1)*	80.4 *(33.8)*
Leaf Litter	5	227.0 *(99.1)*	27.3 *(18.5)*	132.0 *(54.2)*	67.7 *(29.5)*
Snag	42	167.1 *(50.3)*	68.9 *(23.3)*	140.9 *(43.6)*	2.7 *(1.1)*
Sand	15	20.3 *(3.1)*	2.8 *(0.6)*	17.5 *(3.1)*	0.2 *(0.1)*
Silt	37	176.3 *(68.6)*	67.7 *(20.8)*	140.6 *(57.1)*	0.7 *(0.4)*



(a)

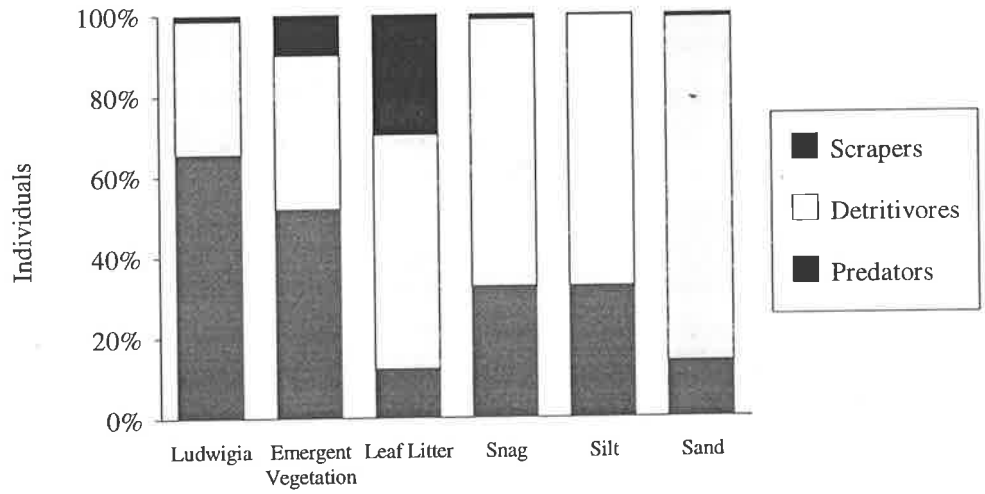


Figure 3.10 Proportion of each functional feeding group in the microhabitats sampled on the Darling floodplain, January 1990, (a) taxa and (b) individuals.

Multivariate Analysis of Samples

TWINSPAN on the log-transformed data yielded twelve groups (A-L) at the fourth level of division (Figure 3.11). Below this were small groups adding little additional information. The first division separated the mainly lentic habitats (Groups A-E) from the lotic habitats (Groups F-L). Indicator species for this division were the corixids *Micronecta* spp., notonectids *Anisops* spp., the ephemeropteran *Cloeon* sp., the leptocerid caddis *Triplectides australis*, the gastropod *Ferrissia* sp. and the chironomid *Parachironomus* sp.

The lentic sites were divided at the second division into two groups. The first (Groups A and B) contained the temporary billabongs Culpaulin (CPBB) and Winbar (WBBB). The second (Groups C and D) the permanent billabongs, Bourke (BKBB) and Orange Tree Lagoon (OTBB), and seven samples from upper pool sites, Bourke (BKUP), Tilpa (TWUP) and Wilcannia (WWUP) (Table 3.10). The weir pool samples in Group F were collected from the *L. peploides* microhabitat (Table 3.11). The temporary billabongs were characterised by large numbers of the predatory caddis *Oecetis* sp., which suggests the absence of vertebrate predators. The permanent lentic sites contained high numbers of the hemipterans *Micronecta* spp. and *Anisops* spp.

The 84 lotic samples separated on a second division into two broad groups. The first (and largest) contained groups F to I and included all samples from sites immediately below weirs (lower pool sites) and a mix of samples from weir pools and those main-channel sites unaffected by weirs (Table 3.10). The second, smaller group (J to L), contained samples from sites above weirs and main-channel sites unaffected by weirs. Indicator species for the first group were *Micronecta* spp., *Ecnomus* sp. and *Macrobrachium australiense*. Indicators for the second group were *Cladopelma* sp., *Coelopynia* sp. and *Procladius* sp. (Figure 3.11).

The most meaningful separations of the lotic sites were related to microhabitats (cf. Table 3.11, Figure 3.12). Groups F, G, J and L contained a majority of samples from snag and silt substrata open littoral sites, where detritus was abundant. Groups H, I and K comprised samples from unvegetated littoral sites with sand substrata that were detritus poor. Significant positive associations of the TWINSPAN groups occurred with temperature and depth. Significant negative associations with CPOM, site salinity and oxygen concentration (Table 3.12).

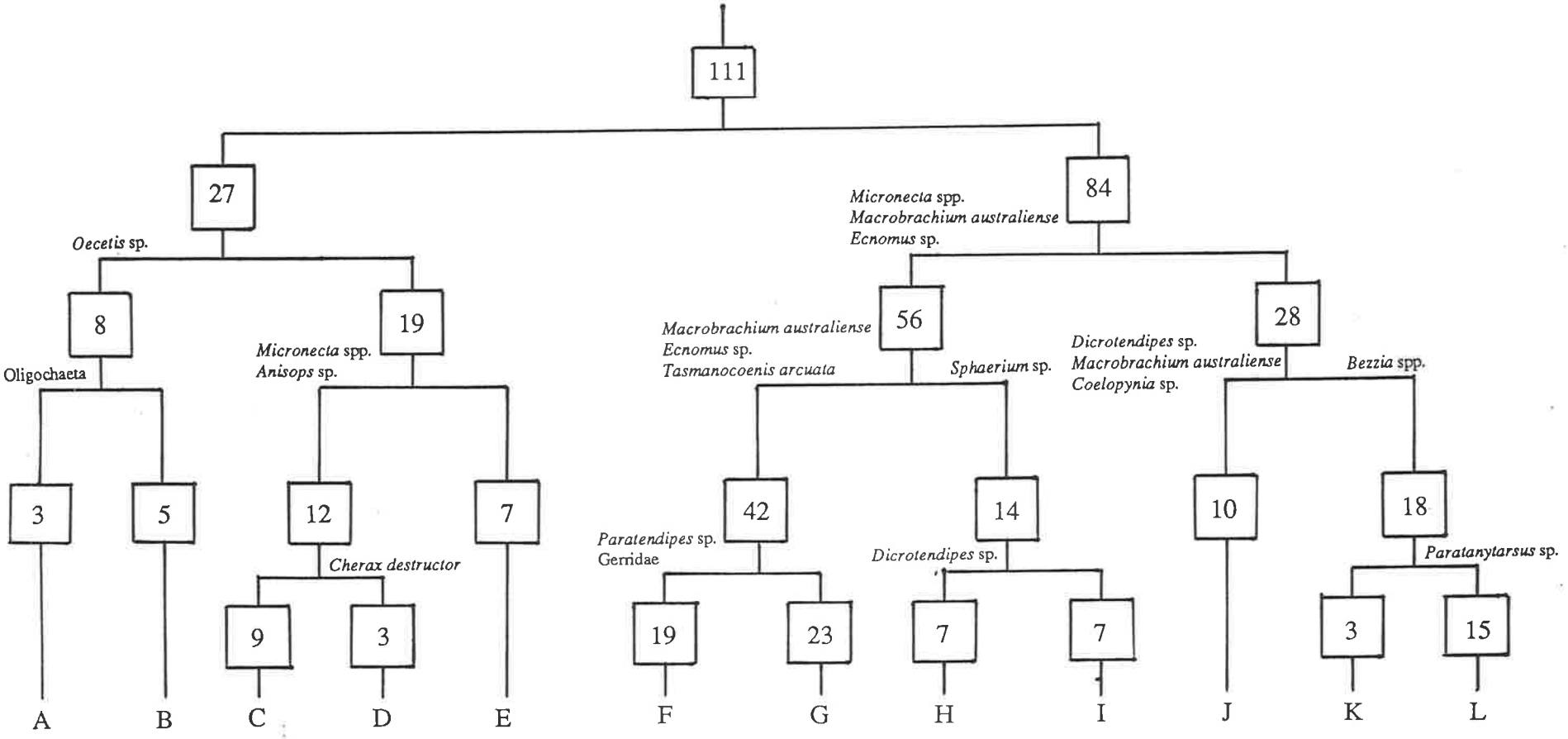


Figure 3.11 TWINSPAN dendogram of the 111 samples collected from the Darling River, in January 1990. Indicator species are listed above the relevant divisions. Entities in sample groups A-L are listed in Table 3.10.

Table 3.10 Samples according to mesohabitat in the eleven sample groups (A-L) yielded by the TWINSPAN of all habitats sampled on the Darling River floodplain in January 1990.

Group	Sample Composition
A	Three Temporary Billabong samples (CPBB)
B	Five Temporary Billabong samples (WBBB)
C	Nine Permanent Billabong samples (OTBB)
D	Three Permanent Billabong samples (BKBB)
E	Seven Upper Pool samples (BWUP, TWUP, WWUP)
F	Seven Upper Pool, five Lower Pool and seven Main Channel samples (GWUP, TWUP, GWLP, TWLP, WYMC, CPMC, WBMC)
G	Ten Upper Pool, four Lower Pool and nine Main Channel samples (BWUP, WWUP, TWUP, TWLP, WBMC, WYMC)
H	One Upper Pool and six Main Channel samples (TWUP, WBMC, WYMC, CPMC)
I	Three Lower Pool and four Main Channel samples (WBMC, WYMC, CPMC, GWLP)
J	Five Upper Pool and five Main Channel samples (TWUP, WWUP, WBMC, WYMC, NBMC< CPMC)
K	One Upper Pool and two Main Channel samples (TWUP, WYMC, CPMC)
L	Six Upper Pool and nine Main Channel samples (TWUP, WWUP, WBMC, NBMC, WYMC, CPMC)

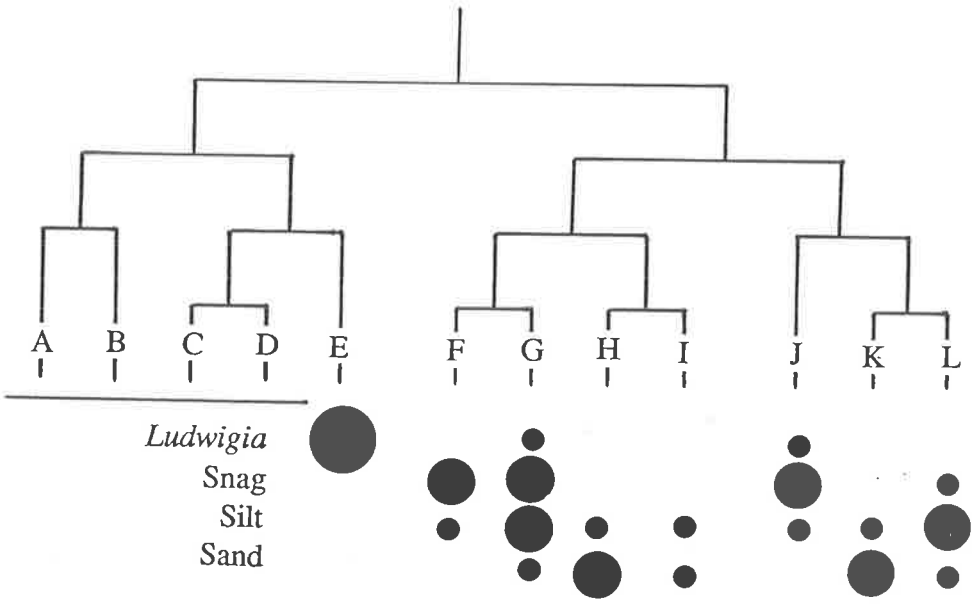


Figure 3.12 A pictorial summary of the microhabitat representation of samples in TWINSPAN groups E to L, as listed in Table 3.11. Large circles depict greater than 70% of samples from the microhabitat occur in the sample group, medium circles 30-70% and small circles 1-30%.

Table 3.11 Samples according to microhabitat in the eleven sample groups (A-L) yielded by the TWINSPAN of all habitats sampled on the Darling River floodplain in January 1990.

Group	Sample Composition
A	Three Temporary Billabong samples (CPBB)
B	Five Temporary Billabong samples (WBBB)
C	Nine Permanent Billabong samples (OTBB)
D	Three Permanent Billabong samples (BKBB)
E	Seven *Ludwigia peploides* samples
F	Eighteen Snag and one Silt sample
G	Nine Snag, ten Silt, three Sand, and one *Ludwigia peploides* sample
H	Two Silt and five Sand samples
I	Four Silt and three Sand samples
J	Six Snag, three Silt and one *Ludwigia peploides* sample
K	One Silt and two Sand samples
L	One Snag, twelve Silt and two Sand samples

Table 3.12 Spearman Rank correlation coefficients (r_S) between environmental variables and the samples in the eleven groups (A-L) yielded by the TWINSPAN of all habitat samples on the Darling River floodplain in January 1990.

Variable	r_S	Significance
CPOM	-0.299	p<0.01
FPOM	-0.115	ns
Shade	-0.344	p<0.001
Salinity	-0.295	p<0.01
Oxygen	-0.241	p<0.01
Temperature	0.408	p<0.001
Secchi Depth	-0.017	ns
Depth	0.291	p<0.01

When the data were analysed using flexible-UPGMA 13 major clusters (A-M) resulted (Figure 3.13). Samples from the four billabong sites (BKBB, OTBB, WBBB, CPBB) formed cluster groups distinct from main channel samples. The similarity of samples from the main channel reflected the microhabitat from which they were collected. This pattern is not substantially different to that produced by TWINSPAN, with the major separations relating to different mesohabitats, particularly lentic billabong and lotic main channel habitats.

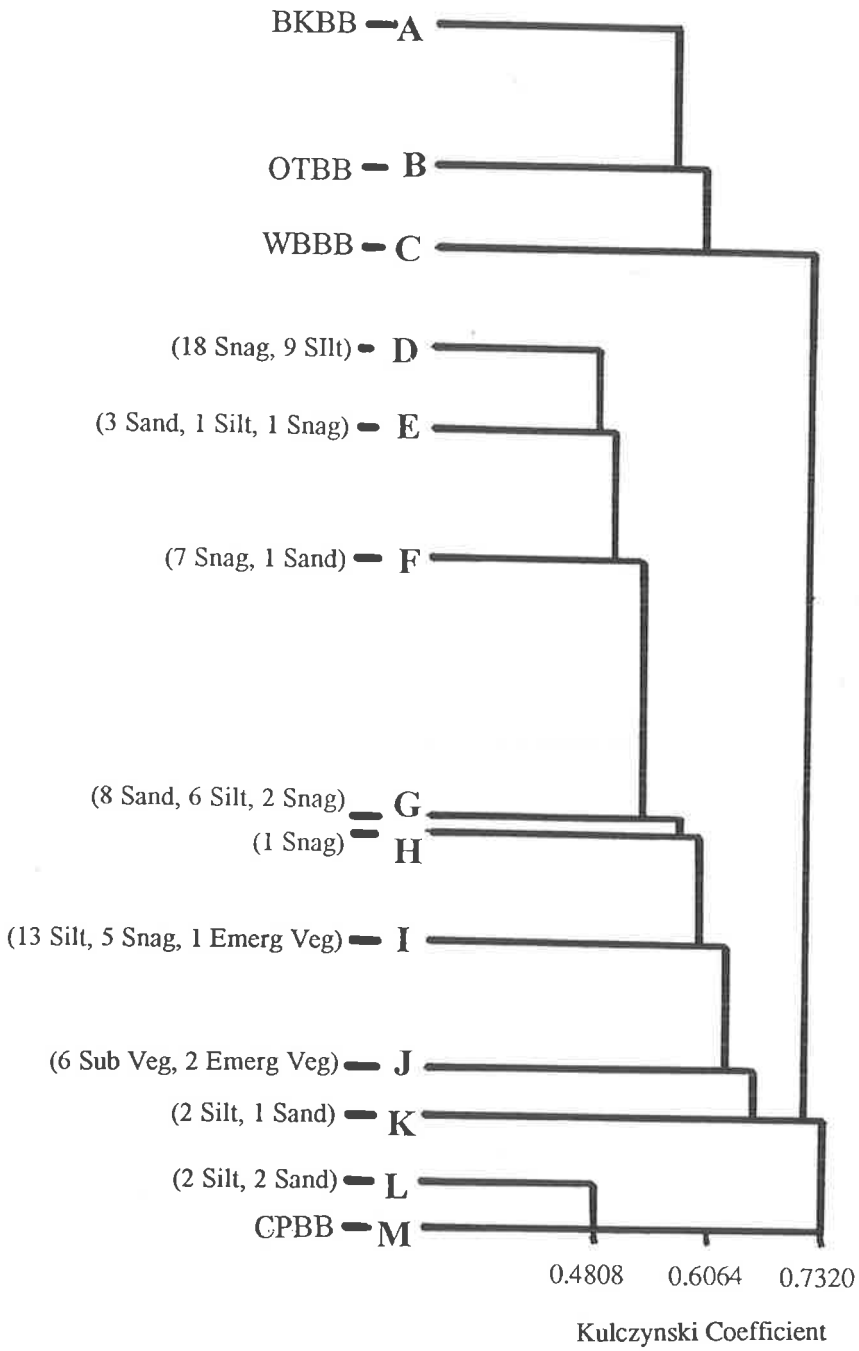


Figure 3.13 Major clusters (A-M) resulting from flexible-UPGMA on samples collected from the Darling River floodplain (January 1990). The sample composition of each cluster is summarised.

Multivariate ordination of the sample data confirmed the distinctiveness of the lentic sites. Figure 3.14 shows the distribution of samples on the first and second axis of the SSH plot. When samples were labelled according to mesohabitat the distinctiveness of the assemblages occupying the permanent (BKBB and OTBB) and temporary (WBBB and CPBB) billabongs was visible (Figure 3.15). The first axis of the SSH ordination was significantly correlated with CPOM (Table 3.13), with samples from the permanent billabongs containing more CPOM than channel samples. Axis 2 showed significant correlations with FPOM, salinity, temperature and depth (Table 3.13).

Samples from permanent billabongs clustered low on Axis 1 and in the centre of Axis 2 whereas those from temporary billabongs grouped low on Axis 2 and in the centre of Axis 1. Although most lower pool sites grouped high on both Axis 1 and Axis 2 and upper pool sites grouped low on Axis 1 and high on Axis 2, samples from the different regions of the main channel did not form distinct clusters. Samples from main channel sites unaffected by weirs were also variable forming no distinct patterns (Figure 3.15).

The various microhabitats represented tended to disperse along Axis 1 which is evident when the microhabitat of each sample is mapped onto the SSH plot (Figure 3.16). The observed pattern is similar to that obtained from TWINSPAN of the samples. There is a gradient along Axis 1 from samples collected in the complex microhabitats, emergent vegetation and *L. peploides,* through to samples collected from coarse organic matter, snags and unvegetated littoral sites with silt substrata. Samples from unvegetated sand substrata have high scores on Axis 1.

The extent of the habitat dissimilarity was illustrated by mapping the sample groups derived from TWINSPAN onto the plot produced from SSH (Figure 3.17). The lotic groups A, B, C and D show distinct clusters. When envelopes enclose the TWINSPAN groupings of main channel sites, sample group similarity for these sites becomes evident. Samples in Group E, mostly from *L. peploides*, cluster low on Axis 1 and high on Axis 2, overlapping some snag samples. The samples in Groups F and G, mainly from snag and silt microhabitats, form a large group also low on Axis 1 and high on Axis 2. Those samples in Groups H and I, unvegetated silt and sand substrata, group high on Axis 1. The remaining samples in Groups J, K and L, mostly snag and silt substrata, form a cluster high on Axis 1 and low on Axis 2.

Table 3.13 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first and second axes of the SSH of faunal data from the Darling River, January 1990. (n = 66)

CPOM	1.00									
FPOM	0.224	1.00								
Shade	0.471	-0.036	1.00							
Salinity	-0.039	0.255	-0.139	1.00						
Oxygen	0.205	0.307	-0.119	0.480	1.00					
Temperature	-0.054	-0.138	0.018	-0.506	-0.221	1.00				
Secchi Depth	0.198	0.153	0.425	0.486	0.341	-0.198	1.00			
Depth	-0.058	-0.178	0.027	-0.463	-0.687	0.318	-0.349	1.00		
Axis 1	**-0.367**	**0.004**	**-0.562**	**-0.047**	**-0.085**	**0.140**	**-0.272**	**-0.047**	**1.00**	
Axis 2	**-0.008**	**-0.341**	**0.344**	**-0.566**	**-0.432**	**0.207**	**-0.088**	**0.241**	**-0.154**	**1.00**

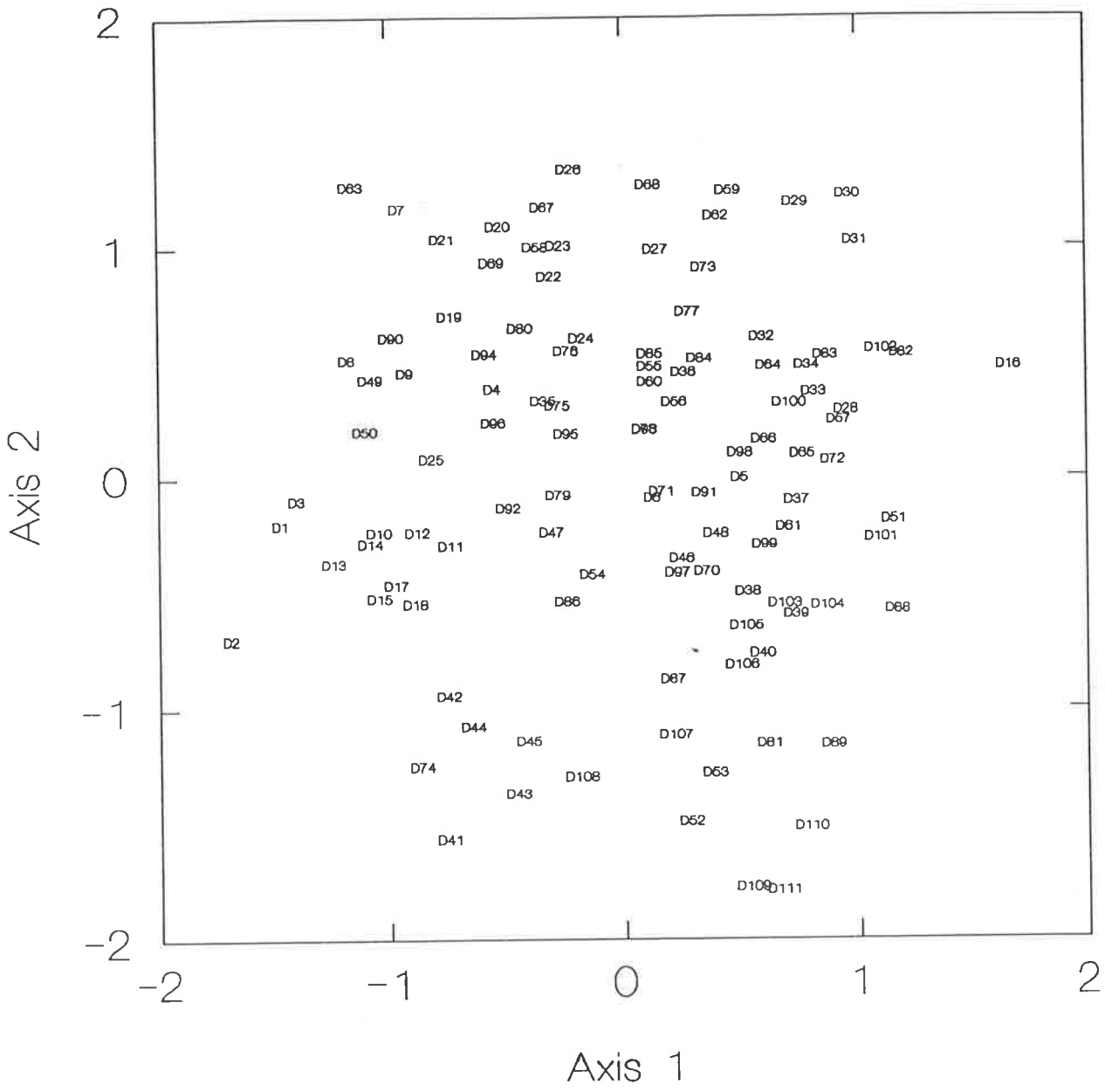
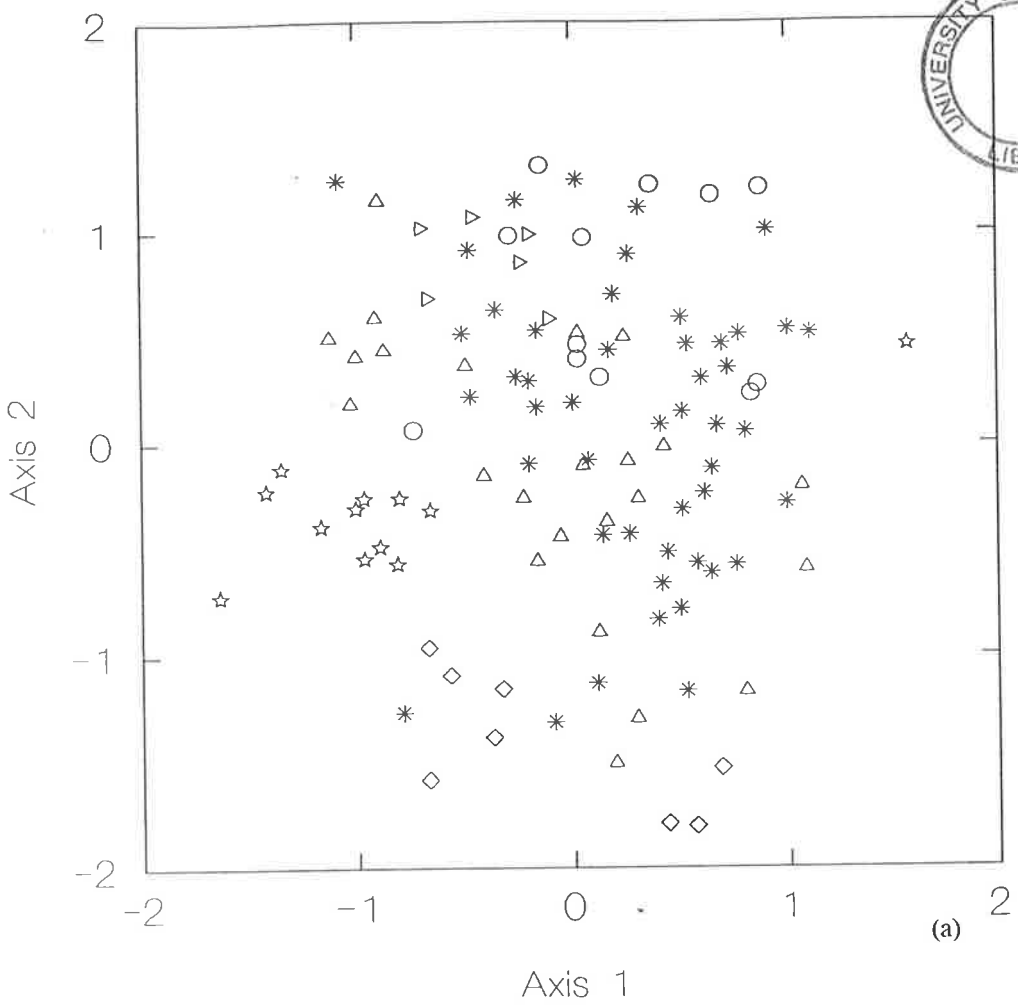
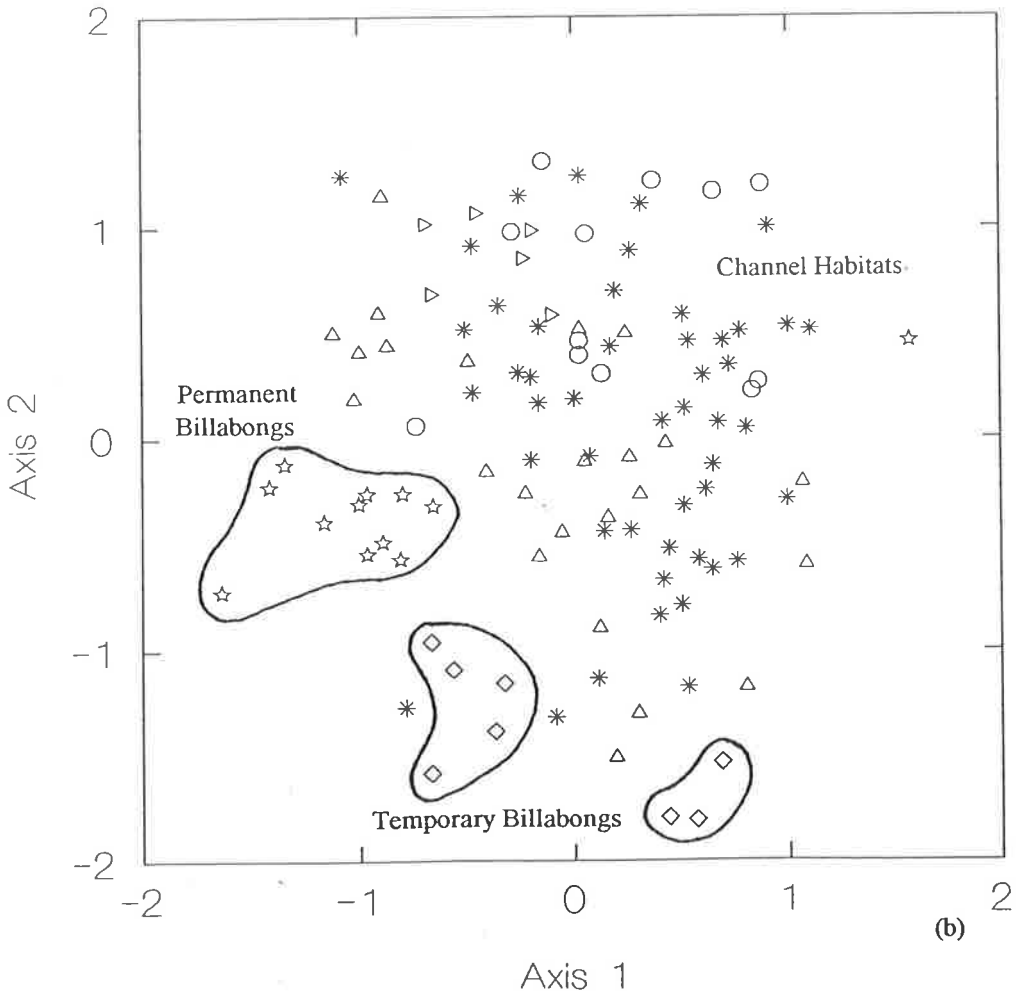


Figure 3.14 Distribution of samples on the first and second axes of the SSH plot of all samples collected from habitats on the Darling River in January 1990.

Figure 3.15 (a) SSH plot on the first and second axes of samples collected from all habitats on the Darling River, January 1990. Samples are labelled according to the mesohabitat from which they were collected; 'diamonds', temporary billabongs; 'stars', permanent billabongs; 'triangles', upper pool main channel sites; 'circles', lower pool main channel sites; 'asterisk', unregulated main channel sites.
(b) highlights the suggested groupings of mesohabitats.

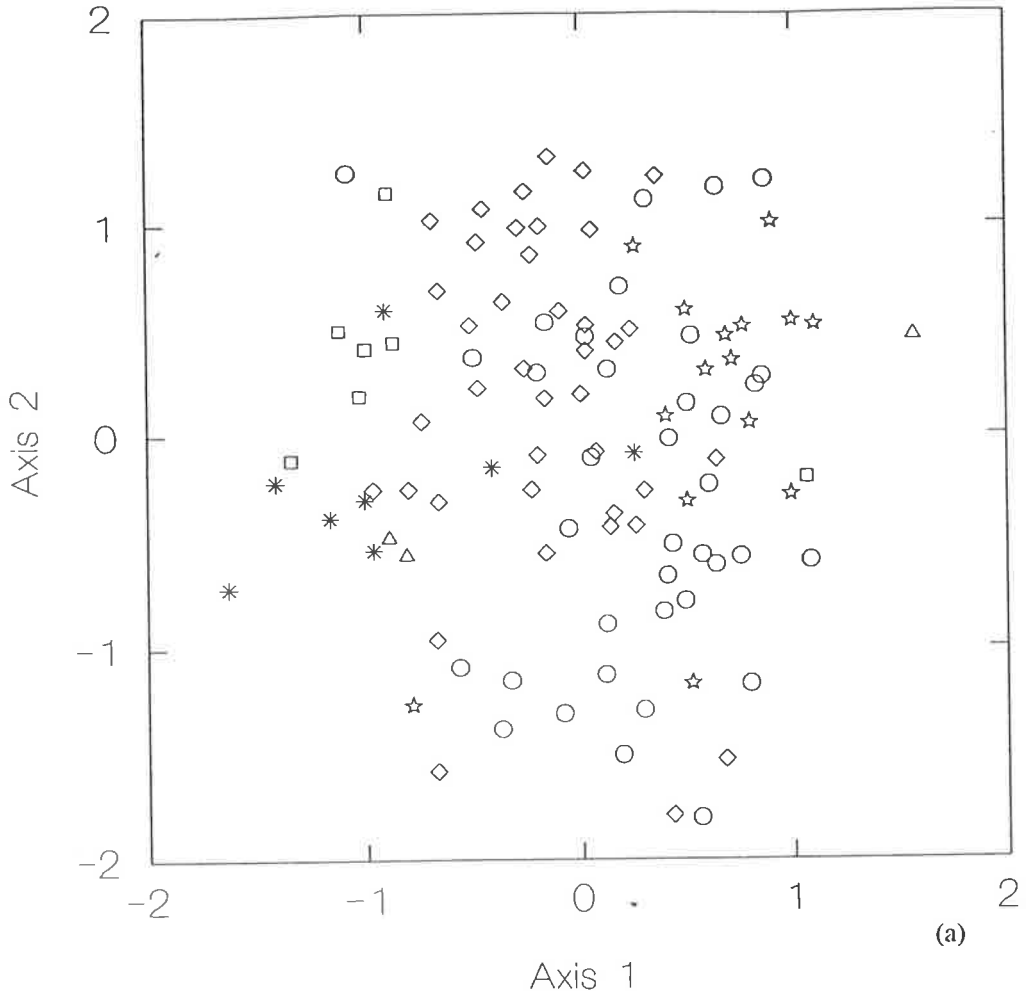


(a)

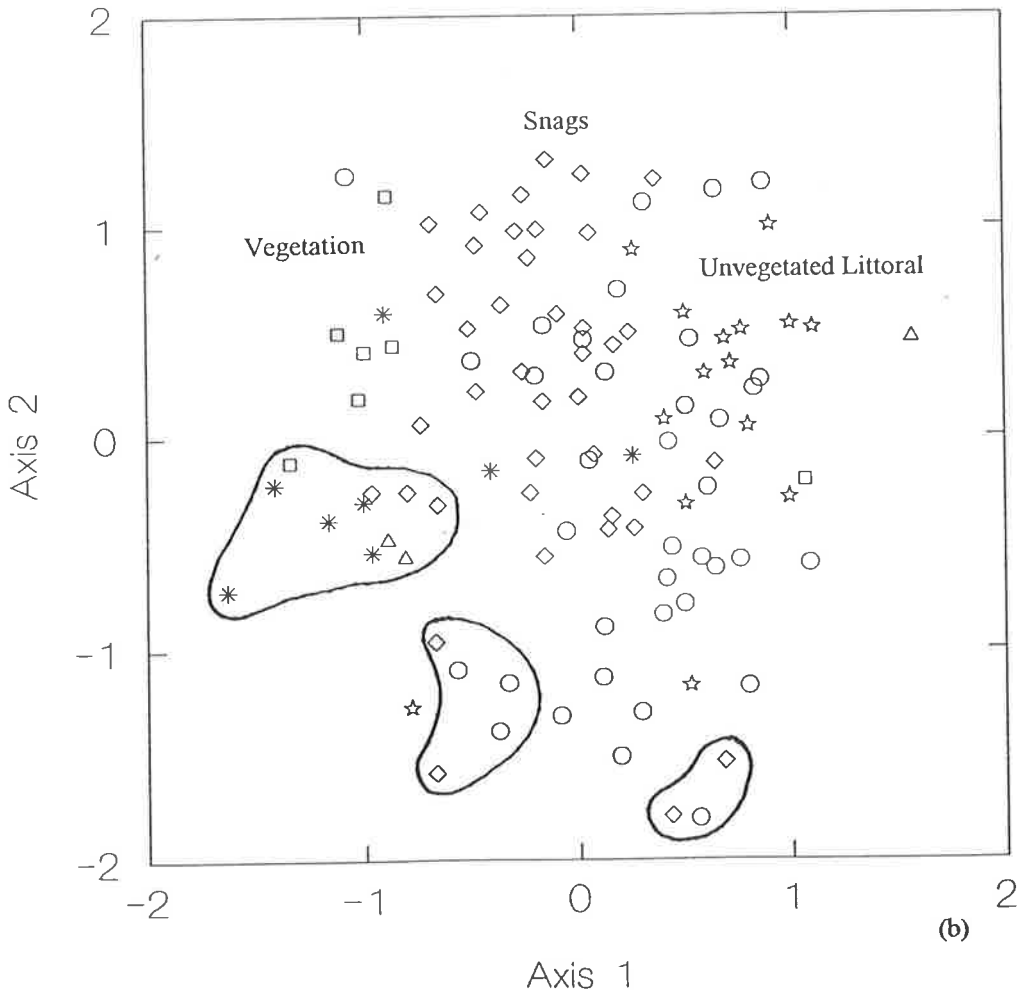


(b)

Figure 3.16 (a) SSH plot on the first and second axes of samples collected from all habitats on the Darling River, January 1990. Samples are labelled according to the microhabitat from which they were collected; 'asterisk', emergent vegetation; 'squares', submerged vegetation; 'diamonds', snags; 'circles', unvegetated open littoral with a silt substrata; 'stars', unvegetated open littoral with a sand substrata. (b) redefines the distinctive mesohabitats and highlights the suggested trend along Axis 1 from vegetation microhabitats to unvegetated littoral regions, this gradient may reflect microhabitat complexity.

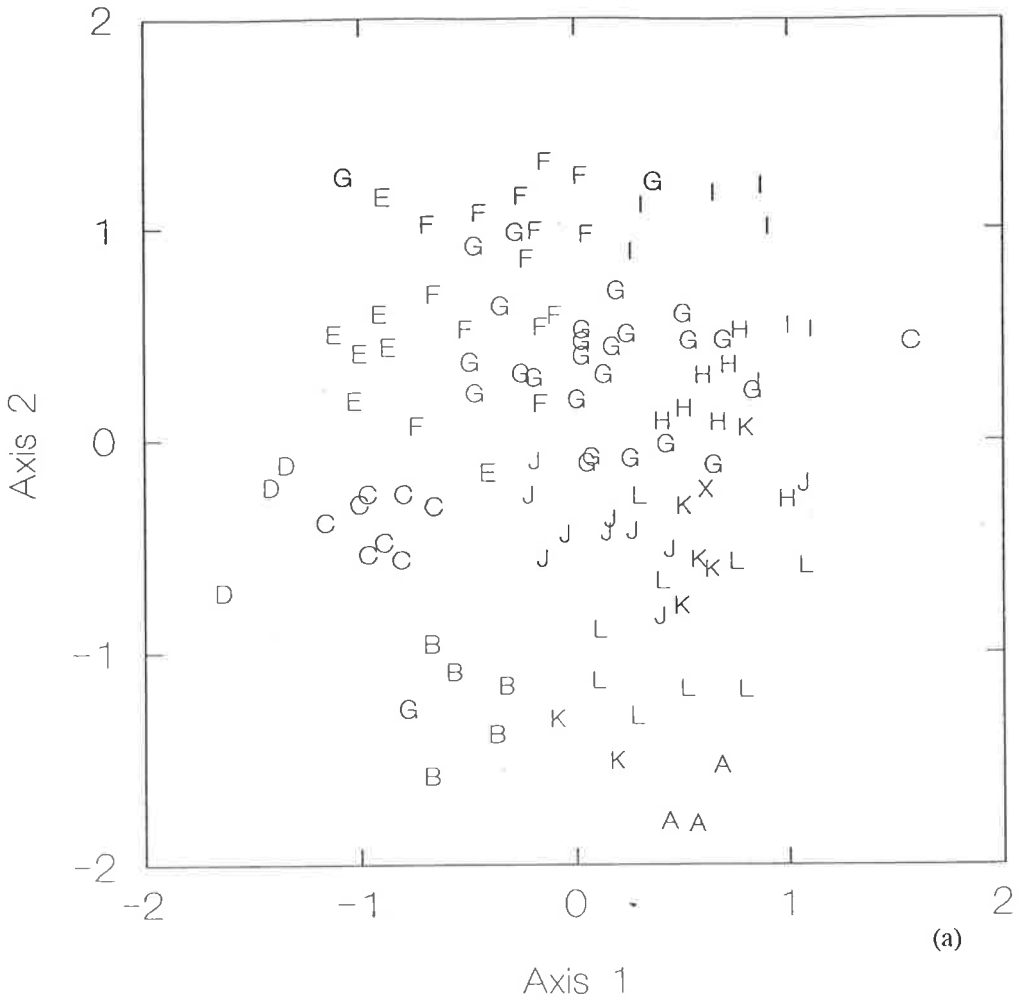

2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
Axis 1

(a)

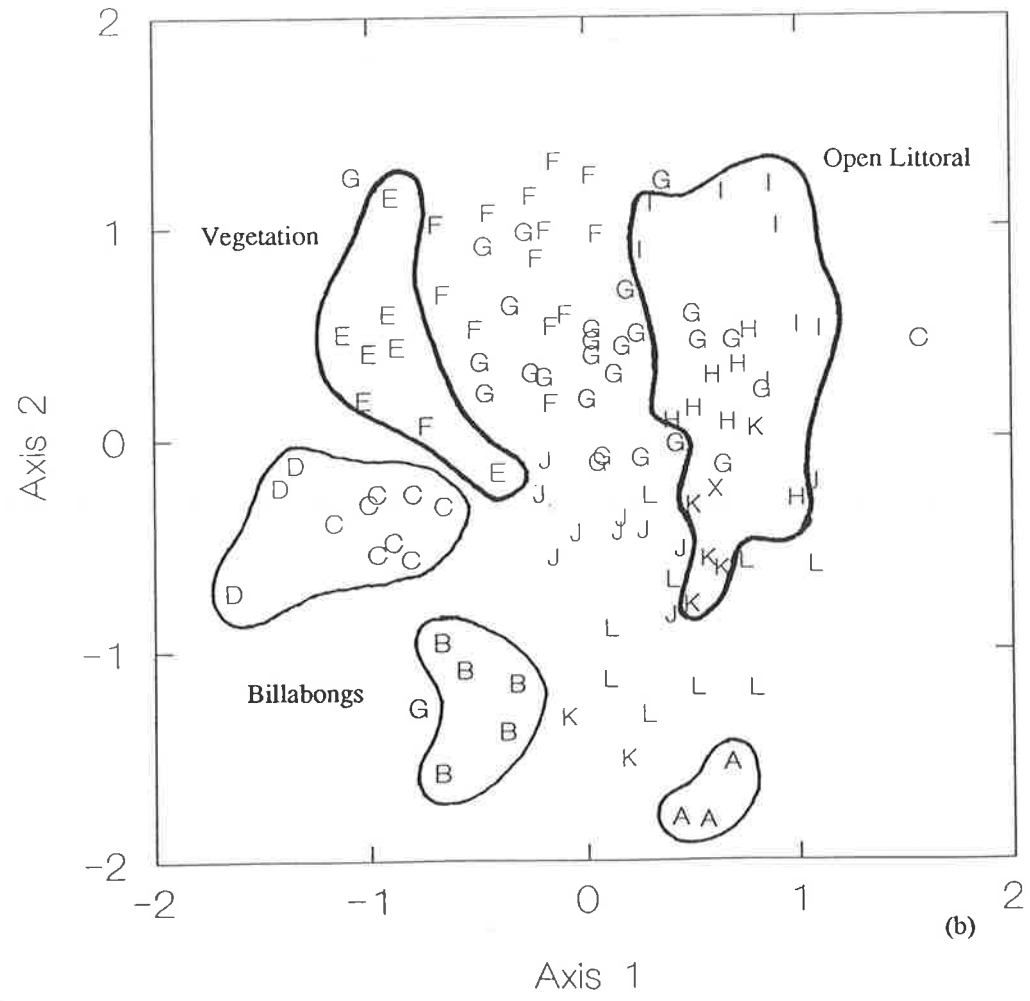

Snags
Vegetation
Unvegetated Littoral
2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
Axis 1

(b)

Figure 3.17 (a) SSH plot on the first and second axes of samples collected from all habitats on the Darling River, January 1990. Groups derived from the TWINSPAN are superimposed (cf. Tables 3.10 and 3.11).
(b) redefines the distinctive mesohabitats and highlights those sample groups dominated by vegetation microhabitats and unvegetated open littoral microhabitats, the remainder comprised mostly snag microhabitats.


Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(a)


Vegetation
Open Littoral
Billabongs
Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(b)

Multivariate Analysis of Species

TWINSPAN of the species in the samples produced seven groups (S1 to S7) (Table 3.14). The first division separated a majority of collectors (Groups S1 to S3) from groups in which predators and scrapers were abundant (Groups S4 to S7) (Figure 3.18). The predators in groups S1 to S3 were rare with less than 10 individuals in total. A similar situation was apparent for scrapers: only three specimens of *Ochthebius* sp. (Group S2) were found. Groups S4 to S7 contained a diverse range of taxa with an increasing dominance of predators (Figure 3.18). The dominance of scrapers in group S7 relates to the presence of *Ferrissia* spp. in that group, found in large numbers in the permanent billabong OTBB. Collectors cover such a diverse range of taxa that they are represented in all TWINSPAN groups.

When preferences of species groups for particular sample groups were examined using the 'fidelity index', species groups S5, S6 and S7 contained a higher proportion of invertebrate predators than species groups S1 to S4. Groups S5 to S7 were dominated by hemipteran collectors and contained nearly all the scraper taxa. These groups showed a preference for lentic sites, sample groups A to F (Figure 3.19). Species groups S1 to S4, dominated by collectors, included most of the chironomids, a number of coleopteran taxa and the three abundant shrimp species. These species groups showed a preference for lotic sites, sample groups F to L.

Multivariate ordination of the species data highlighted the overlap of the three functional feeding groups. The distribution of species on Axis 1 and Axis 2 of the SSH plot is shown in Figure 3.20. When the FFG of each species was mapped onto this plot (Figure 3.21) there was no apparent clustering. Scrapers tended to fall higher on Axis 1, however, the taxa assigned to collectors and predators did not form clusters.

When the species groupings produced by TWINSPAN of the species data (cf. Table 3.14) are mapped onto the SSH ordination (Figure 3.22) the assemblage characteristics (cf. Figure 3.19) are more obvious. Species groups S1, S2, S3 and S4, containing mainly collectors, cluster high on Axis 2 and low on Axis 1. These assemblages are characteristic of lentic sites with unvegetated silt and sand microhabitats. Species group S5 clustered low on both Axis 1 and 2 and showed a preference for billabong habitats and those containing *V. spiralis*. This group comprised mostly hemipteran and coleopteran taxa. Species groups S6 and S7

clustered high on Axis 1 with both assemblages characteristic of billabong habitats (cf. Figure 3.19).

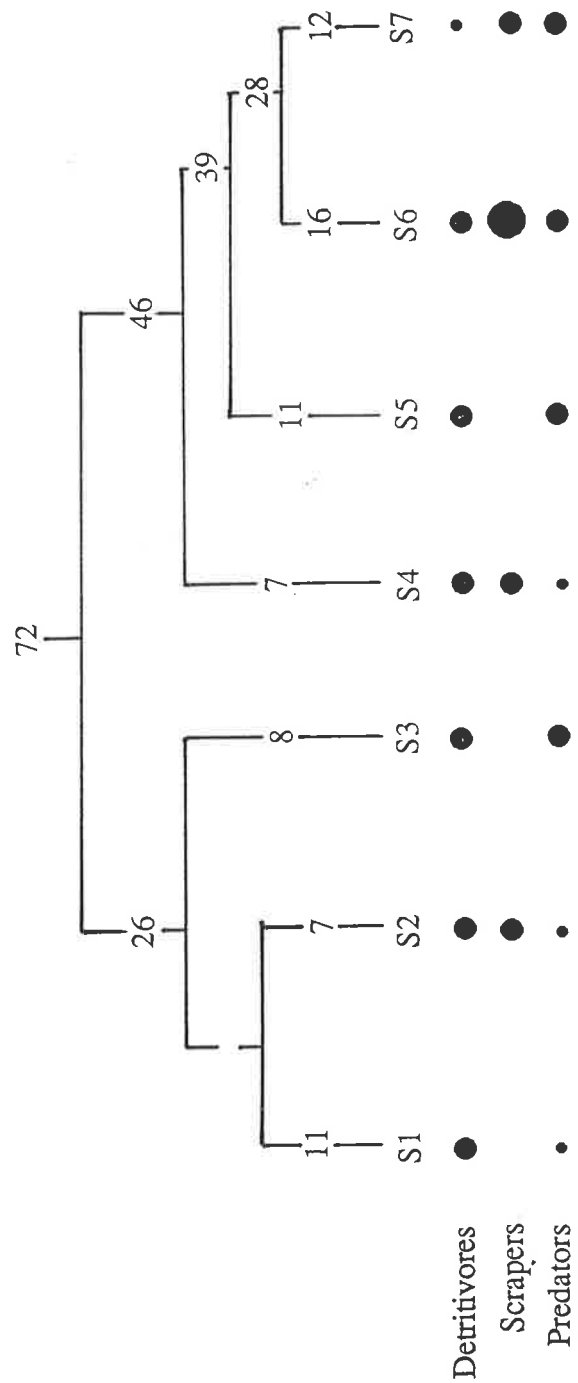


Figure 3.18 TWINSPAN dendogram of the species data from the 111 samples collected from the Darling River floodplain in January 1990. Taxa in species groups S1 to S7 are listed in Table 3.14. The proportional representation of each FFG in the species groups is depicted as follows, large circle >70%, medium circle 30-70%, small circle 1-30%.

Table 3.14 Species and their FFG for the seven species groups (A-G) yielded by the TWINSPAN of all habitat samples on the Darling River floodplain in January 1990.

	Species	FFG
Group S1	*Sphaerium*	Collector
	Austroargathona picta	Collector
	Atalophlebia australis	Collector
	Virgatanytarsus sp.	Collector
	Chironomus sp.	Collector
	Stenochironomus sp.	Collector
	Paratendipes sp.	Collector
	Harnishia? sp.	Collector
	Cheumatopsyche sp.	Collector
	Coxelmis sp. (larvae)	Predator
	Muscidae sp.1	Predator
Group S2	*Paratya australiensis*	Collector
	Macrobrachium australiense	Collector
	Tasmanocoenis arcuata	Collector
	Cryptochironomus sp.	Collector
	Gerridae sp.	Predator
	Ecnomus sp.	Predator
	Ochthebius sp.	Scraper
Group S3	Oligochaeta spp.	Collector
	Cherax destructor	Collector
	Cladotanytarsus sp.	Collector
	Dicrotendipes sp.	Collector
	Cladopelma sp.	Collector
	Microvelia sp.	Predator
	Coelopynia sp.	Predator
	Bezzia sp.	Predator
Group S4	*Caridina mccullochi*	Collector
	Paracymus sp.	Collector
	Parakiefferiella sp.	Collector
	Tiny Chironomids	Collector
	Antiporus femoralis	Predator
	Empididae sp.	Predator
	Enochrus sp.	Scraper

Group S5	*Agraptocorixa* sp.	Collector
	Sigara sp.	Collector
	Micronecta spp.	Collector
	Polypedilum spp.	Collector
	Antiporus gilberti	Predator
	Megaporus sp.	Predator
	Allodessus sp.	Predator
	Paroster sp.	Predator
	Macrogyrus sp. (larvae)	Predator
	Procladius sp.	Predator
	Oecetis sp.	Predator
Group S6	*Chironomus cloacalis*	Collector
	Dicrotendipes conjunctus	Collector
	Kiefferulus martini	Collector
	Cricotopus spp.	Collector
	Triplectides australis	Collector
	Triplectidina sp.	Collector
	Hydracarina sp. 1	Predator
	Xanthagrion erythroneurum	Predator
	Anisops spp.	Predator
	Eretes ? sp. (larvae)	Predator
	Parachironomus sp.	Predator
	Tabanidae sp. 1	Predator
	Ferrissia spp.	Scraper
	Isidorella sp.	Scraper
	Physa sp.	Scraper
	Berosus sp.	Scraper
Group S7	*Cloeon* sp.	Collector
	Tanytarsus spp.	Collector
	Culicinae sp.	Collector
	Austrogomphus sp.	Predator
	Austagrion watsoni	Predator
	Calagrion billinghursti	Predator
	Tiny Zygoptera	Predator
	Mesovelia sp. 1	Predator
	Liodessus sp.	Predator
	Hydrophilidae (larvae) sp. 1	Predator
	Ablabesmyia sp.	Predator
	Hydraena sp.	Scraper

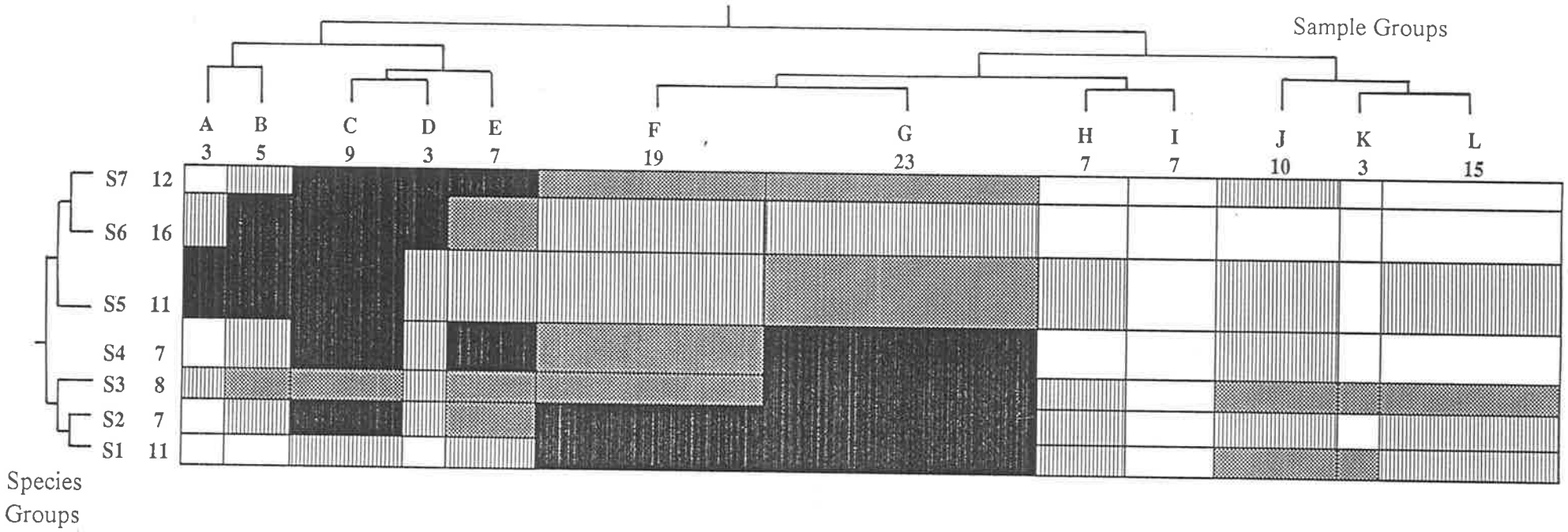


Figure 3.19 Two-way table of species group fidelities (Fij) to sample groups. Both species groups (S1-S7) and sample groups (A-L) are derived from the TWINSPAN of the faunal data in the 111 samples from the Darling River floodplain collected in January 1990. The numbers of elements in each group are near the label. Values of $F_{ij} > 2.0$ (full-shading) or $F_{ij} > 1.0$ (cross-hatching) indicate 'preference' while values of $F_{ij} < 1.0$ (vertical lines) or F_{ij} (no shading) indicate 'avoidance'.

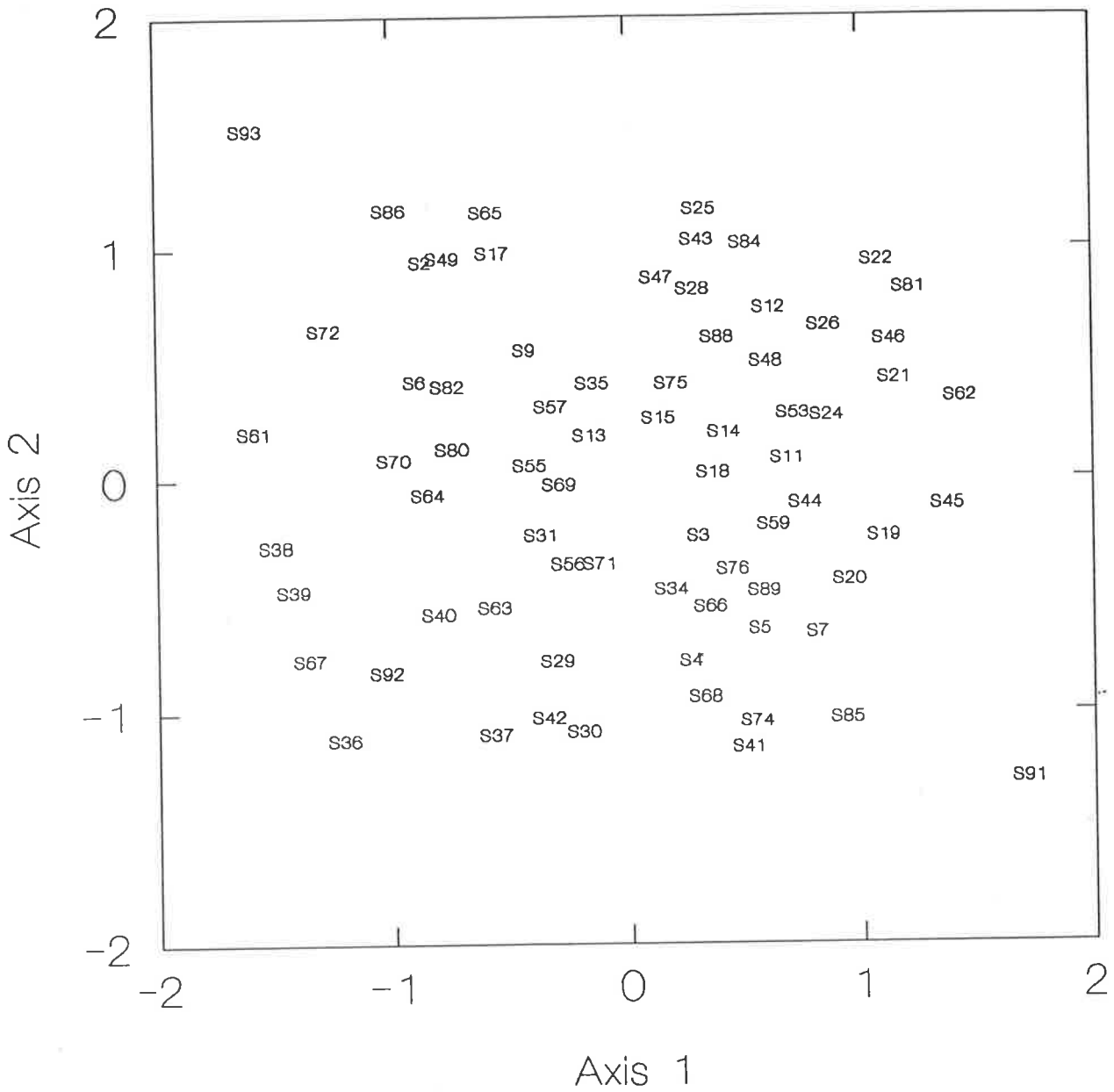
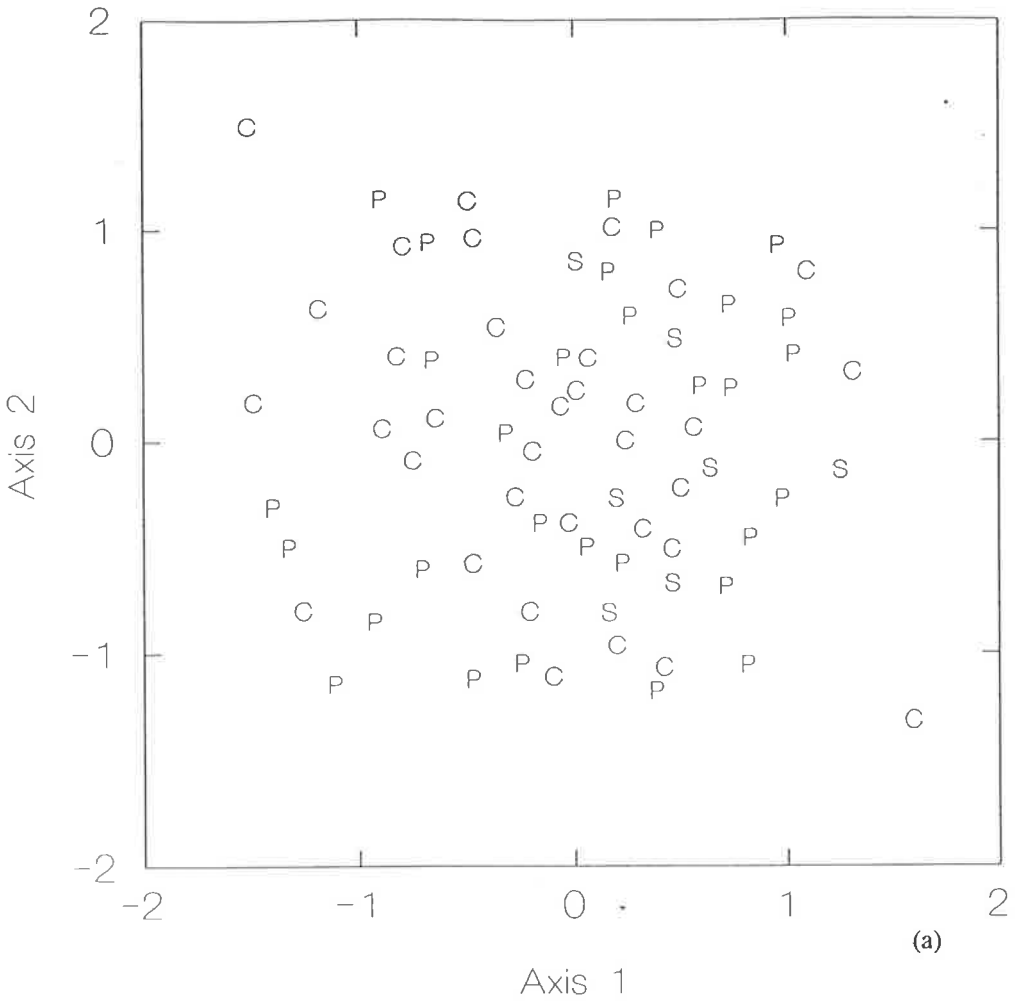
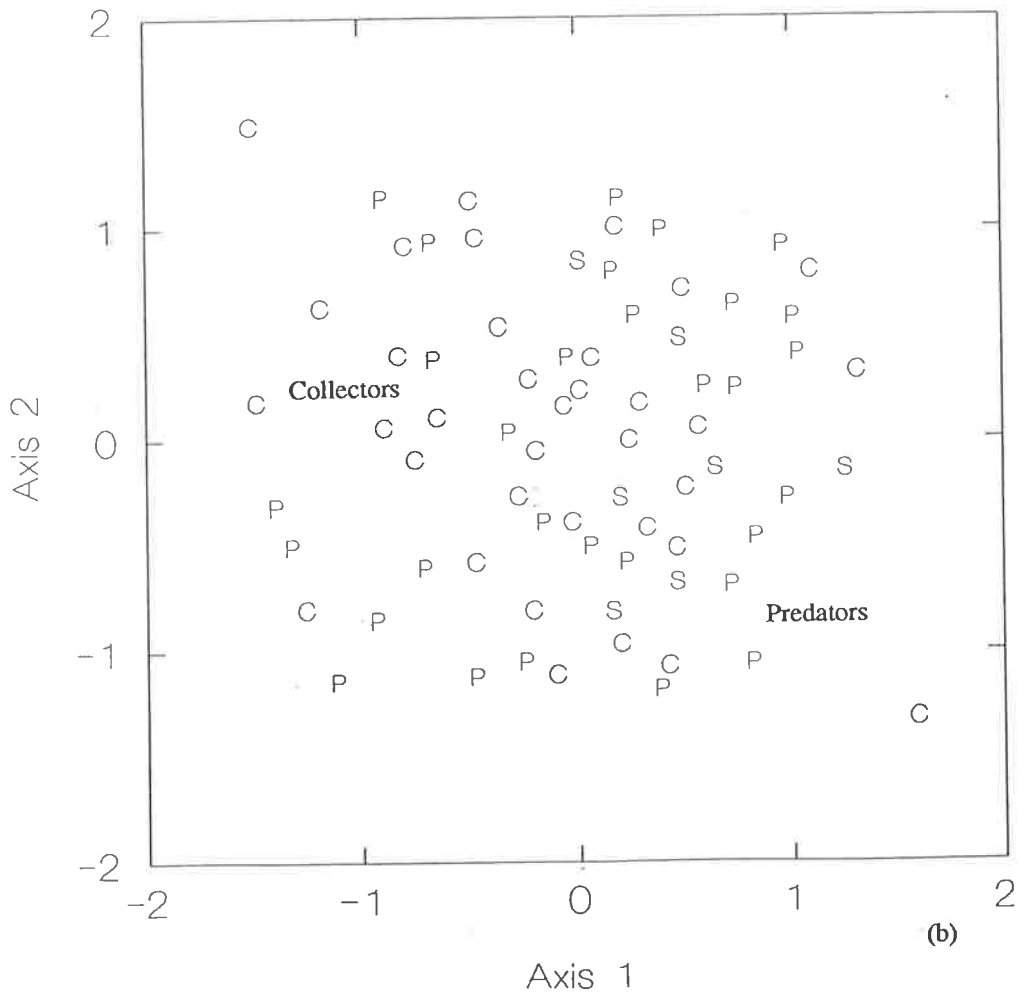


Figure 3.20 SSH ordination of the species in sample data from the 111 samples collected from the Darling River floodplain in January 1990. Distribution of species on the first and second axes.

Figure 3.21 SSH ordination of the species in sample data from the 111 samples collected from the Darling River floodplain in January 1990. Species are labelled according to their respective FFG; 'C' collector, 'P' predator and 'S' scraper. There is no apparent clustering of species.


Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(a)


Axis 2
Axis 1
Collectors
Predators
2
1
0
-1
-2
-2
-1
0
1
2

(b)

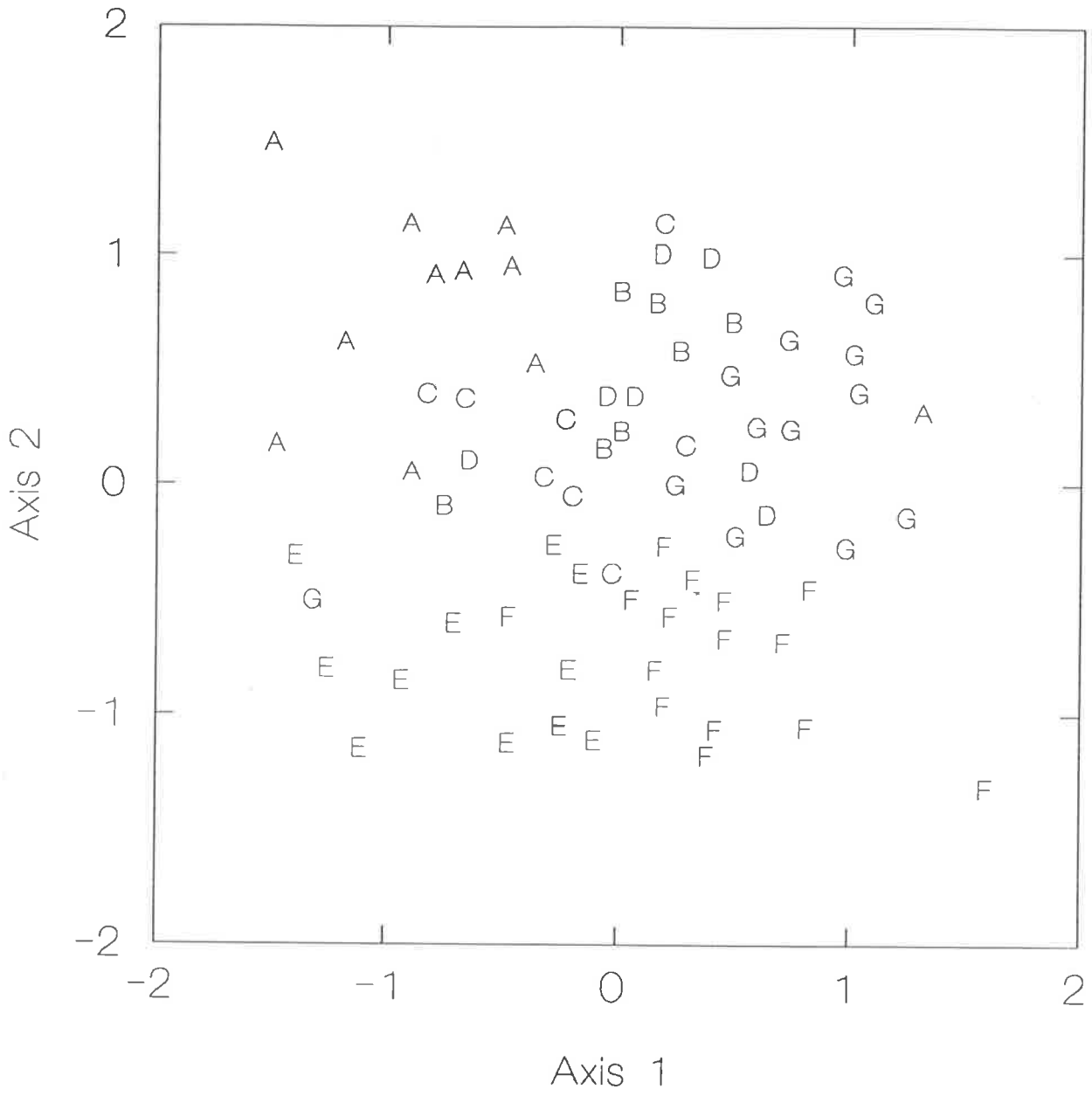


Figure 3.22 SSH ordination of the species in sample data from the 111 samples collected from the Darling River floodplain in January 1990. Species groups derived from TWINSPAN are superimposed (cf. Table 3.14); 'A' = S1; 'B' = S2; 'C' = S3; 'D' = S4, 'E' = S5, 'F' = S6; 'G' = S7.

Gastropods in the Darling River

There have been no studies of the abundance and distribution of gastropods in the lower Darling River. Personal observations of shells in Aboriginal middens along the banks of the Darling identified both large prosobranch taxa previously recorded from the lower Murray, *Notopala* sp. and *Thiara balonnensis,* which indicates relatively recent presence (cf. Section 1.2.5). The gastropod collection held by the Australian Museum, Sydney, contains specimens of both *Notopala* species, *N. hanleyi* and *N. sublineata*, as well as *T. balonnensis* from the Darling River (Sheldon and Walker, 1993b). The majority of *Notopala* specimens are *N. sublineata* with only a few shells assigned to the *N. hanleyi* group. From the geographical distributions in Smith and Kershaw (1979), most of the gastropod species listed in Table 1.3 (Chapter 1), as occurring in the lower River Murray, would be also expected in the lower Darling River.

The most extensive recent assessment of gastropod abundance and distribution in both the River Murray and the lower Darling River is the Murray-Darling Basin Commission macroinvertebrate survey (1983 until 1986) (Bennison *et al.,,* 1989). The survey covered the entire River Murray but included only one site on the Darling, Burtundy, close to the junction of the Darling and the Murray. Only *Ferrissia* spp. (162 specimens) was collected from the Burtundy site during the survey, providing an indication of the paucity of gastropod populations in the lower Darling. In the present study, covering the river between Bourke and Wilcannia, three gastropod species were recorded: *Ferrissia* spp., *Isidorella hainesii* and *Physa acuta* (cf. Appendix B). *Ferrissia* spp. was the most abundant taxon with a total of 534 specimens collected from billabong habitats. The other taxa were comparatively rare with only eight *I. hainesii* and 168 *P. acuta* collected.

3.4.2 Lower River Murray Floodplain

Environmental Conditions

The environmental conditions for all sites on the lower River Murray floodplain at the time of sampling are given in Table 3.15. Salinity levels for channel sites increased with distance downstream, levels at Chowilla were approximately 250 mg/L compared with 450 mg/L downstream at Morgan. Billabong sites had higher salinities than channel sites, especially Coongaleena Billabong on the Pike River floodplain which was extremely shallow, having a salinity three times higher than the corresponding channel sites. Monoman Creek, on the Chowilla floodplain, had a higher salinity than adjacent sites as it intercepts the flow of saline groundwater from the floodplain into the channel (cf. NEC, 1988). All sites were well oxygenated with water temperatures ranging from 23 to 32 °C. Recorded Secchi depths were in the range characteristic of the lower River Murray in summer, when light penetration is usually highest (Mackay *et al.*, 1988). Light penetration was greatest at channel sites.

Table 3.15 Environmental conditions measured in the littoral zone of each site on the lower River Murray in January 1990.

	Site	Salinity (mg/L)	Oxygen (% saturation)	Secchi depth (cm)	Temperature °C
1	SLAB	260.4	74	16	25
2	SLBB	499.5	34	16	26
3	SIMC	255	75	25	26
4	IMBW	245	94	24	32
5	QBMC	266	81	25	25
6	MNAB	940	100	22	26
7	PRAB	456	100	24	28
8	PRBW	466	100	8	32
9	PRMC	316	100	25	25
10	CGBB	2897	100	25	25
11	MGMC	431	100	31	24
12	SCBW	439	100	31	24

Community Composition

A total of 18,292 individuals from 62 taxa (Appendix C) was collected in 63 samples. Insects were the dominant group, comprising 84 percent of taxa and 52 percent of individuals. Although only comprising 9 percent of taxa, crustaceans accounted for 47 percent of individuals (Figure 3.23). Of the Insecta, the Diptera comprised 22 taxa with Coleoptera (12) and Hemiptera (9) also dominant. The Odonata (4), Trichoptera (3) and Ephemeroptera (2) were less so. Within the Insecta, the Diptera accounted for 54 percent and the Hemiptera 39 percent of the individuals, other orders each accounted for less then 5 percent of the total abundance (Figure 3.24). Overall, the shrimp *Paratya australiensis* was the most abundant taxon, and comprised the greatest biomass. Other abundant taxa included *Caridina mccullochi*, the corixids *Micronecta* spp., the zygopteran *Ischnura heterosticta*, the ceratopogonid *Bezzia* sp. and the chironomids *Chironomus* sp. and *Cladotanytarsus* sp. Nine taxa occurred only once.

Table 3.16 gives the mean (SE) number of taxa and individuals for each site. Both the median number of taxa and individuals varied significantly between sites (Kruskal-Wallis $H = 28.37$, $p<0.01$ for taxa and $H = 35.48$, $p<0.001$ for individuals). When the sites were grouped into mesohabitats the differences remained (Kruskal-Wallis $H = 13.16$, $p<0.01$ for taxa and $H = 25.63$, $p<0.001$ for individuals). The billabongs (SLBB and CGBB) contained significantly more taxa and individuals than the other mesohabitats. There were no differences for taxa or individuals among the other mesohabitats.

There were significant differences between mesohabitats for collectors and predators but not for scrapers (Table 3.17). Collectors comprised both the greatest number of taxa and the greatest abundance across all habitats (Figure 3.25; Table 3.18). There were more collectors in the slow-flowing anabranch and billabong sites with the greatest abundance in billabongs, mostly *Micronecta* spp. and *Chironomus* spp. There were fewer predatory taxa and individuals than collectors across all habitats. The billabongs contained more predatory taxa than either anabranch or main channel sites, with greater abundances also occurring in billabongs. In SLBB the abundant predators were *Anisops* spp. and *Procladius* sp. whereas in CGBB the zygopteran *I. heterosticta* was dominant. Scrapers were rare across all habitats with no differences in either the number of taxa or the abundance of individuals.

The median number of taxa and the median number of individuals also varied significantly amongst microhabitats ($H = 15.67$, 17.65, respectively, $p<0.01$). Fewer taxa were collected from unvegetated sand habitats than from unvegetated silt and emergent vegetation. More individuals were collected from unvegetated silt habitats than from submerged vegetation or snags (Table 3.19; Figure 3.26). Significant differences exist between microhabitats for both richness and abundance of collectors, as well as abundance of predators; there were no microhabitat differences for scrapers (Table 3.17). A greater number of collectors was found in unvegetated littoral areas with silt substratum than all other microhabitats.

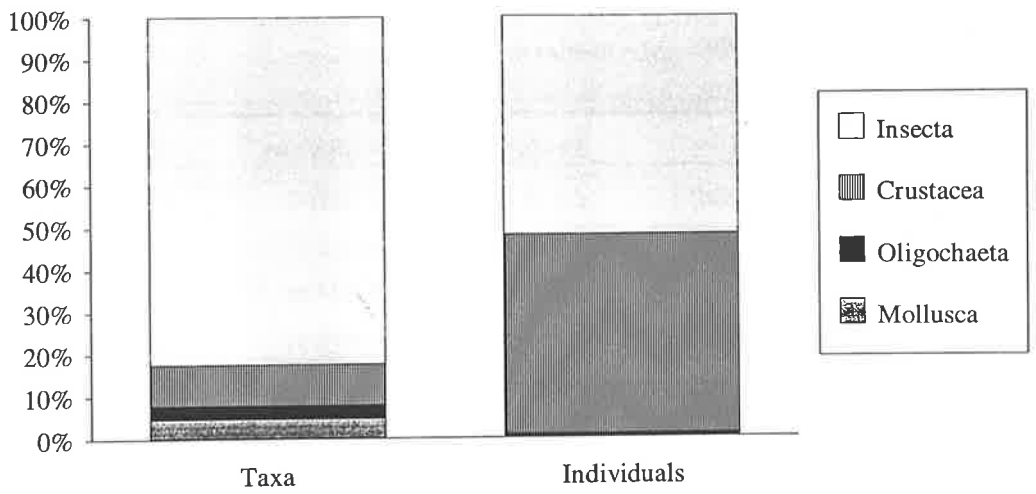


Figure 3.23 Percent representation of the major invertebrate groups in the lower River Murray samples (January 1990), in terms of the number of taxa of each group and the abundance of individuals.

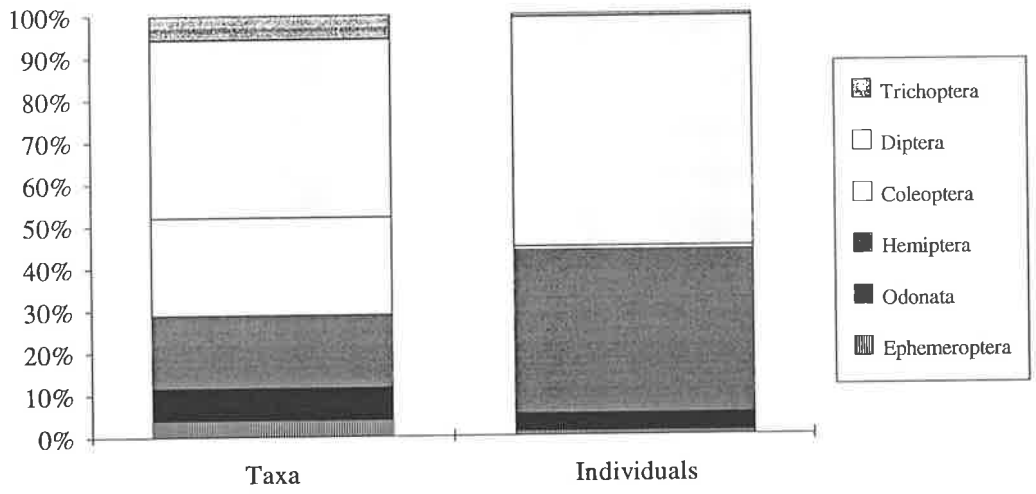


Figure 3.24 Percent representation of the major Insect orders from the lower River Murray (January 1990), in terms of the number of taxa within each order and the abundance of individuals.

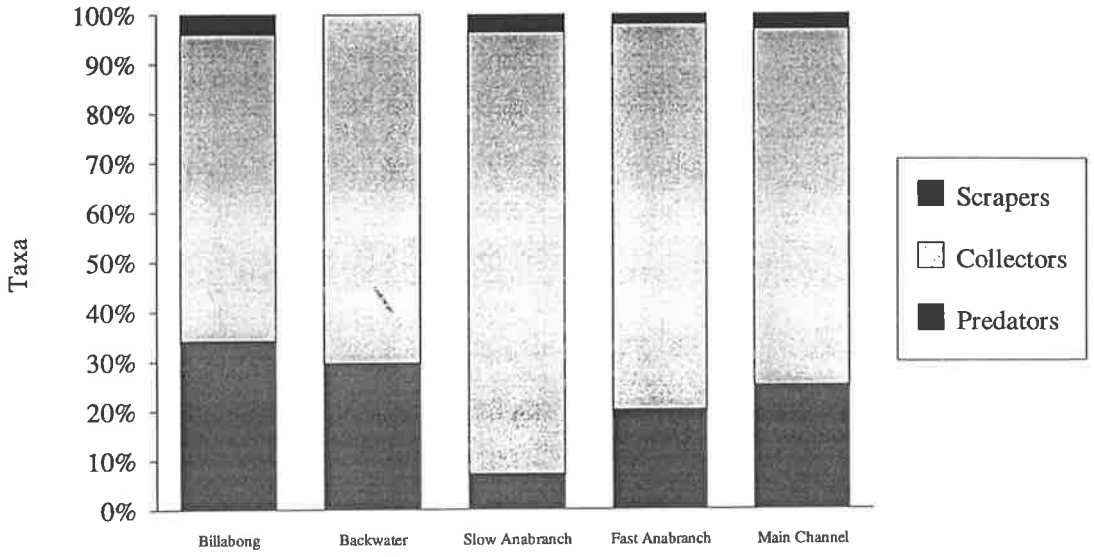
Table 3.16 The mean number *(SE)* of (a) taxa and (b) individuals in total and for three functional feeding groups at each site from the lower River Murray collected in January 1990. (n) = number of samples

(a)

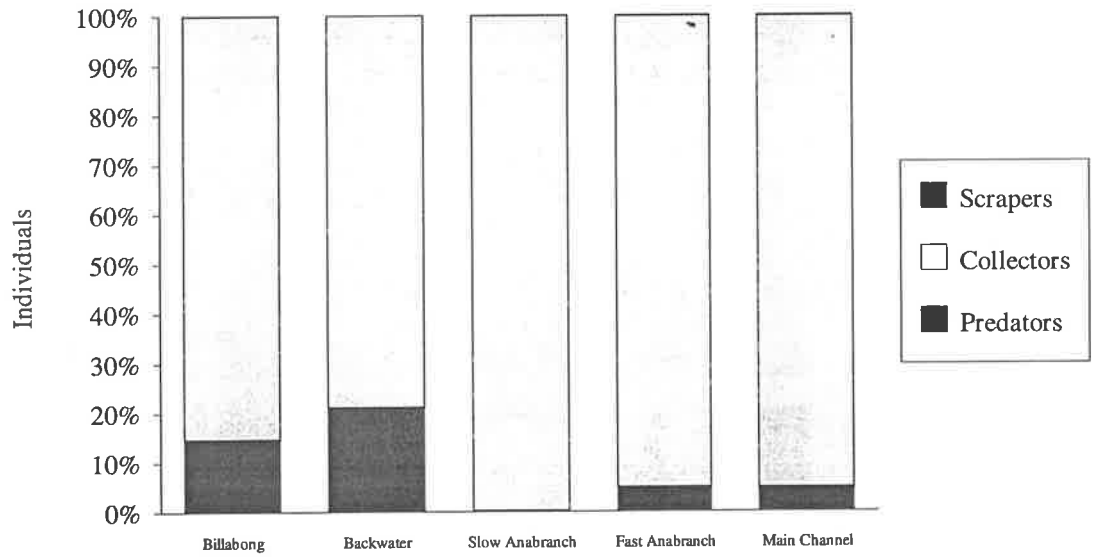
	(n)	Total	Predators	Collectors	Scrapers
SLAB 1	5	10.0 *(0.6)*	2.0 *(0.4)*	7.8 *(0.6)*	0.2 *(0.2)*
SLBB 2	3	13.7 *(1.2)*	4.7 *(0.7)*	9.0 *(0.6)*	0
SIMC 3	5	10.0 *(1.7)*	2.0 *(0.8)*	8.0 *(1.0)*	0
IMBW 4	4	13.7 *(3.1)*	5.2 *(1.2)*	8.5 *(1.9)*	0
QBMC 5	9	12.8 *(1.1)*	4.4 *(0.7)*	7.4 *(0.5)*	0.9 *(0.4)*
MNAB 6	6	12.7 *(0.9)*	1.0 *(0.3)*	11.0 *(0.4)*	0.7 *(0.3)*
PRAB 7	6	10.7 *(0.6)*	0.7 *(0.3)*	9.8 *(0.4)*	0.2 *(0.2)*
PRBW 8	4	8.0 *(0.9)*	2.0 *(0.8)*	6.0 *(0.7)*	0
PRMC 9	6	11.2 *(0.6)*	2.0 *(0.4)*	9.2 *(0.4)*	0
CGBB 10	4	20.5 *(0.8)*	7.0 *(0.8)*	12.2 *(0.6)*	1.2 *(0.2)*
MGMC 11	7	8.3 *(1.3)*	1.4 *(0.5)*	6.7 *(1.1)*	0.1 *(0.1)*
SCBW 12	4	13.0 *(1.6)*	3.0 *(0.7)*	10.0 *(1.1)*	0

(b)

	(n)	Total	Predators	Collectors	Scrapers
SLAB 1	5	110.0 *(32.4)*	5.4 *(2.2)*	104.4 *(31.7)*	0.2 *(0.2)*
SLBB 2	3	667.7 *(147.6)*	110.7 *(32.2)*	557.0 *(117.7)*	0
SIMC 3	5	64.6 *(10.8)*	6.2 *(3.5)*	58.4 *(8.9)*	0
IMBW 4	4	118.0 *(41.8)*	69.0 *(35.1)*	49.0 *(17.3)*	0
QBMC 5	9	138.5 *(19.5)*	16.9 *(6.1)*	120.4 *(18.1)*	1.2 *(0.7)*
MNAB 6	6	206.8 *(13.2)*	1.0 *(0.4)*	204.3 *(12.9)*	0.8 *(0.4)*
PRAB 7	6	546.7 *(169.3)*	0.7 *(0.3)*	545.8 *(169.5)*	0.2 *(0.2)*
PRBW 8	4	41.8 *(9.8)*	8.7 *(7.4)*	33.0 *(9.4)*	0
PRMC 9	6	199.0 *(53.9)*	3.7 *(1.9)*	195.3 *(52.3)*	0
CGBB 10	4	1225.2 *(127.0)*	170.2 *(34.2)*	1052.7 *(97.1)*	2.2 *(0.5)*
MGMC 11	7	275.0 *(86.8)*	3.1 *(1.1)*	271.7 *(86.7)*	0.1 *(0.1)*
SCBW 12	4	248.2 *(80.6)*	8.2 *(1.9)*	240.0 *(79.9)*	0



(a)



(b)

Figure 3.25 Proportion of each functional feeding group in the mesohabitats sampled on the lower River Murray floodplain, January 1990, (a) taxa and (b) individuals.

Table 3.17 Values for Kruskal-Wallis H for differences in the number of taxa and number of individuals in each FFG for mesohabitats and microhabitats on the lower Murray floodplain, January 1990.

	Number of Taxa	Number of Individuals
Mesohabitat		
Collector	H=18.47, p<0.001	H=27.03, p<0.001
Predator	H=23.99, p<0.001	H=30.65, p<0.001
Scraper	H=9.24, p>0.01	H=10.28, p<0.01
Microhabitat		
Collector	H=14.01, p>0.01	H=17.73, p<0.01
Predator	H=9.584, p>0.01	H=11.26, p>0.01
Scraper	H=7.33, p>0.01	H=7.54, p>0.01

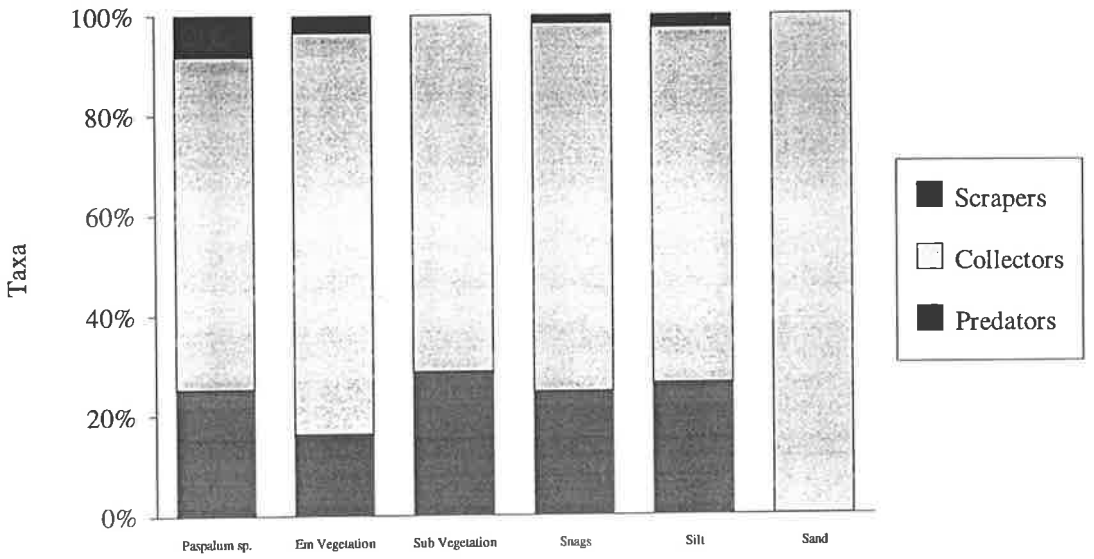
Table 3.18 The mean number *(SE)* of (a) taxa and (b) individuals in total and for three functional feeding groups for each mesohabitat sampled from the lower River Murray in January 1990. (n) = number of samples

(a)

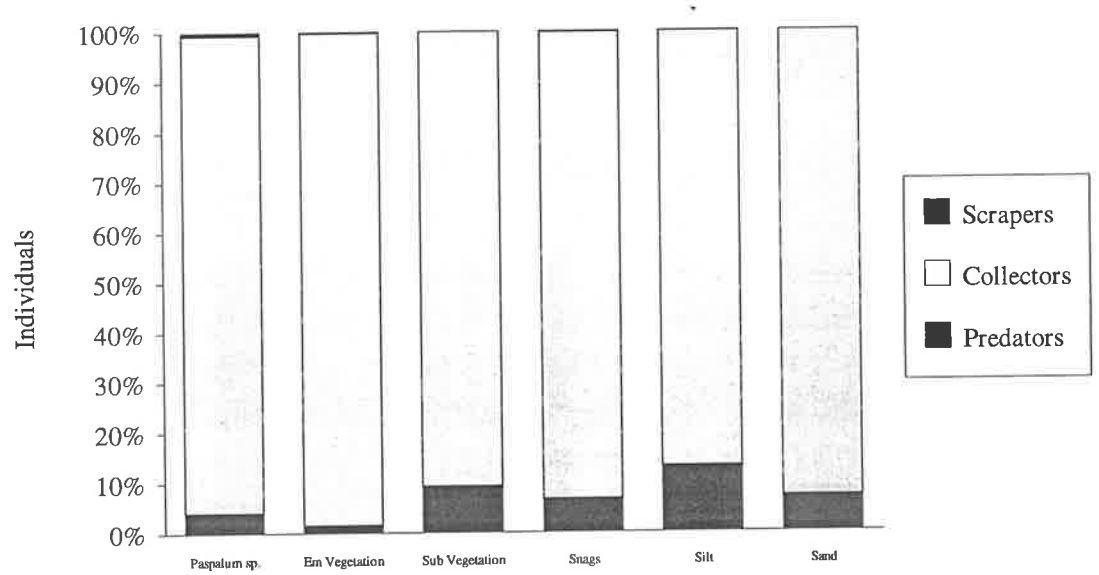
	(n)	Total	Predators	Collectors	Scrapers
Billabong	7	17.6 *(1.5)*	6.0 *(0.7)*	10.8 *(0.8)*	0.7 *(0.3)*
Backwater	12	11.6 *(1.3)*	3.4 *(0.6)*	8.2 *(0.8)*	0 *(0.0)*
Slow Anabranch	12	11.7 *(0.6)*	0.8 *(0.2)*	10.4 *(0.4)*	0.4 *(0.2)*
Fast Anabranch	5	10.0 *(0.6)*	2.0 *(0.4)*	7.8 *(0.6)*	0.2 *(0.2)*
Main Channel	27	10.7 *(0.7)*	2.7 *(0.4)*	7.7 *(0.4)*	0.3 *(0.2)*

(b)

	(n)	Total	Predators	Collectors	Scrapers
Billabong	7	986.3 *(142.9)*	144.7 *(25.1)*	840.3 *(121.2)*	1.3 *(0.5)*
Backwater	12	136.0 *(37.7)*	28.7 *(13.8)*	107.3 *(37.7)*	0
Slow Anabranch	12	376.4 *(95.8)*	0.8 *(0.2)*	375.1 *(96.0)*	0.5 *(0.2)*
Fast Anabranch	5	110.0 *(32.4)*	5.4 *(2.2)*	104.4 *(31.7)*	0.2 *(0.2)*
Main Channel	27	173.7 *(28.7)*	8.4 *(2.4)*	164.8 *(28.8)*	0.4 *(0.2)*



(a)



(b)

Figure 3.26 Proportion of each functional feeding group in the microhabitats sampled on the lower River Murray floodplain, January 1990, (a) taxa and (b) individuals.

Table 3.19 The mean number (SE) of (a) taxa and (b) individuals in total and for three functional feeding groups for each microhabitat samples from the lower River Murray floodplain in January 1990. (n) = number of samples.

(a)

	(n)	Total	Predators	Collectors	Scrapers
Paspalum sp.	5	14.2 *(0.97)*	3.6 *(0.41)*	9.5 *(0.98)*	1.2 *(0.71)*
Emergent Vegetation	18	11.0 *(0.73)*	1.8 *(0.39)*	8.8 *(0.49)*	0.4 *(0.16)*
Submerged Vegetation	13	12.4 *(0.94)*	3.5 *(0.84)*	8.8 *(0.49)*	0
Snag	11	10.4 *(0.91)*	2.5 *(0.36)*	7.6 *(0.78)*	0.2 *(0.12)*
Silt	13	14.1 *(1.35)*	3.7 *(0.81)*	10.1 *(0.57)*	0.4 *(0.18)*
Sand	3	4.7 *(0.31)*	0	3.7 *(0.33)*	0

(b)

	(n)	Total	Predators	Collectors	Scrapers
Paspalum sp.	5	262.6 *(48.5)*	10.6 *(1.1)*	250.2 *(48.8)*	1.8 *(1.1)*
Emergent Vegetation	18	185.4 *(32.5)*	2.78 *(0.8)*	182.2 *(32.5)*	0.4 *(0.2)*
Submerged Vegetation	13	321.0 *(98.9)*	29.7 *(13.2)*	291.3 *(103.2)*	0
Snag	11	134.2 *(43.3)*	8.9 *(2.7)*	125.1 *(44.4)*	0.2 *(0.1)*
Silt	13	606.0 *(140.4)*	78.9 *(24.3)*	526.4 *(117.1)*	0.7 *(0.3)*
Sand	3	38.0 *(19.1)*	2.7 *(1.2)*	35.2 *(17.9)*	0

Multivariate Analysis of Samples

TWINSPAN (of the log-transformed data) yielded six groups (A-F) at the fifth level of division (Figure 3.27). The first division placed samples from lentic billabong habitats in a single group (Group F), separating them from the remaining lotic samples (Groups A-E). The indicator species for this division was the chironomid *Procladius* sp. Group F contained seven samples from silt substrata littoral sites in the billabongs CGBB and SLBB with one silt substratum sample from the backwater IMBW.

The 55 lotic samples separated on the second division into two groups. The first, Group A, contained samples from both main-channel (QBMC) and backwater (IMBW) mesohabitats (Table 3.20). All Group A samples were from aquatic vegetation microhabitats (Table 3.21). Indicator species for this group were the zygopterans, *I. heterosticta* and *Calagrion billinghursti,* and the shrimp *C. mccullochi.*

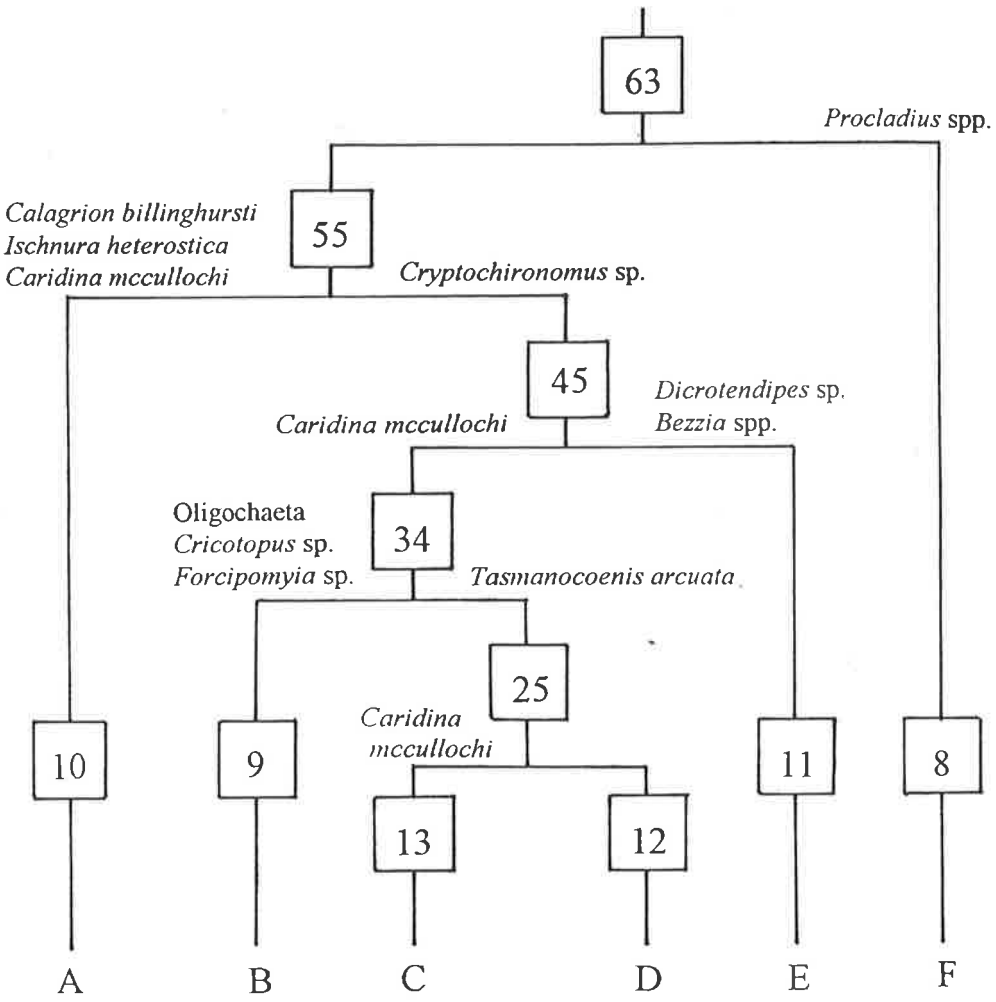


Figure 3.27 TWINSPAN dendogram of samples collected from the lower Murray (January 1990). Indicator species are listed above the relevant divisions. Entities in sample groups A-F are listed in Table 3.20 and Table 3.21.

The second group (B to E) contained a majority of samples from main-channel and anabranch habitats (Table 3.20); the indicator species was the chironomid *Cryptochironomus* sp. Further separations were related to microhabitat differences (Table 3.21; Figure 3.28). Samples from emergent vegetation microhabitats occurred in small numbers in all TWINSPAN groups. Groups A and C, which contained a mix of samples from channel and backwater sites, also contained the majority of samples from *V. spiralis*. Group D, mostly flowing channel and anabranch sites, comprised samples from unvegetated littoral areas with both sand and silt substrata. Group E contained samples from snag microhabitats, while Group F comprised billabong and backwater samples from unvegetated silt substrata. There were significant associations of TWINSPAN groups with FPOM, site salinity and Secchi depth (Table 3.22).

Table 3.20 Samples according to mesohabitat in the six sample groups (A-F) yielded by TWINSPAN of all samples on the lower River Murray floodplain in January 1990.

Group	Sample Composition
A	Eight main channel, two backwater (QBMC, IMBW)
B	Seven main channel, two slow anabranch (PRMC, MGMC, PRAB)
C	Five main channel, five slow anabranch, three backwater (SIMC, QBMC, PRMC, MNAB, PRAB, IMBW, PRBW)
D	Four main channel, five slow anabranch, three fast anabranch (SIMC, MGMC, MNAB, SLAB)
E	Six backwater, three main channel, two fast anabranch (IMBW, PRBW, SCBW, SIMC, PRMC, SLAB)
F	Seven billabong, one backwater (SLBB, CGBB, PRBW)

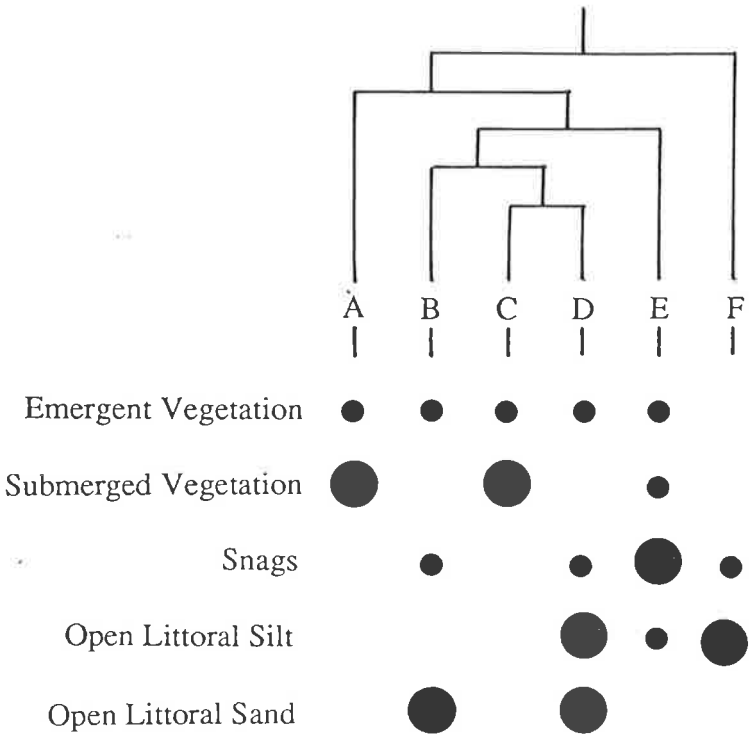


Figure 3.28 A pictorial summary of the microhabitat representation of samples in the TWINSPAN groups A to F, as listed in Table 3.21. Large circles depicts greater than 70% of samples from the microhabitat occur in this sample group, medium circles 30-70% and small circles 1-30%.

Table 3.21 Samples according to microhabitat in the six sample groups (A-F) yielded by the TWINSPAN of all habitat samples on the lower River Murray floodplain in January 1990

Group	Sample Composition
A	Five emergent vegetation, five submerged vegetation
B	Six emergent vegetation, two snag, one sand
C	Seven submerged vegetation, six emergent vegetation
D	Four emergent vegetation, five silt, two sand, one snag
E	Seven snag, two Paspalum, one submerged vegetation, one silt
F	Seven silt, one snag

Table 3.22 Spearman Rank correlation coefficients (r_S) between environmental variables and the samples in the eleven groups (A-F) yielded by the TWINSPAN of all habitat samples on the lower River Murray floodplain in January 1990.

Variable	r_S	Significance
CPOM	-0.161	ns
FPOM	0.248	$p<0.05$
Shade	-0.077	ns
Salinity	0.362	$p<0.01$
Oxygen	-0.005	ns
Temperature	0.236	ns
Secchi	-0.459	$p<0.001$

When analysed using flexible-UPGMA, 14 major clusters (A-N) resulted (Figure 3.29). Samples from silt substrata in billabongs and samples from backwaters were distinctly different to samples from lotic habitats, main channel and anabranches. Within lotic habitats the similarity of samples reflected microhabitat differences. The pattern was similar to that produced by TWINSPAN, where major differences were between samples from lentic and lotic habitats.

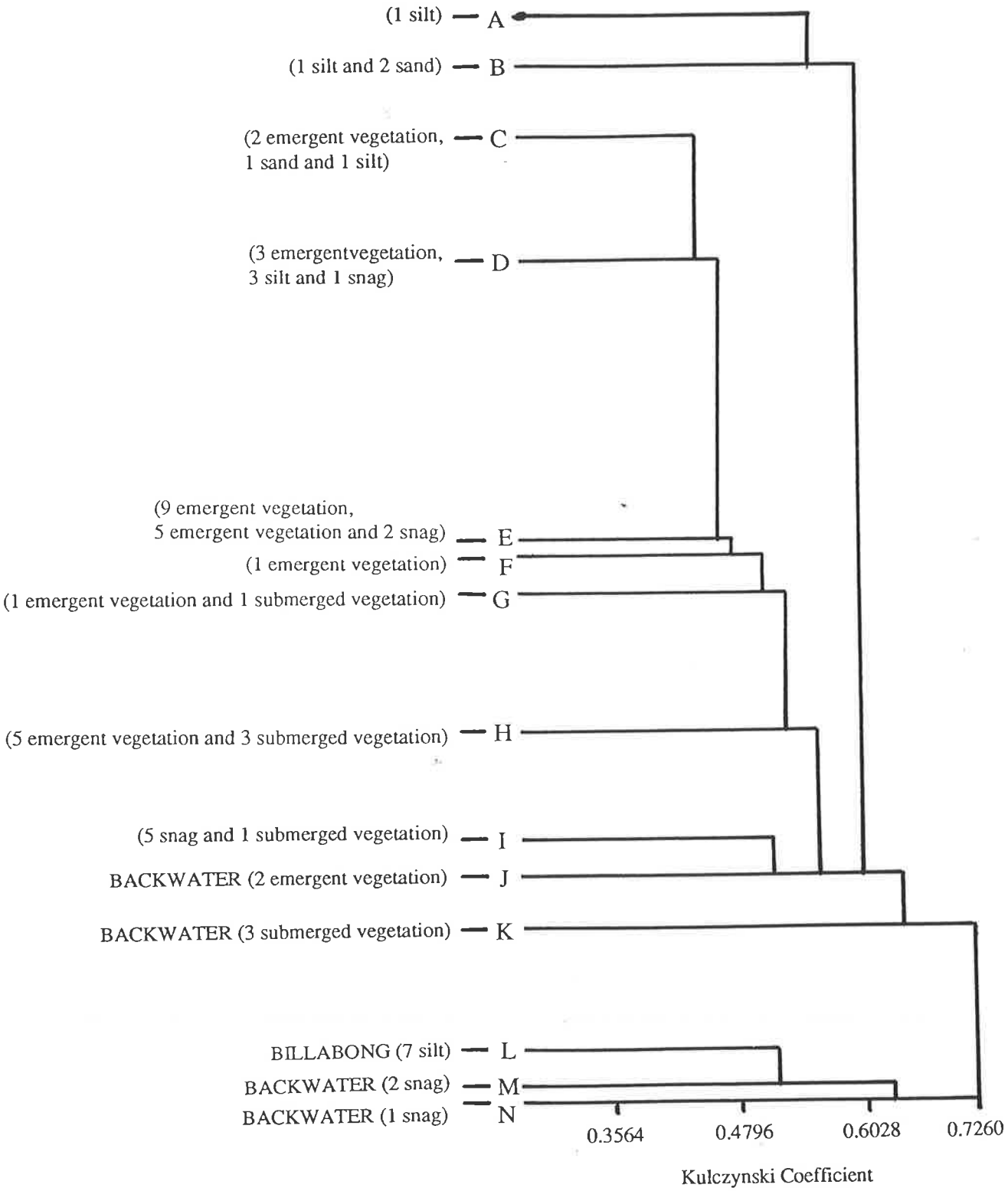


Figure 3.29 Major clusters (A-N) resulting from flexible-UPGMA on samples collected from the lower River Murray floodplain (January 1990). The sample composition of each cluster is summarised.

Multivariate ordination of the sample data demonstrated assemblage differences between habitats. Figure 3.30 shows the distribution of samples on the first and second axes of the SSH plot. When samples were labelled according to mesohabitat, the distinctiveness of samples from billabong sites was evident (Figure 3.31). These formed a distinct cluster with low scores on both Axis 1 and Axis 2. The backwater samples were more dispersed but also had low scores on both Axis 1 and 2. Comparatively, samples from fast and slow anabranches had high scores on both Axis 1 and 2, with a 'gradient' extending from habitats of low flow to those of higher flow. Samples taken from main channel sites were dispersed, forming no distinct clusters. As only three sites on the main channel of the lower Murray were sampled, sites were not further sub-divided into pool section. The effect of pool section on littoral macroinvertebrate assemblage composition will be examined in more detail in Chapter 4. The differences in position within pools of the three main channel sites (QBMC, PRMC and MGMC) may have contributed to dispersion of the samples from these sites on the SSH plot.

When samples are labelled according to microhabitat the unvegetated silt substrata samples were distinctive, clustering low on both Axis 1 and Axis 2 (Figure 3.32). Samples from submerged vegetation fall low on Axis 2 and on the higher portion of Axis 1. There was minimal overlap between samples from submerged vegetation, snag or unvegetated littoral habitats. Snag samples had low scores on Axis 1, overlapping with channel and backwater samples from unvegetated silt substrata. Emergent vegetation samples, mostly *Phragmites australis*, did not form distinct clusters and overlapped with snag and submerged vegetation samples. The silt samples from main channel and backwater mesohabitats fall high on Axis 2, distinctly separated from billabong silt samples. The first axis of the SSH ordination was significantly correlated with Secchi depth and the quantity of FPOM present in samples (Table 3.23). Axis 2 also showed a significant correlation with FPOM as well as temperature (Table 3.23).

When the groups derived from TWINSPAN were mapped onto the SSH plot (Figure 3.33), Group F formed a distinct cluster of billabong samples from unvegetated silt substrata. Groups A and E were also distinctive; Group A dominated by samples from submerged vegetation and Group E by snags. Groups B, C and D covered the large amorphous group of main channel samples from vegetation, snag and silt microhabitats. TWINSPAN suggested that sample groups B, C, and D were most similar, which is confirmed by the ordination. This suggests that assemblages of

different microhabitats in the main channel sites are not substantially different (cf. Figure 3.26).

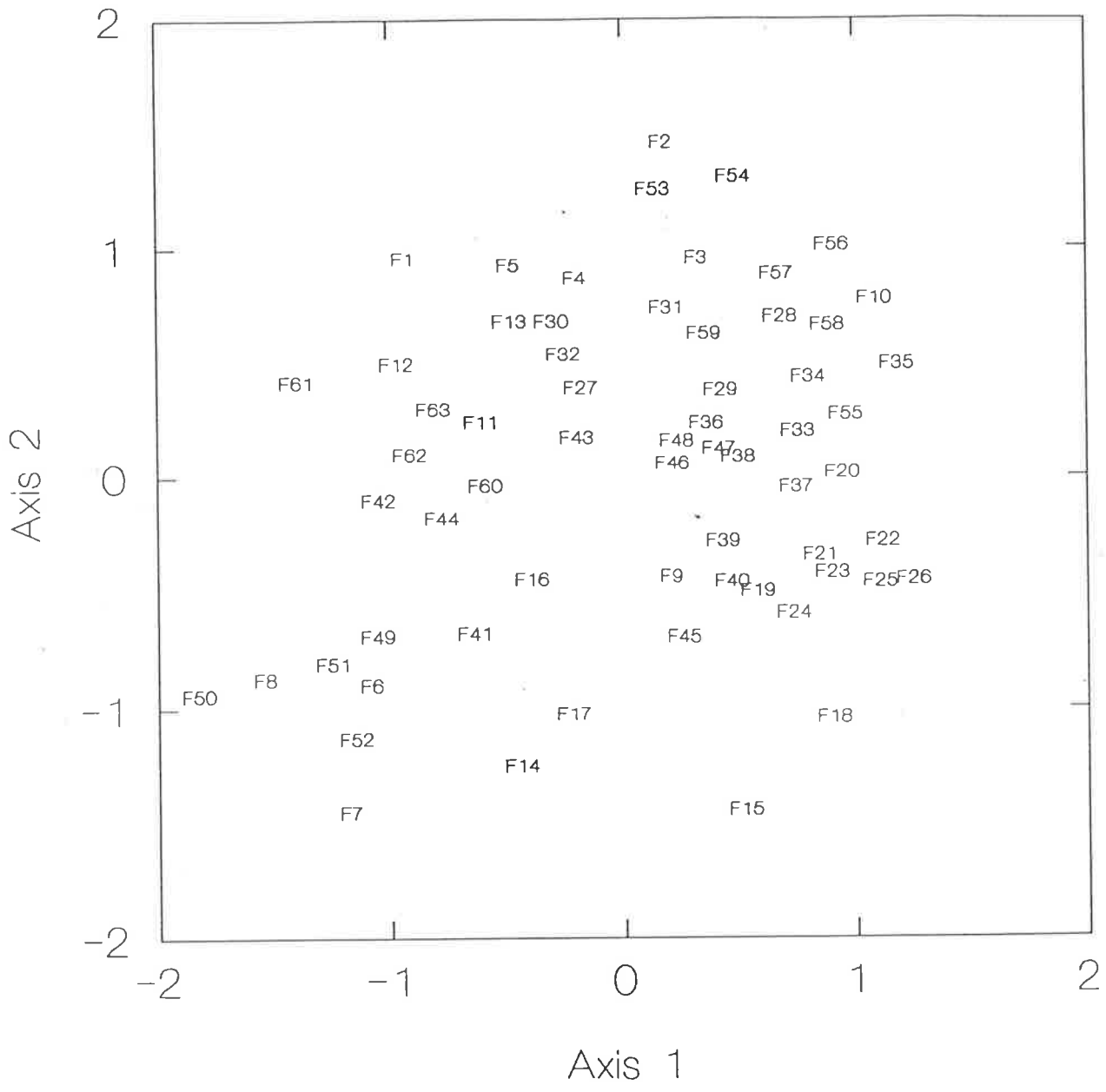
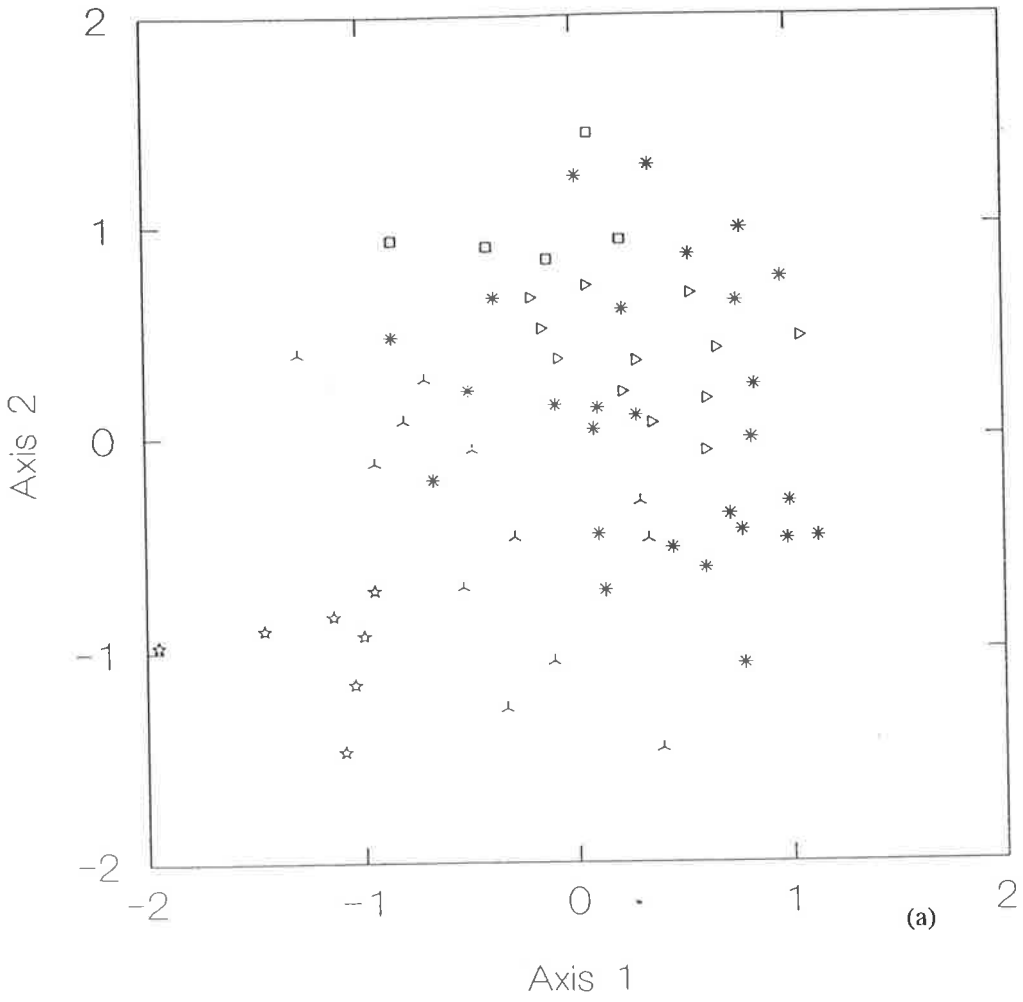
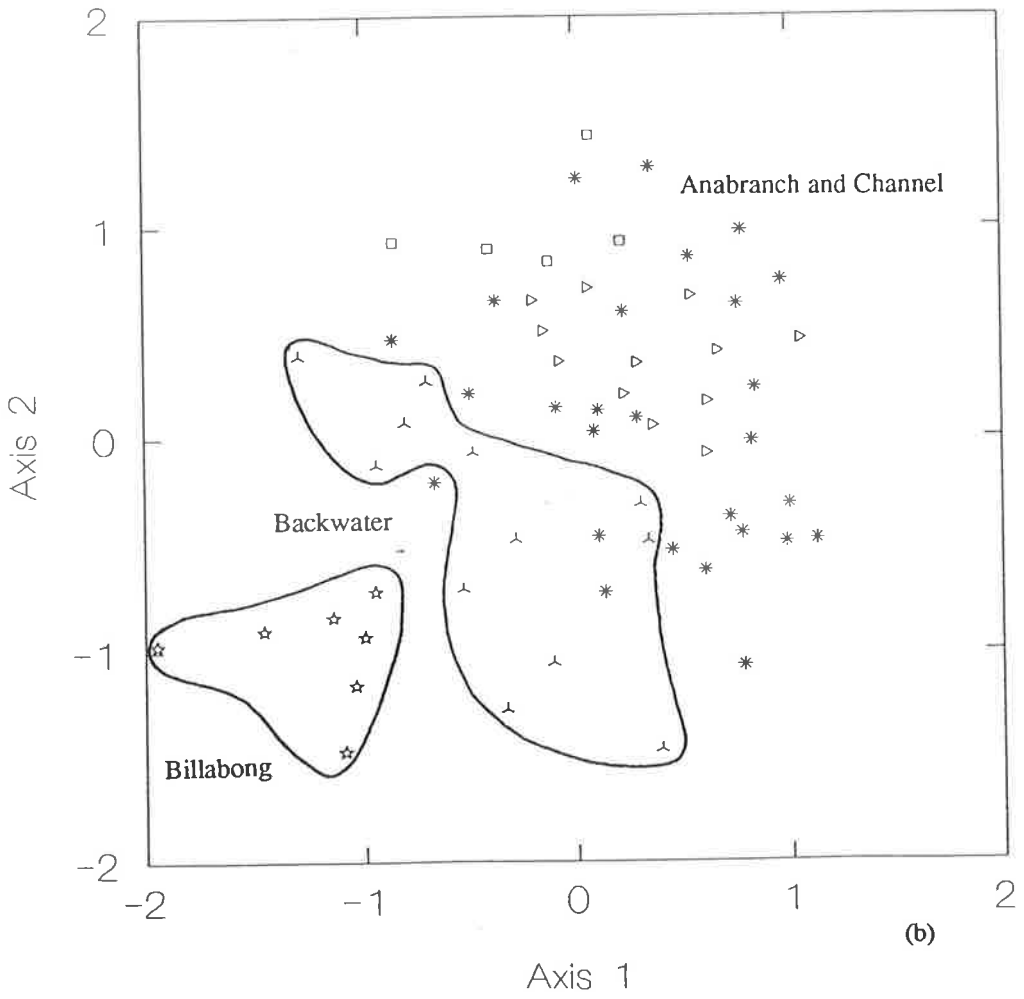


Figure 3.30 Distribution of samples on the first and second axes of the SSH plot of all samples collected from habitats sampled on the lower River Murray in January 1990.

Figure 3.31 (a) SSH plot on the first and second axes of samples collected from all habitats on the lower River Murray, January 1990. Samples are labelled according to the mesohabitat from which they were collected; 'stars', billabongs; 'three corners', backwaters; 'squares'; fast anabranches; 'triangles', slow anabranches; 'asterisk', main channel sites.
(b) highlights the suggested groupings of mesohabitats.

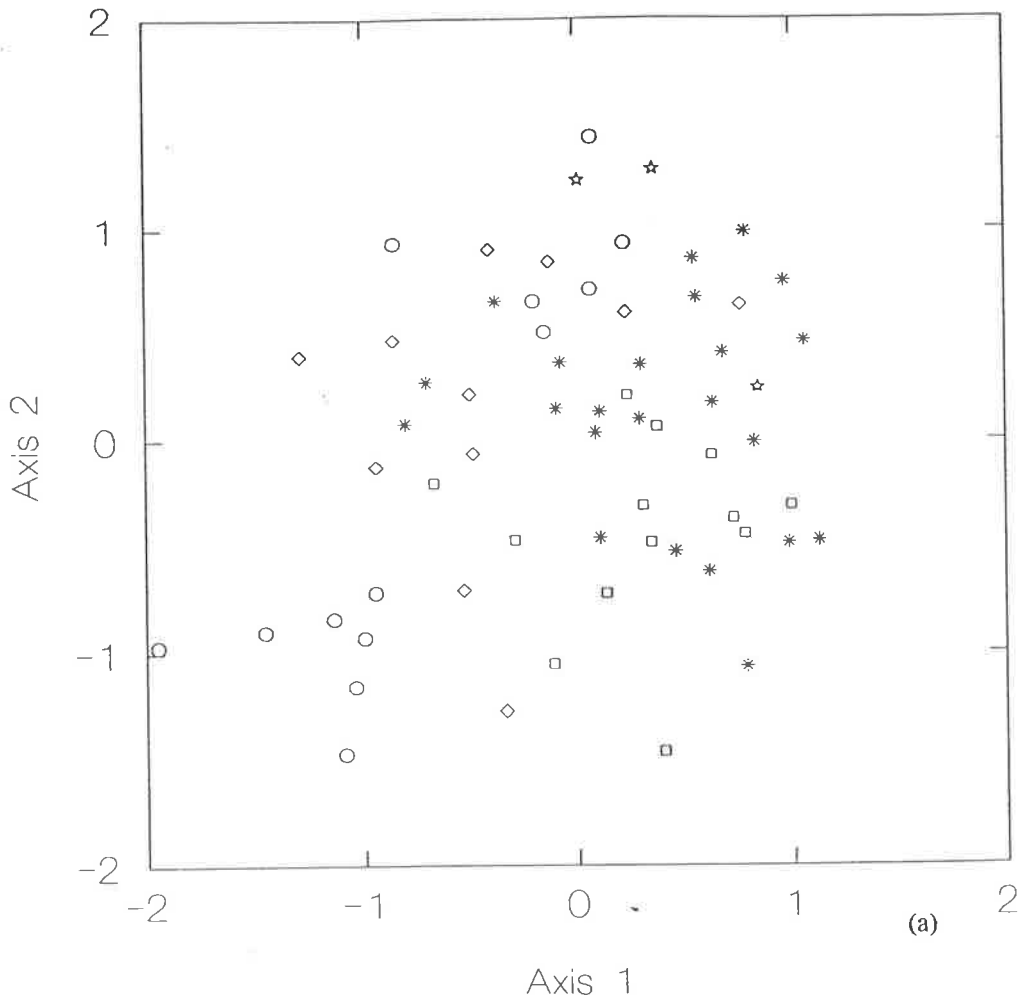

Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(a)


Anabranch and Channel
Backwater
Billabong
Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(b)

Figure 3.32 (a) SSH plot on the first and second axes of samples collected from all habitats on the lower River Murray, January 1990. Samples are labelled according to the microhabitat from which they were collected; 'asterisk', emergent vegetation; 'squares', submerged vegetation; 'diamonds', snags; 'circles', unvegetated open littoral with a silt substrata; 'stars', unvegetated open littoral with a sand substrata. (b) redefines the distinctive mesohabitats and highlights the suggested trend along Axis 1 from unvegetated littoral regions towards vegetation which may reflect microhabitat complexity.


2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
(a)
Axis 1

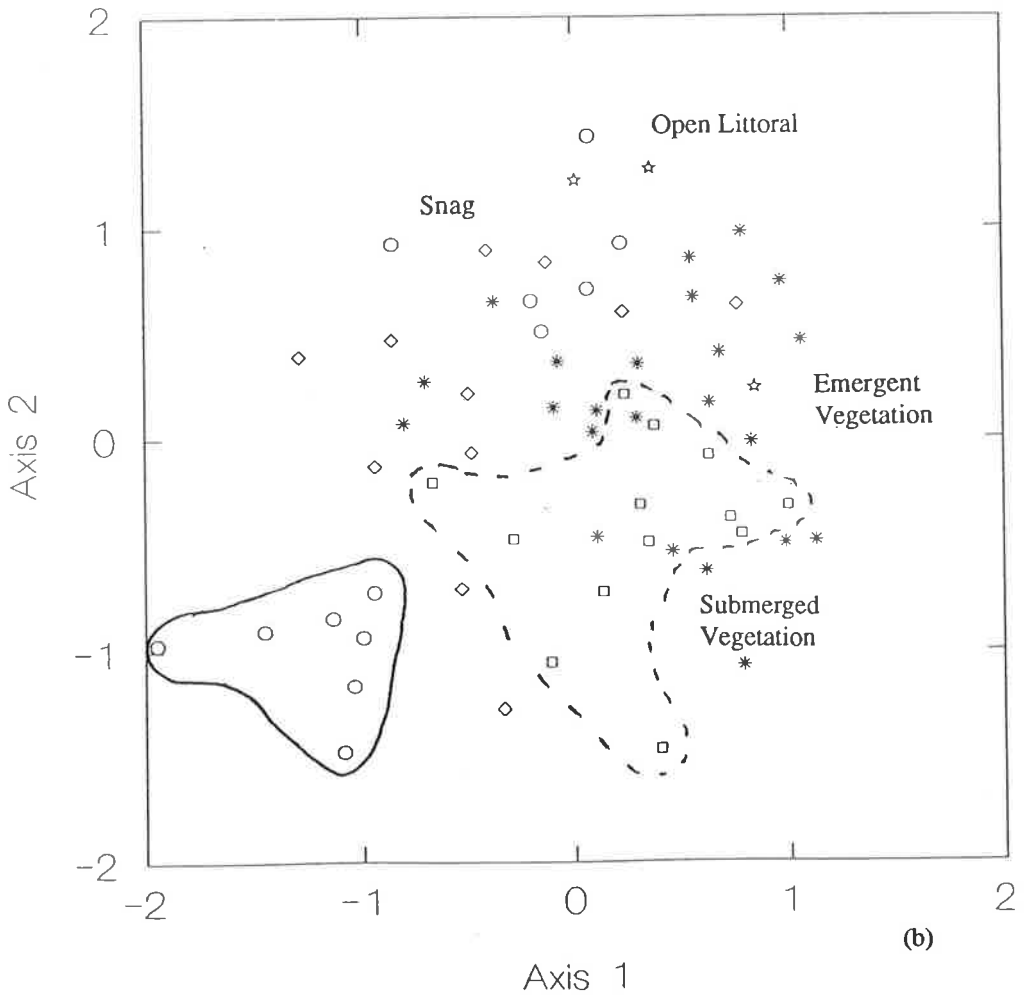
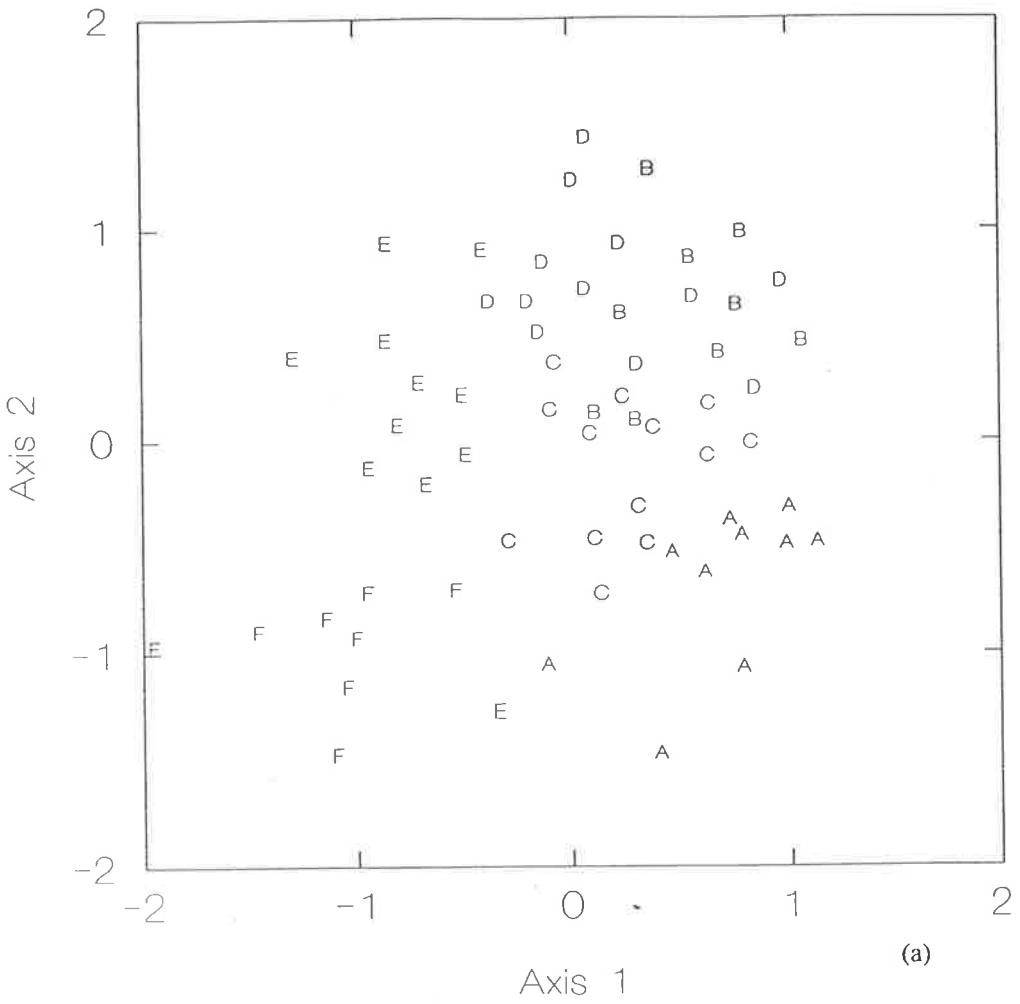
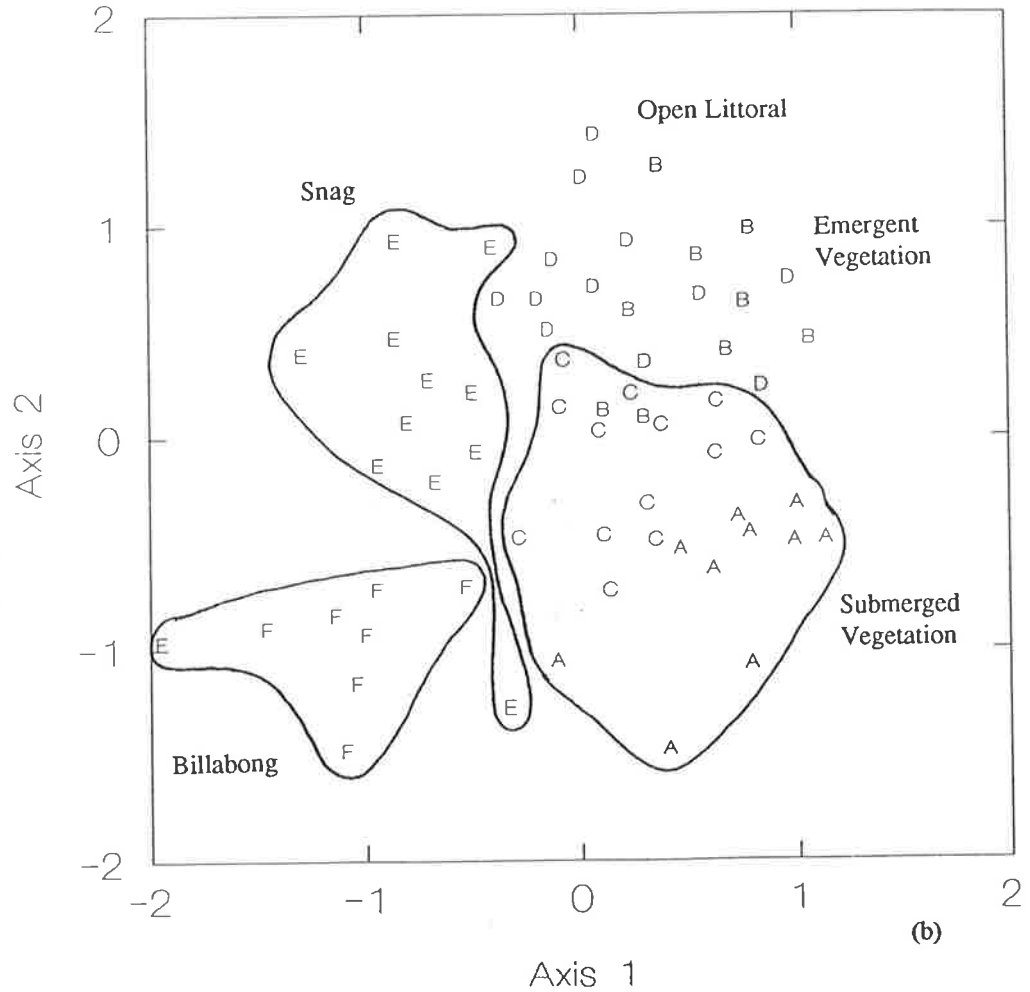

Open Littoral
Snag
Emergent
Vegetation
Submerged
Vegetation
2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
(b)
Axis 1

Figure 3.33 (a) SSH plot on the first and second axes of samples collected from all habitats on the lower River Murray, January 1990. Groups derived from the TWINSPAN are superimposed (cf. Tables 3.20 and 3.21).
(b) redefines the distinctive mesohabitats and highlights those samples groups dominated by submerged vegetation samples and snags, the remainder comprised mostly emergent vegetation samples.


Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(a)


Open Littoral
Snag
Emergent Vegetation
Submerged Vegetation
Billabong
Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(b)

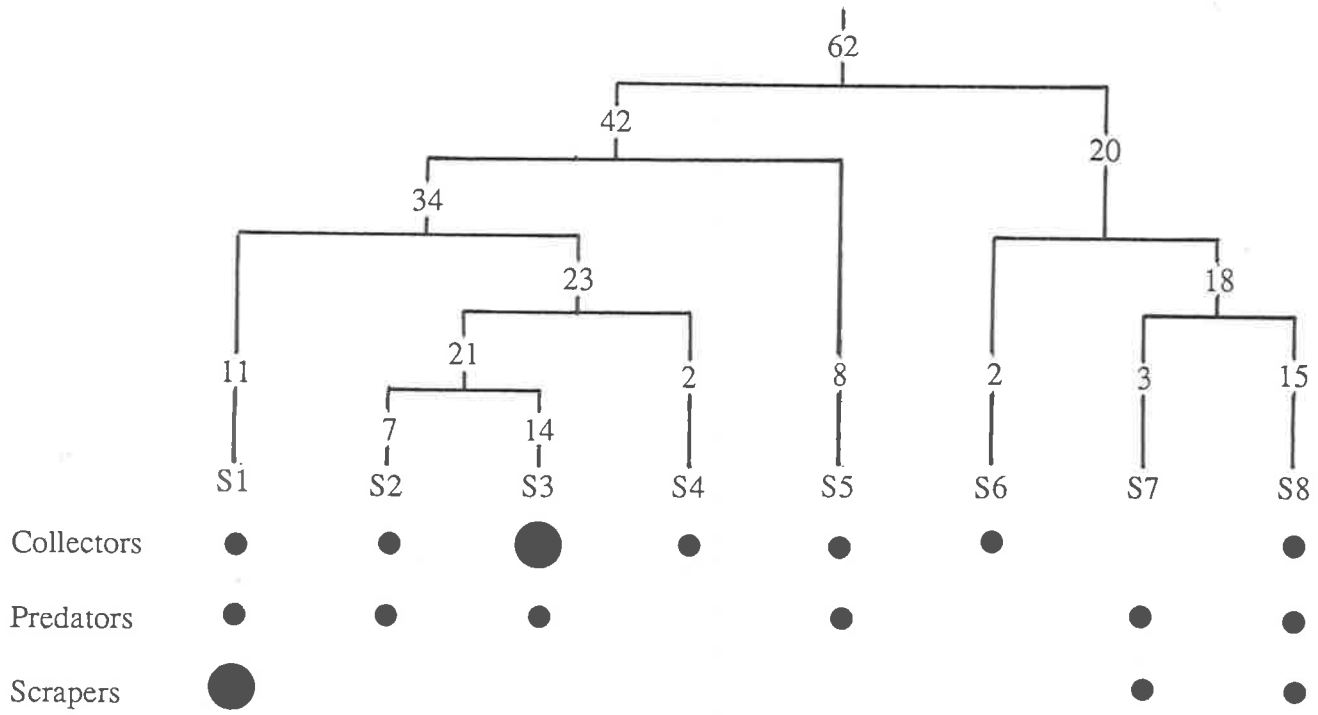


Figure 3.34 TWINSPAN dendogram of the species data from the samples collected from the lower River Murray floodplain in January 1990. Taxa in species groups S1 to S8 are listed in Table 3.24. The proportional representation of each FFG in the species groups is depicted as follows, large circle >70%, medium circle 30-70%, small circle 1-30%.

Table 3.23 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first and second axes of the SSH of faunal data from the lower River Murray floodplain, January 1990. (n = 63)

CPOM	1.00								
FPOM	-0.277	1.00							
Shade	0.089	0.127	1.00						
Salinity	-0.127	0.103	-0.279	1.00					
Oxygen	-0.059	0.045	-0.395	0.647	1.00				
Temperature	-0.030	0.190	0.095	0.267	0.027	1.00			
Secchi Depth	-0.188	-0.456	-0.005	-0.176	-0.069	-0.446	1.00		
Axis 1	**0.146**	**-0.388**	**-0.006**	**-0.268**	**0.014**	**-0.230**	**0.500**	**1.00**	
Axis 2	**0.153**	**-0.430**	**-0.083**	**-0.097**	**0.080**	**-0.448**	**0.216**	**0.161**	**1.00**

Multivariate Analysis of Species

TWINSPAN of the species in samples produced 8 groups (S1-S8) (Table 3.24). When each species group was characterised with respect to the relative abundance of each FFG, there was no obvious pattern (Figure 3.34). Both collectors and predators occurred in small numbers in nearly all groups, only Group S3 was dominated by collectors. The majority of scrapers occurred in Group S1, including gastropods *Ferrissia* spp. and the coleopteran *Ochthebius* sp. The most meaningful division of the TWINSPAN was the separation at the first division of groups containing abundant taxa (S1-S5) from groups containing less abundant taxa (S6-S8).

When the preferences of species groups for sample groups were examined, species groups S2-S5 were relatively ubiquitous, showing a 'preference' for nearly all sample groups (Figure 3.35). These groups contained the abundant shrimps *P. australiensis*, *C. mccullochi,* the prawn *M. australiense* and the chironomids *Cladotanytarsus* sp. and *Tanytarsus* sp. Species group S1 had a preference for sample group A which is dominated by submerged vegetation samples. This species group contained the yabbie *Cherax destructor* and hemipterans *Micronecta* spp. Species groups S6-S8, comprising the rarer taxa, displayed a preference for samples from billabongs, Group F. Species in these groups included a number of coleopteran larvae, hemipterans and chironomids such as *Chironomus cloacalis,* found predominantly in billabongs (cf. Table 3.24).

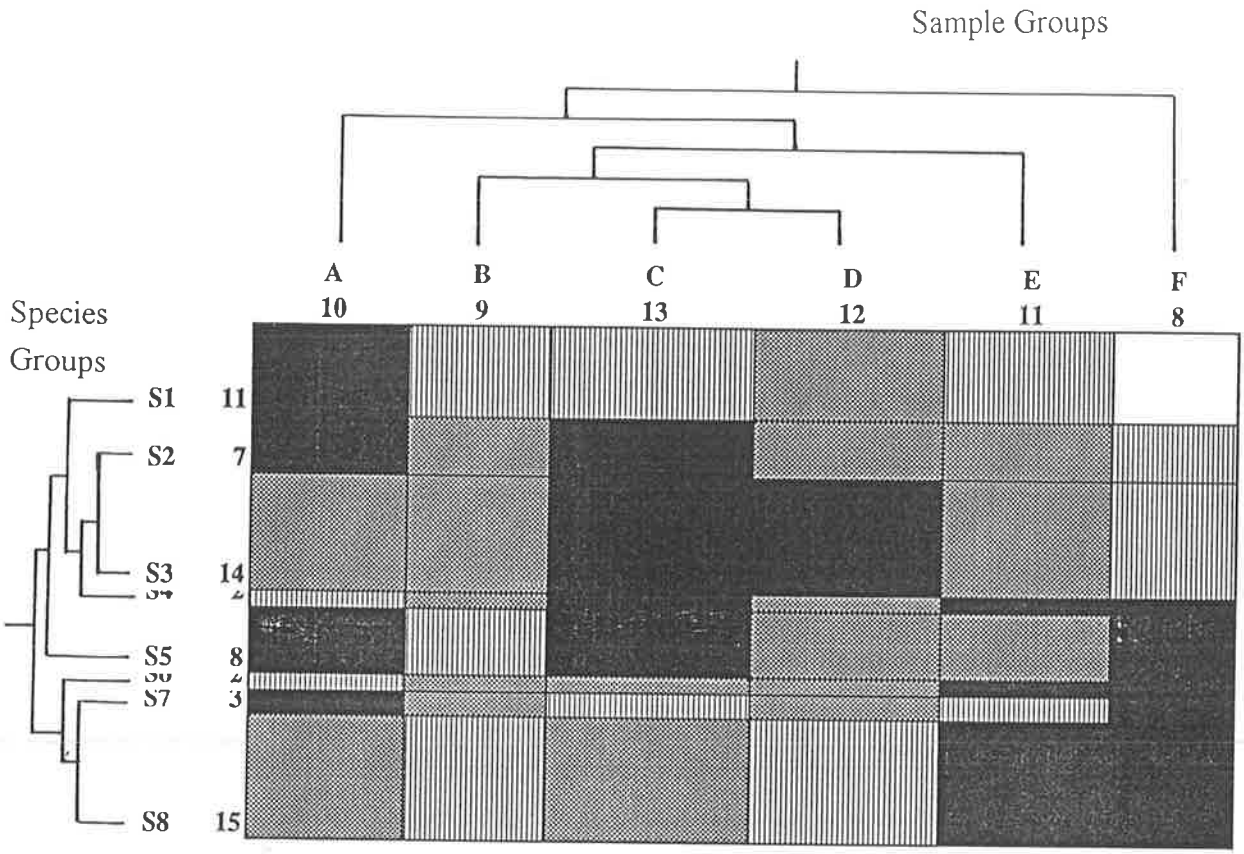


Figure 3.35 Two-way table of species group fidelities (*Fij*) to sample groups. Both species groups (S1-S8) and sample groups (A-f) are derived from the TWINSPAN of the faunal data in the 63 samples from the lower River Murray floodplain collected in January 1990. The numbers of elements in each group are near the label. Values of $F_{ij} > 2.0$ (full-shading) or $F_{ij} > 1.0$ (cross-hatching) indicate 'preference' while values of $F_{ij} < 1.0$ (vertical lines) or F_{ij} (no shading) indicate 'avoidance'.

Table 3.24 Species and their FFG for the seven species groups (A-G) yielded by the TWINSPAN of all habitat samples on the lower River Murray floodplain in January 1990.

	Species	FFG
Group S1	*Austrochiltonia australis*	Collector
	Cherax destructor	Collector
	Micronecta spp.	Collector
	Saldura sp.	Collector
	Calagrion billinghursti	Predator
	Mesovelia sp. 1	Predator
	Allodessus sp.	Predator
	Empididae sp.	Predator
	Stratiomyidae sp.	Predator
	Ferrissia spp.	Scraper
	Ochthebius sp.	Scraper
Group S2	Oligochaeta spp.	Collector
	Paratya australiensis	Collector
	Macrobrachium australiense	Collector
	Cricotopus spp.	Collector
	Coxelmis sp. (larvae)	Predator
	Tipulidae spp.	Predator
	Parachironomus sp.	Predator
Group S3	*Sphaerium* sp.	Collector
	Austroargathona picta	Collector
	Tasmanocoenis arcuata	Collector
	Cloeon sp.	Collector
	Sigara sp.	Collector
	Paracymus sp.	Collector
	Cladotanytarsus sp.	Collector
	Cladopelma sp.	Collector
	Forcipomyia sp.	Collector
	Limnoxenos sp.	Collector
	Ecnomus sp.	Predator
	Oecetis sp.	Predator
	Diplonychus eques	Predator
	Pseudagrion aureofrons	Predator
Group S4	*Stenochironomus* sp.	Collector
	Tanytarsus spp.	Collector
Group S5	*Caridina mccullochi*	Collector
	Paratendipes sp.	Collector
	Naucoris sp.	Predator
	Ablabesmyia sp.	Predator
	Coelopynia sp.	Predator
	Ischnura heterosticta	Predator
	Hemicordulia tau	Predator
	Hydraena sp.	Scraper

Group S6	*Cryptochironomus* sp.	Collector
	Dicrotendipes sp.	Collector
Group S7	*Paroster* sp.	Predator
	Hydrophilidae (larvae) sp. 1	Predator
	Enochrus sp.	Scraper
Group S8	Culicinae sp.	Collector
	Triplectides australis	Collector
	Kiefferulus martini	Collector
	Chironomus cloacalis	Collector
	Dicrotendipes conjunctus	Collector
	Chironomus sp.	Collector
	Agraptocorixa sp.	Collector
	Anisops spp.	Predator
	Procladius sp.	Predator
	Bezzia sp.	Predator
	Microvelia sp.	Predator
	Antiporus femoralis	Predator
	Berosus sp. (larvae)	Predator
	Eretes sp. (larvae)	Predator
	Physa sp.	Scraper

Ordination of the species data suggested a weak separation of the FFG's on two axes. Figure 3.36 shows the distribution of species on Axis 1 and Axis 2 of the SSH plot, the overlay of the relative FFG's is given in Figure 3.37. Collector taxa have higher scores on Axis 2 than predators. When groups produced by TWINSPAN (cf. Table 3.24) are mapped onto the SSH plot only Groups S3 and S8 form distinct clusters (Figure 3.38). Species groups S6-S8, the least abundant taxa, form a cluster low on Axis 2. Species group S3, which shows a strong preference for sample groups C and D, formed a cluster high on both Axis 1 and Axis 2.

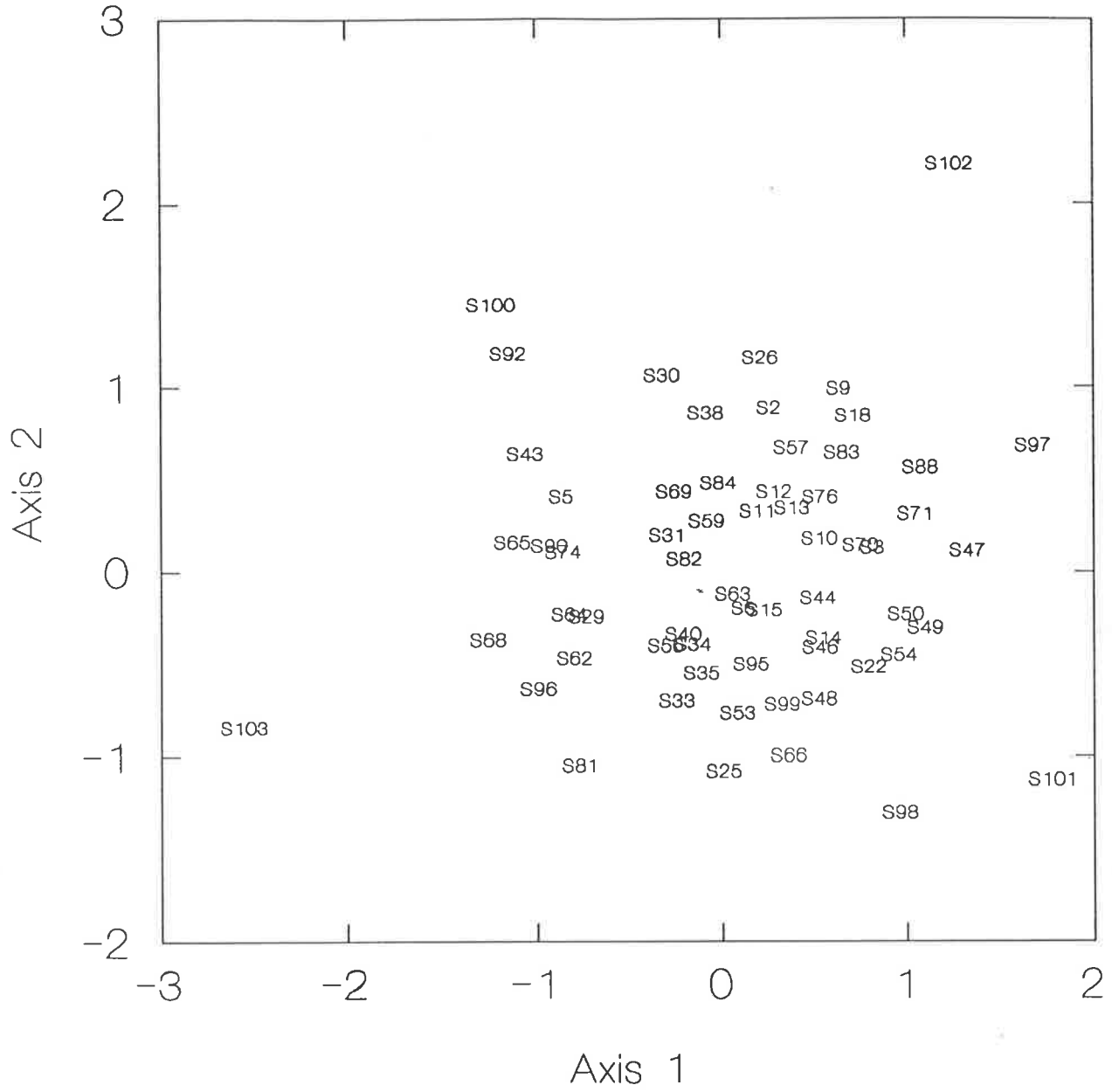
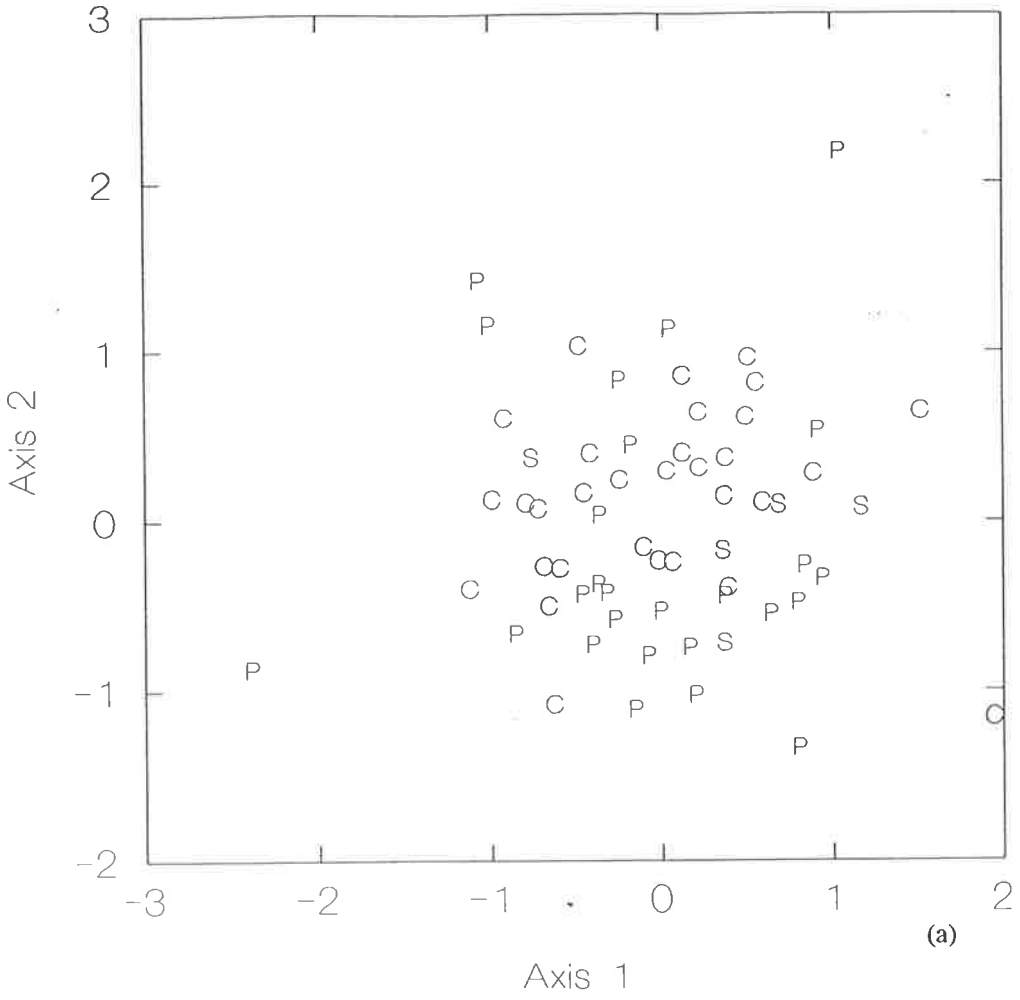
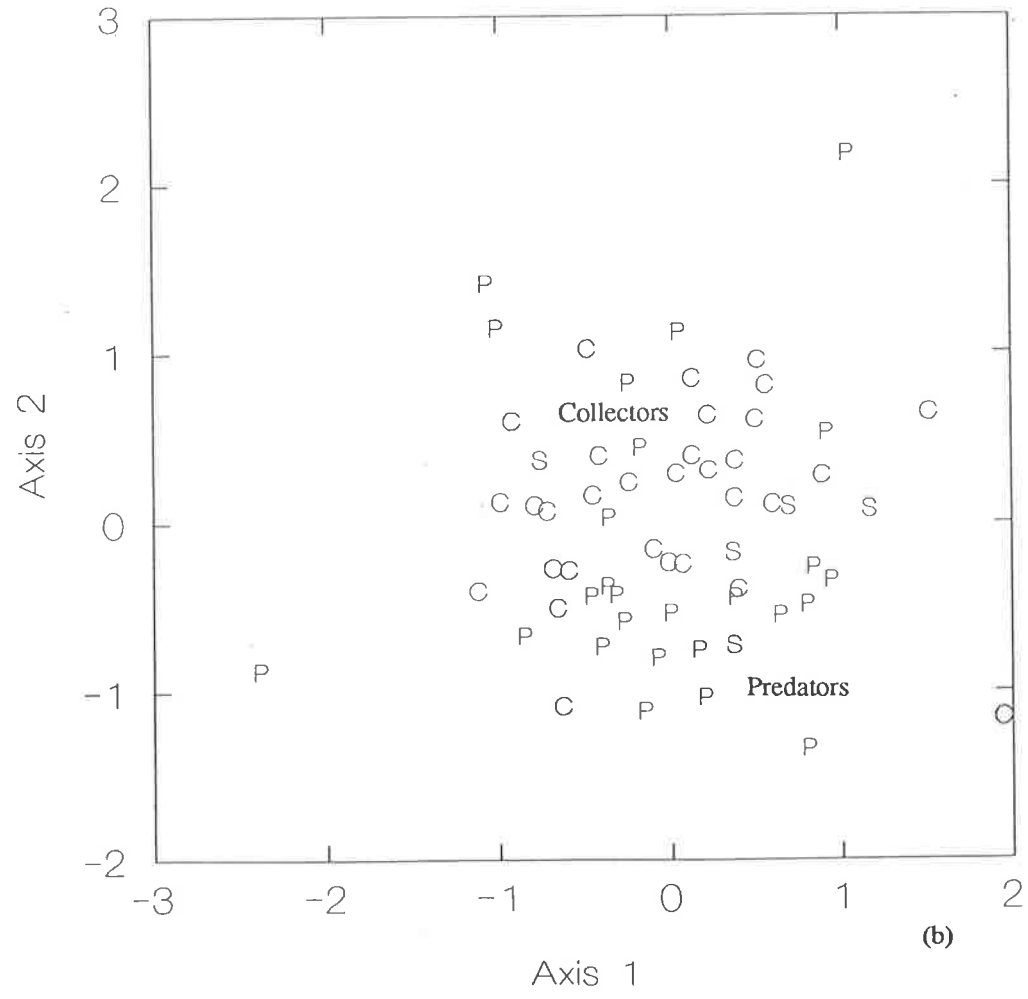


Figure 3.36 SSH ordination of the species in sample data from the 63 samples collected from the lower River Murray floodplain in January 1990. Distribution of species on the first and second axes.

Figure 3.37 SSH ordination of the species in sample data from the 63 samples collected from the lower River Murray floodplain in January 1990. Species are labelled according to their respective FFG; 'C' collector, 'P' predator and 'S' scraper. There is no apparent clustering os species.

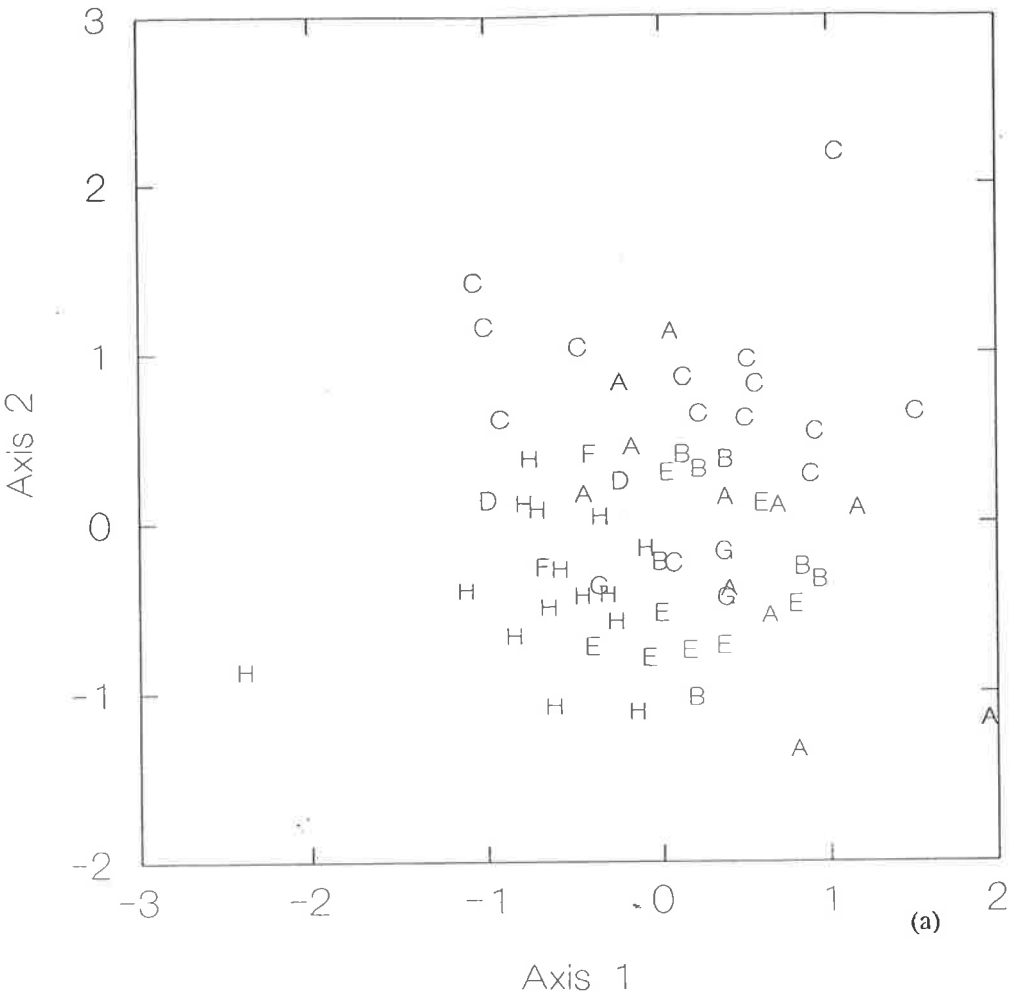

Axis 2
Axis 1
3
2
1
0
-1
-2
-3
-2
-1
0
1
2

(a)

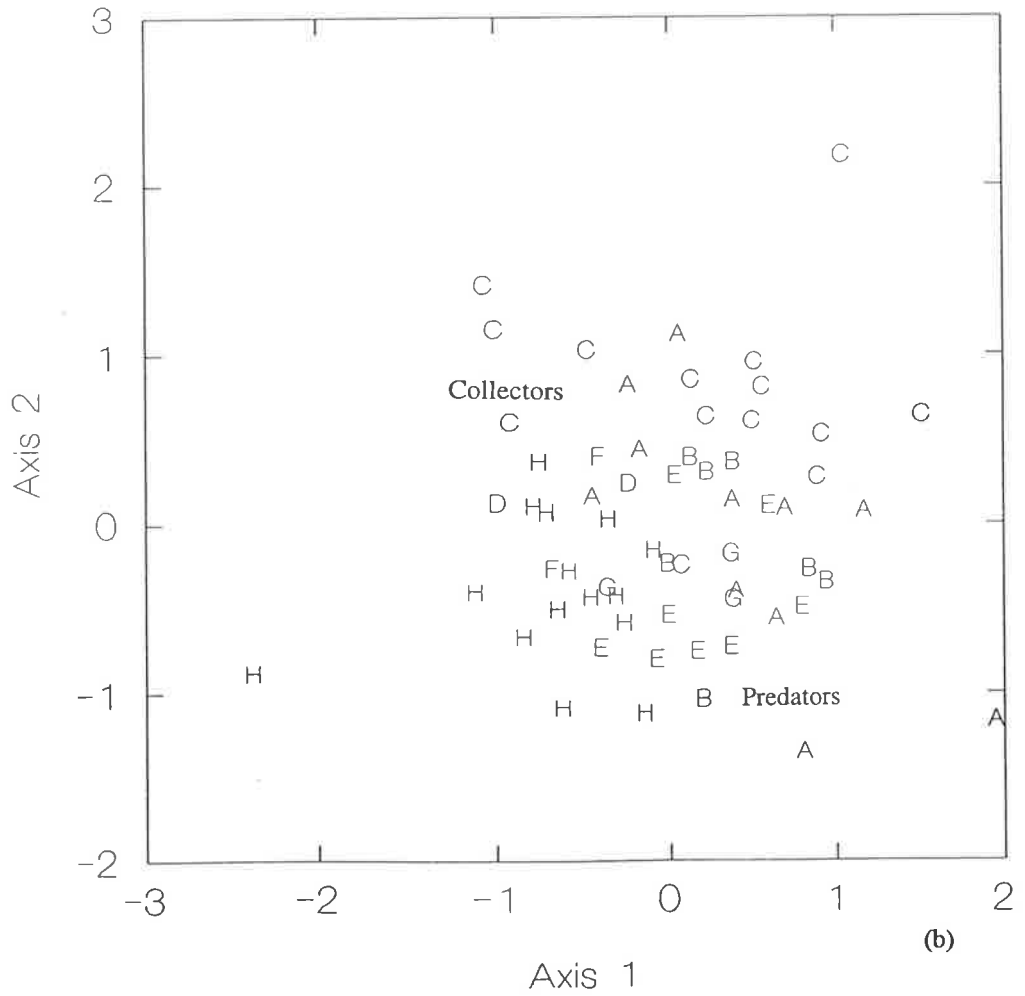

Axis 2
Axis 1
Collectors
Predators
3
2
1
0
-1
-2
-3
-2
-1
0
1
2

(b)

Figure 3.38 SSH ordination of the species in sample data from the 63 samples collected from the lower River Murray floodplain in January 1990. Species groups derived from TWINSPAN are superimposed (cf. Table 3.24); 'A' = S1; 'B' = S2; 'C' = S3; 'D' = S4, 'E' = S5, 'F' = S6; 'G' = S7; 'H' = S8.


Axis 2
Axis 1
3
2
1
0
-1
-2
-3
-2
-1
0
1
2

(a)


Axis 2
Axis 1
Collectors
Predators
3
2
1
0
-1
-2
-3
-2
-1
0
1
2

(b)

Gastropods in the lower River Murray

A summary of the historical abundances of gastropod taxa in the lower River Murray is provided in Chapter 1. Bennison *et al.* (1989) recorded 10 gastropod taxa in the lower section of the river (Table 3.25). Three of these occurred at Site 12 (upstream from Lock 5) and four at Site 13 (Morgan), with the gastropods *Ferrissia* spp. and the introduced *P. acuta* the most abundant. The large prosobranch *T. balonnensis* was rare (Table 3.25). The difference in both richness and abundance of the gastropods at Site 14 (Woods Point) is unclear, but perhaps related to the position of this site on the lower river. The Woods Point area is relatively disturbed, with the surrounding floodplain developed for irrigated agriculture and the riparian vegetation dominated by willows (*Salix babylonica*) (Bennison *et al.*, 1989). These conditions may be favourable for the introduced taxa *Potamopyrgus* sp. and *P. acuta*, both highly abundant at this site (cf. Table 3.25). *Physa* spp. have been found to thrive in polluted, eutrophic environments (cf. Elstad, 1986).

In the present study, only *Ferrissia* spp. and *P. acuta* were recorded from the lower Murray, these were rare. The same situation was observed by Boulton and Lloyd (1991) and Jenkins (unpubl. Hons Thesis). Neither large prosobranch taxa (*Notopala* spp. or *T. balonnensis*) were collected from any of the habitats along the lower Murray during this survey. It is apparent that there have been drastic reductions in both the distribution and abundance of these taxa since the 1950's.

Table 3.25 Gastropods collected at the three sites on the lower Murray as part of the Murray-Darling Basin Commission macroinvertebrate survey (Bennison *et al.*, 1989)

Species	Site 12	Site 13	Site 14
Notopala sp.			1
Potamopyrgus sp.	1	1	556
Glacidorbis hedleyi			39
Thiara balonnensis		5	
Ferrissia spp.	110	11	87
Glyptophysa aliciae			2
Isidorella hainesii			1
Gyraulis meridionalis			11
Isidorella sp.			62
Physa acuta	60	5	494

3.4.3 Spatial Patterns in Both Rivers

The three diversity indices Margalef's (D_{Mg}), Menhinick's (D_{Mn}) and Berger-Parker (d) suggest similarities for the macroinvertebrate assemblages collected from both rivers (cf. Table 3.26). Although more samples were collected from the Darling a similar number of taxa (S) and individuals (N) were recorded from the two systems. In the Darling insects dominated the abundance (cf. Figure 3.7), whereas in the Murray insects comprised only 52% of the individuals with crustaceans more abundant (cf. Figure 3.23). Similar values were obtained for the diversity indices for both rivers.

Table 3.26 Diversity indices calculated from total abundance data for all samples from the lower Darling River and the lower River Murray, January 1990.

Description		Lower Darling	Lower Murray
No. of Samples Collected		111	63
No. of Taxa	S	72	62
No. of Individuals	N	18303	18292
N in most abundant species	N_{max}	6557	6579
Margalef Index	D_{Mg}	7.23	6.21
Menhinick's Index	D_{Mn}	0.53	0.46
Berger-Parker Index	d	0.36	0.36
	$1/d$	2.79	2.78

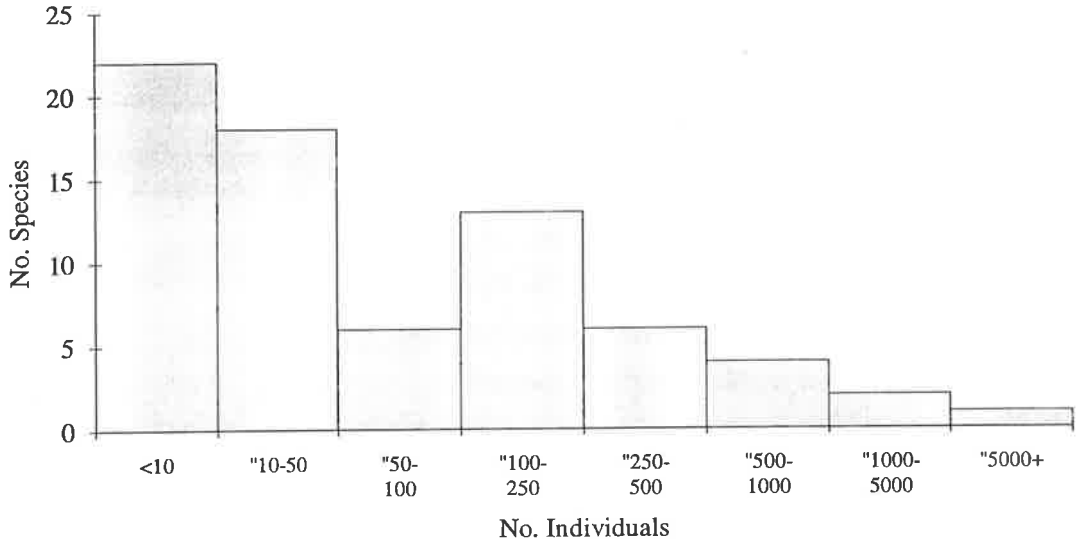
When the number of species in eight abundance classes was plotted (Figure 3.39) the uneven form of the assemblage was evident. Most taxa were moderately rare (less than 50 individuals) with only a few classed as abundant (greater than 500 individuals). In the Darling *Micronecta* spp. dominated the assemblage, occurring in enormous numbers in the temporary billabongs. In the lower Murray the shrimp *P. australiensis* dominated.

TWINSPAN and SSH ordination (cf. Section 3.2.3) were used on the combined sample data to examine broad patterns in littoral zone macroinvertebrate assemblages. TWINSPAN yielded 13 groups (A-M) in five divisions (Figure 3.40). The first division separated lentic samples from the Darling floodplain (Groups A and B) and samples from all habitats on the lower Murray floodplain (Groups C-F) from lotic main channel sites of the Darling (Groups G-M). Lentic sites on the

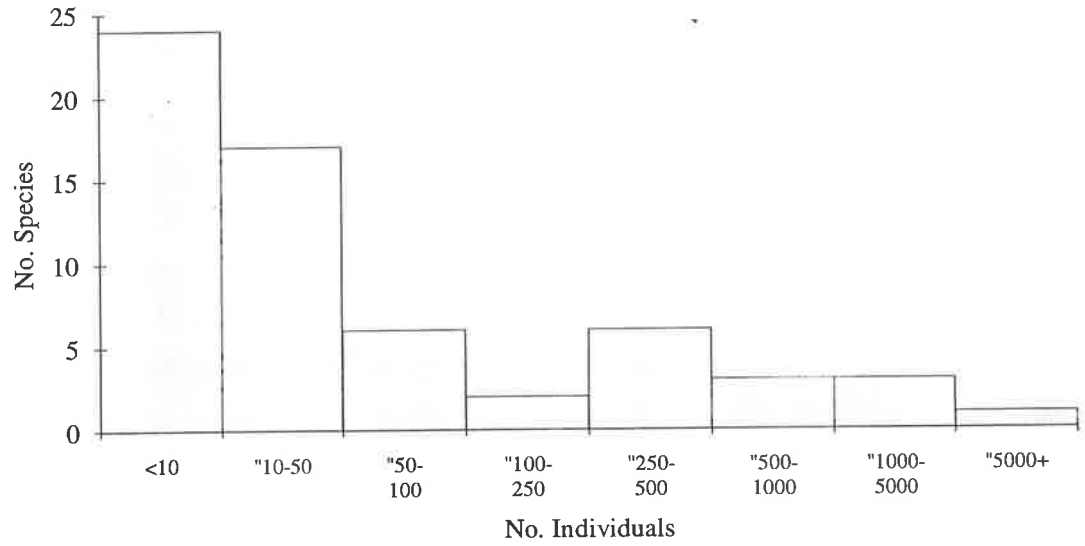
Darling floodplain and samples from the lower Murray were characterised by the midges *Tanytarsus* sp. and *Cricotopus* sp., the shrimps *P. australiensis* and *C. mccullochi* and notonectids *Anisops* spp. The lotic Darling samples were typified by the prawn *M. australiense* and the isopod *Austroargathona picta,* both were found in large numbers in Darling main channel samples but in reduced abundances in the lower Murray.

Table 3.27 Samples according to mesohabitat in the thirteen sample groups (A-M) yielded by TWINSPAN of all samples from both the Darling River floodplain and the lower Murray floodplain in January 1990.

Group	Sample Composition
A	Three Darling River billabong (CPBB), Seven lower Murray Billabong (SLBB, CGBB)
B	Seventeen Darling River billabong (BKBB, OTBB, WBBB)
C	Murray: Seven backwater, three main channel, one fast anabranch (IMBW, PRBW, SCBW, SIMC, PRMC, SLAB)
D	Murray: Seven main channel, seven slow anabranch, four fast anabranch, three backwater (SIMC, QBMC, PRMC, MGMC, MNAB, SLAB, IMBW, PRBW)
E	Murray: Nine main channel, five slow anabranch (SIMC, PRMC, MGMC, PRAB)
F	Two Darling River upper pool (BWUP), Eight lower Murray main channel and two backwater (QBMC, IMBW)
G	Darling: Six upper pool (BWUP, TWUP, WWUP)
H	Darling: Six main channel, five upper pool, two lower pool (WYMC, CPMC, GWUP, GWLP, TWLP)
I	Darling: Eight main channel, two upper pool (WBMC, WYMC, NBMC, BWUP, WWUP)
J	Darling: Seven upper pool, six main channel, one lower pool (BWUP, TWUP, WWUP, WBMC, WYMC, NBMC, CPMC, GWLP)
K	Darling: Ten main channel, five upper pool (WBMC, WYMC, CPMC, TWUP. WWUP)
L	Darling: Nine main channel;, five lower pool, one upper pool (WBMC, WYMC, CPMC, TWLP, GWUP)
M	Darling: Ten main channel, four lower pool, two upper pool (WBMC, WYMC, NBMC, CPMC, GWLP, WWUP)



(a)



(b)

Figure 3.39 The number of species in eight abundances classes for (a) the Darling River floodplain and (b) the lower Murray floodplain, in January 1990.

Table 3.28 Samples according to microhabitat in the thirteen sample groups (A-M) yielded by TWINSPAN of all samples from both the Darling River floodplain and the lower Murray floodplain in January 1990.

Group	Sample Composition
A	Three Darling River billabong (CPBB), Seven lower Murray billabong (SLBB, CGBB)
B	Seventeen Darling River billabong (BKBB, OTBB, WBBB)
C	Murray: Seven snag, three vegetation, one silt.
D	Murray: Nine vegetation, five silt, five snag, two sand
E	Murray: Twelve vegetation, one snag, one sand
F	Two Darling River upper pool, vegetation, Eight lower Murray vegetation
G	Darling: Six vegetation
H	Darling: Eleven snag, two silt
I	Darling: Six snag, four silt
J	Darling: Eleven snag, two silt, one vegetation
K	Darling: Fourteen silt, one snag
L	Darling: Six sand, five silt, four snag
M	Darling: Nine sand, six silt, one snag

The 85 lentic and lower Murray samples split on the second division into Groups A and B, containing billabong samples from both the lower Murray and the Darling (Table 3.27), the indicators were the insect predators *Procladius* sp. and *Anisops* spp. and the corixids *Micronecta* spp. The remaining Murray samples were typified by *P. australiensis,* which was the most abundant taxon and constituted the greatest biomass. Further divisions of the Murray samples related to microhabitat (Table 3.28).

The 89 Darling samples separated on the second division into Groups G to I characterised by the prawn *M. australiense* and the isopod *A. picta*, the mayflies *Cloeon* sp. and *T. arcuata* and the caddis *Ecnomus* sp. These groups contained the remaining vegetation samples and a majority of samples collected from snag microhabitats (cf. Table 3.28). Groups J to M were typified by insect predators, the ceratopogonid *Bezzia* sp. and the tanypodine chironomid *Coelopynia* sp. These groups separated further into J and K, comprising samples from snag and silt microhabitats (Table 3.28), with a number of chironomid taxa and the ephemeropteran *T. arcuata* as indicators (Figure 3.40) . Groups L and M contained all samples from the open littoral sand microhabitat, with the bivalve *Sphaerium* sp. an indicator.

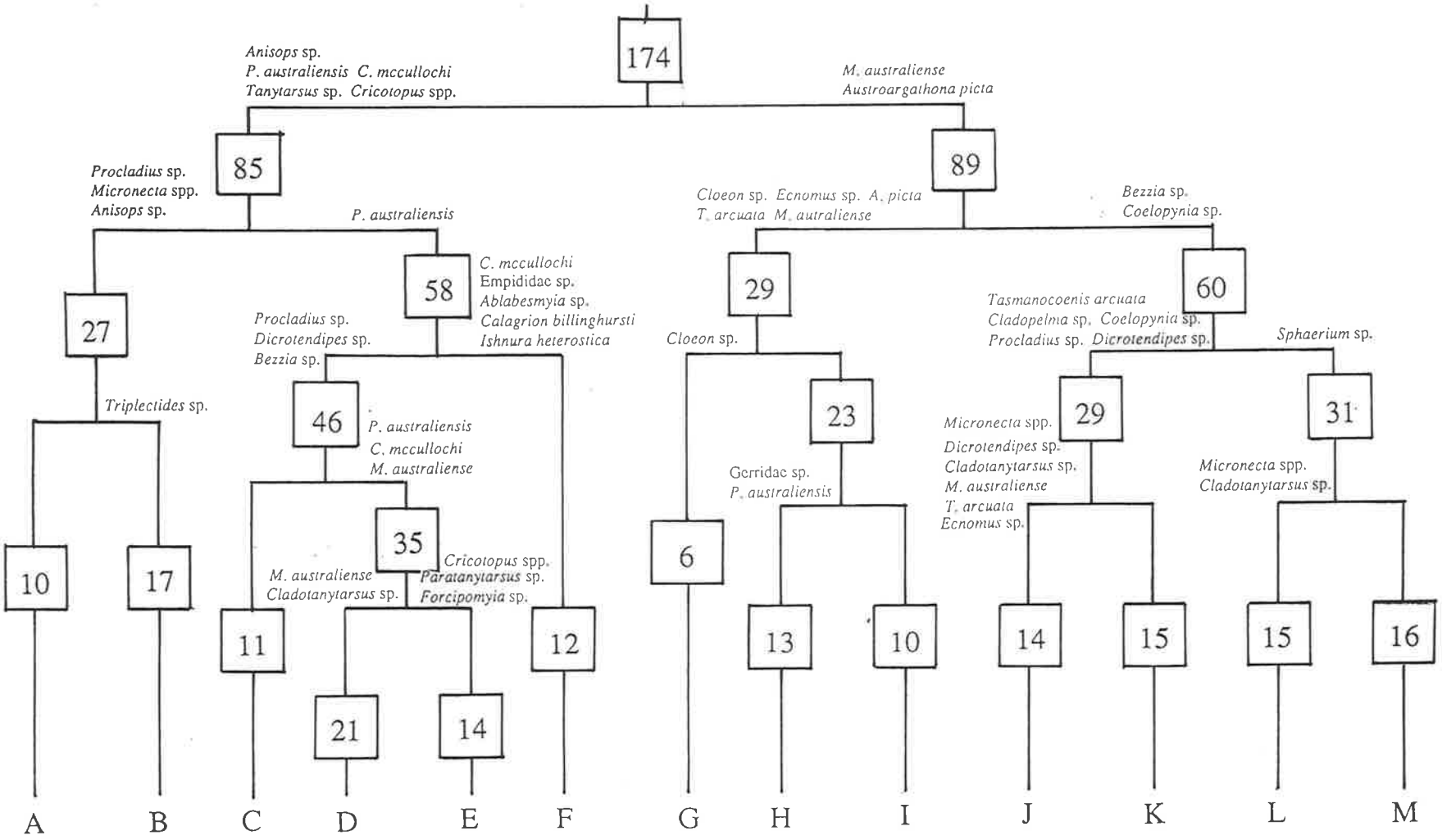


Figure 3.40 TWINSPAN dendogram of the 174 samples from the combined Darling River and lower River Murray samples, January 1990. Indicator species are listed above the relevant divisions. Entities in sample groups A-M are listed in Table 3.27.

Multivariate ordination highlighted the assemblage differences between rivers. Figure 3.41 shows the distribution of samples from the Darling and the lower Murray on the first three SSH axes, with samples from each river showing distinct clusters. The samples collected from the Darling had high scores on Axis 1, were dispersed along Axis 2 and had low scores on Axis 3. In contrast, lower Murray samples had low scores on Axis 1, were also dispersed along Axis 2 but had high scores on Axis 3. Axis 1 was associated with FPOM and site salinity, Axis 2 correlated with site salinity, CPOM and oxygen saturation (cf. Table 3.29). There were associations with Axis 3 and site salinity and Secchi depth.

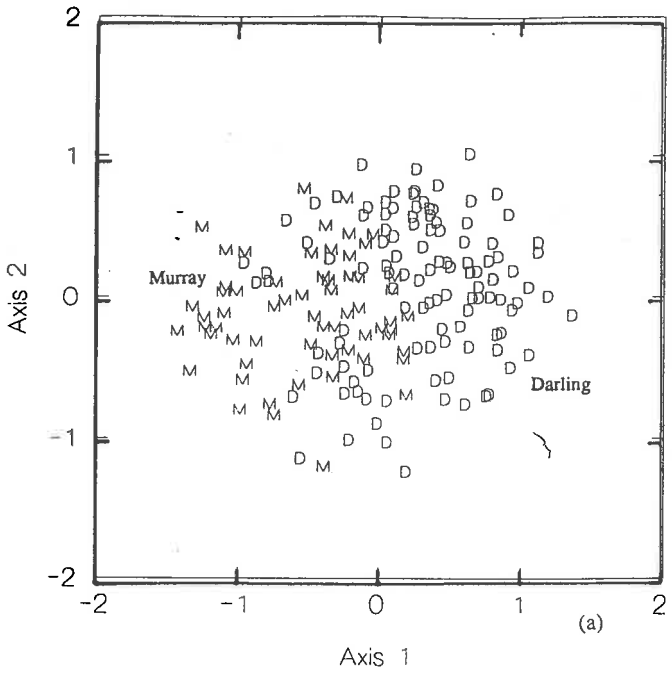
With samples labelled according to mesohabitat (Figure 3.42) differences between lentic and lotic sites, regardless of river, became clear. Samples from billabong and backwater habitats had low scores on both Axes 1 and 2 but separated along Axis 3, with billabong samples having low scores while backwater samples had higher scores. The large group of samples from lotic channel and anabranch sites had higher scores on Axis 1 and Axis 2 but were dispersed along Axis 3. There was some grouping of samples from anabranch sites and a separation of samples from above and below weirs on the Darling (cf. Figure 3.42).

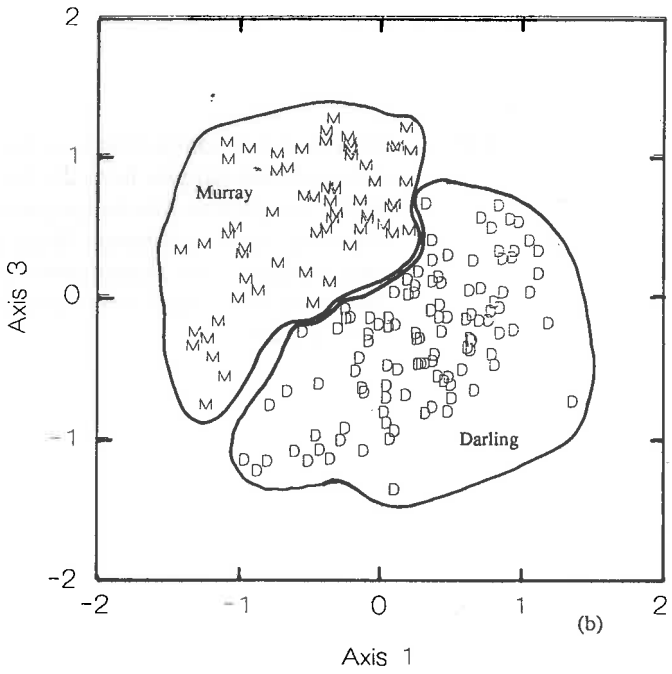
There were also broad patterns in microhabitat assemblage composition, regardless of river (Figure 3.43). The submerged vegetation microhabitats occurred in a group with low scores on Axis 1 and Axis 2 and high scores on Axis 3, while the detritus dominated microhabitats, snag and unvegetated littoral, overlapped the vegetation samples along Axis 1. This indicates some grouping of samples reflecting microhabitat.

Table 3.29 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first three axes of the SSH ordination of faunal data from both the Darling River and the lower River Murray, January 1990.

CPOM	1.00									
FPOM	-0.046	1.00								
Shade	0.251	0.108	1.00							
Salinity	-0.177	0.297	0.095	1.00						
Oxygen	0.032	0.217	-0.117	0.547	1.00					
Temperature	0.048	-0.020	-0.030	-0.348	-0.031	1.00				
Secchi Depth	-0.025	-0.073	0.441	0.330	0.091	-0.444	1.00			
Axis 1	**0.182**	**-0.403**	**0.022**	**-0.692**	**-0.391**	**0.227**	**-0.127**	**1.00**		
Axis 2	**-0.279**	**-0.118**	**-0.388**	**-0.277**	**-0.335**	**0.041**	**-0.190**	**0.080**	**1.00**	
Axis 3	**-0.099**	**-0.074**	**0.337**	**0.363**	**0.116**	**-0.249**	**0.469**	**-0.113**	**-0.170**	**1.00**

Figure 3.41 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3, (c) 2 vs 3 of the SSH plot of the combined samples from the Darling River and the lower River Murray, January 1990. Samples are labelled according to the River from which they were collected, 'M' = lower River Murray and 'D' = Darling River. Overlay highlights the groupings of the rivers.


Murray
Darling
Axis 2
Axis 1
(a)


Murray
Darling
Axis 3
Axis 1
(b)

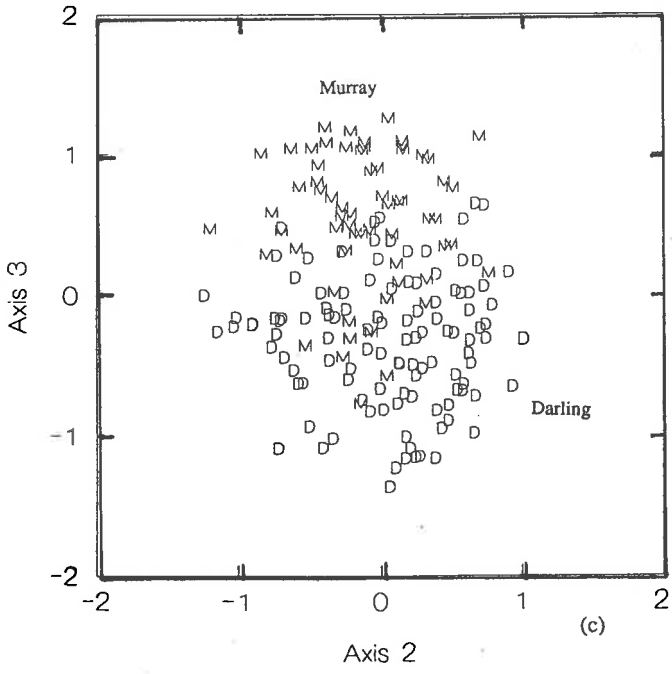
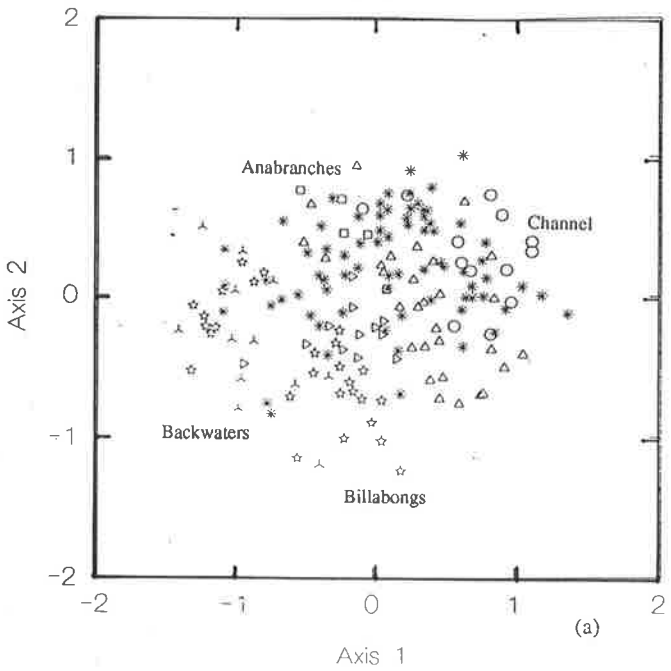
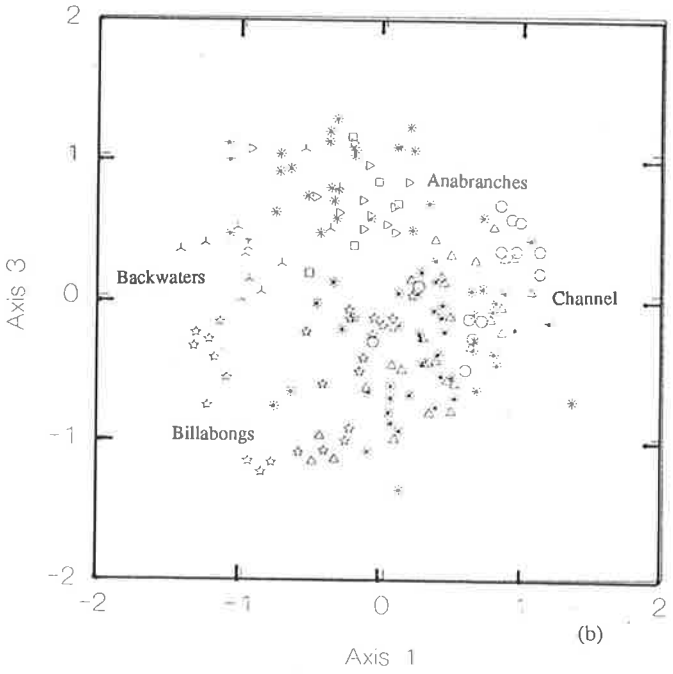

Murray
Darling
Axis 3
Axis 2
(c)

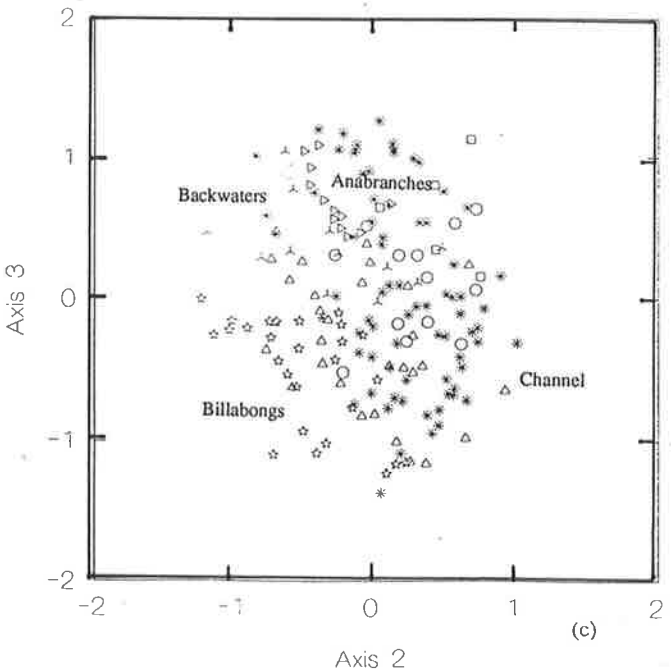
Figure 3.42 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3, (c) 2 vs 3 of the SSH plot of the combined samples from the Darling River and the lower River Murray, January 1990. Samples are labelled according to the mesohabitat from which they were collected, 'stars', billabongs; 'three corners', backwaters; 'squares', fast anabranches; 'side triangles', fast anabranches; 'asterisk', main channel; 'triangle', upper pool Darling River; 'circle', lower pool Darling River. Overlay highlights the groupings of mesohabitats.


Anabranches
Channel
Backwaters
Billabongs
Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

(a)

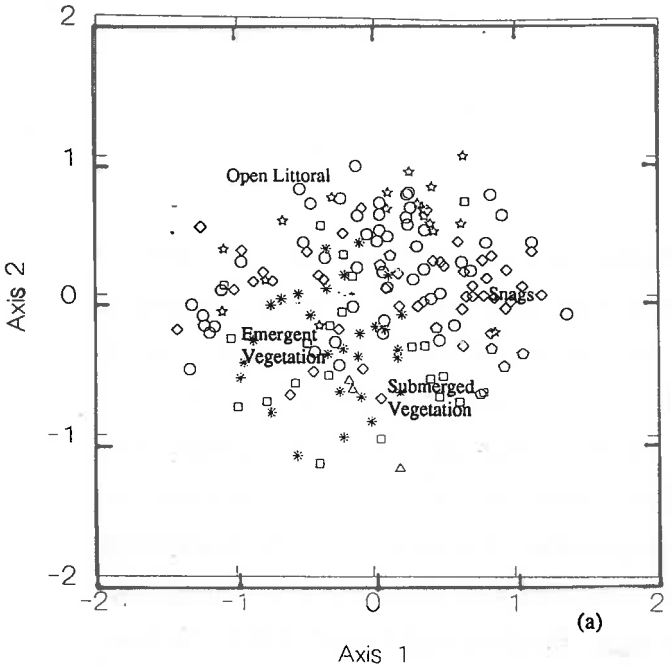

Anabranches
Backwaters
Channel
Billabongs
Axis 3
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2

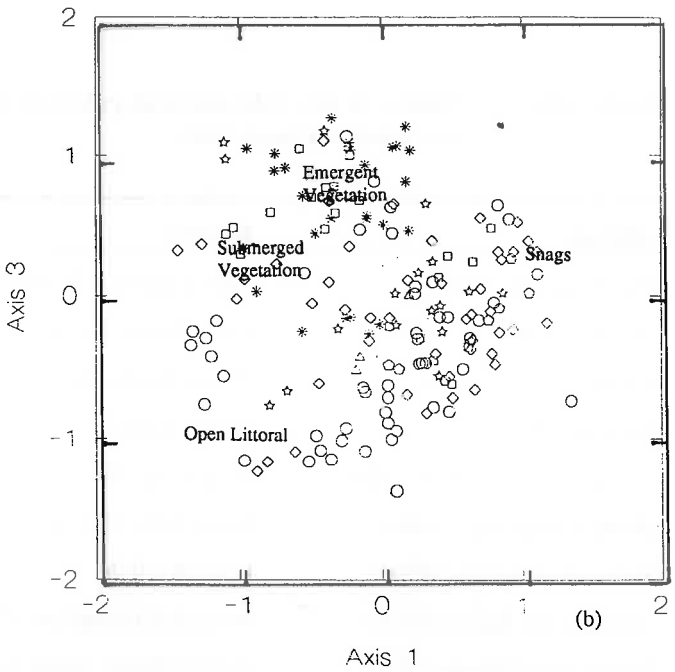
(b)

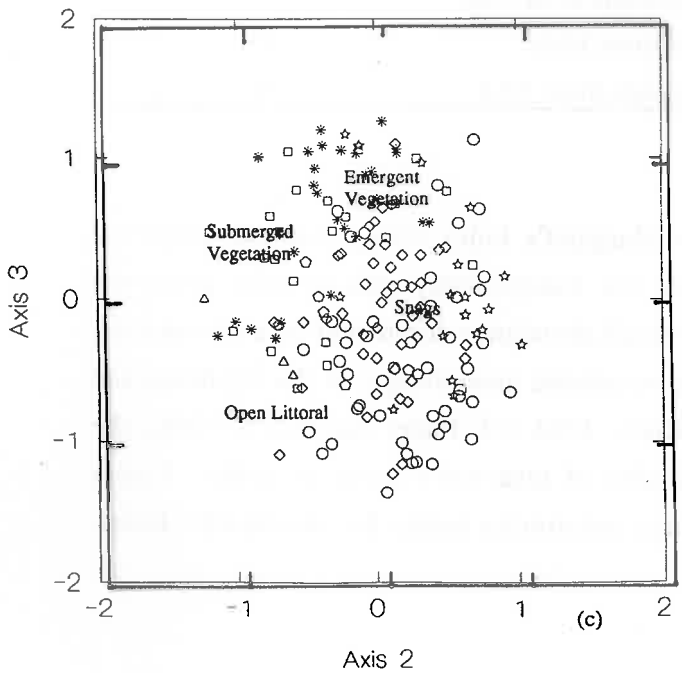

Backwaters
Anabranches
Channel
Billabongs
Axis 3
Axis 2
2
1
0
-1
-2
-2
-1
0
1
2

(c)

Figure 3.43 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3, (c) 2 vs 3 of the SSH plot of the combined samples from the Darling River and the lower River Murray, January 1990. Samples are labelled according to the microhabitat from which they were collected, 'stars', open littoral sand substrata; 'circles', open littoral silt substrata; 'squares', submerged vegetation; 'asterisk', emergent vegetation; 'diamonds', snags; 'octagon', coarse organic matter. Overlay highlights the groupings of microhabitats.


Open Littoral
Snags
Emergent Vegetation
Submerged Vegetation
Axis 2
Axis 1
(a)


Emergent Vegetation
Submerged Vegetation
Snags
Open Littoral
Axis 3
Axis 1
(b)


Emergent Vegetation
Submerged Vegetation
Snags
Open Littoral
Axis 3
Axis 2
(c)

3.5 DISCUSSION

The littoral zone habitats of the lower Darling and lower Murray, in the summer of 1990, supported a total of 80 macroinvertebrate taxa with 50 of these common to habitats in both rivers. This is somewhat depleted when compared to macroinvertebrate faunal assemblages from other large rivers (Table 3.30). It is difficult, however, to make comparisons between rivers as collections are made over different time periods, seasons, and flow conditions using diverse methods; all factors that may influence community composition. The richness of the assemblage collected from the Murray-Darling system compares with that previously reported for approximately the same region (cf. 95 taxa, Boulton and Lloyd, 1991; 78 taxa, Goonan *et al.,* 1992).

Table 3.30 Number of taxa collected from published surveys of macroinvertebrate assemblages in a number of large rivers.

Authors	River(s)	Taxa
Castella *et al.*, (1991)	Rhône and Ain Rivers, France	215
Obrdlik and Fuchs (1991)	Rhine River, Europe	114
Castella *et al.*, (1984)	Rhône River, France	83
Fruget (1991)	Rhône River, France	77
Edwards and Brooker (1984)	Wye River, UK	230
Whitton and Crisp (1984)	River Tees, UK	135
Battegazzore *et al.*, (1992)	River Po, Italy	131
Adamek and Sukop (1992)	Morovian floodplain, Czechoslovakia	206
Palmer and O'Keefe (1991)	Buffalo River, South Africa	103
Elstad (1986)	Upper Mississippi River, USA	144
Munn and Brusven (1991)	Clearwater River, Idaho	~ 35
Rader and Ward (1988)	Upper Colorado River, USA	~ 60

The low diversity values obtained for Margalef's Index (D_{Mg}) and the reciprocal Berger-Parker ($1/d$) reflect assemblages not exceptionally rich in taxa, given the number of individuals collected, with overall abundance dominated by a few species. When compared with the diversity of invertebrate assemblages in the regulated and unregulated sections of the Colorado River, USA (cf. Rader and Ward, 1988), the Murray and Darling have a similar number of taxa but a lower diversity. Lower values are obtained for the Margalef Index and similar values for Menhinick's Index.

These highlight the uneven distribution of individuals amongst the taxa. Unevenness is a feature of invertebrate assemblages in regulated rivers, including the Colorado (Rader and Ward, 1988) and Clearwater (Munn and Brusven, 1991), USA.

The uneven Darling assemblage is the result of over 50% of the total abundance occurring across three taxa, the corixids *Micronecta* spp., the prawn *M. australiense* and the chironomid *Dicrotendipes* sp. (Appendix B) The abundance of *Micronecta* spp. reflects their dominance in the temporary billabongs, where suspended ultrafine organic matter would provide an abundant food source. In the Murray, approximately 70% of the abundance is distributed across four taxa, the shrimps *P. australiensis* and *C. mccullochi*, the corixids *Micronecta* spp. and the chironomid *Chironomus* sp. (Appendix C). Again, *Micronecta* spp. dominate the assemblage of shallow drying billabongs.

Lateral water movements are significant in driving ecological processes in large rivers (cf. Chapter 2); the greatest difference in invertebrate assemblage composition may therefore be expected between mesohabitats of the channel and floodplain (Section 3.1). During this study, water levels in both rivers were low (cf. Figure 3.4 and Figure 3.6) with water confined within mesohabitats. Broad patterns in assemblage composition, however, existed at both mesohabitat and microhabitat scales.

The physical characteristics of mesohabitats (e.g. temperature, flow, depth, and substrata type) have been suggested as influencing their assemblage structure (cf. Pringle *et al.,* 1988). Although billabong habitats were the most saline, owing to receding water levels, the physical conditions of the remaining mesohabitats were somewhat similar (cf. Table 3.5 and Table 3.15), and do not suggest reasons for assemblage differences. Instantaneous values for physical parameters, however, may not be useful indicators of assemblage structure, as assemblages are most likely to respond to combinations of previous and present environmental conditions.

For each river, and the combined data, the three main mesohabitats (billabongs, backwaters and channels) were distinctive, with differences perhaps relating to flow and the extent to which sites were continuous with the main channel (Boulton and Lloyd, 1991). Billabongs of both rivers contained large numbers of mobile insect predators (e.g. notonectids *Anisops* spp., tanypodine chironomids *Procladius* sp. and the caddis *Oecetis* sp.); a situation observed in other temporary environments (cf. Lake *et al.,* 1989; Boulton and Lloyd, 1991). The occurrence of relatively few insect

predators at permanent sites may reflect the presence of small fish occupying this trophic level (Boulton and Lloyd, 1991).

Backwaters of the lower Murray also contained invertebrate predators, mainly zygopteran larvae *I. heterosticta* and *C. billinghursti*; odonates are characteristics of lentic habitats (Ward, 1992). The shrimp *C. mccullochi* was also common in backwaters of the lower Murray, more so than in channel habitats. This differs from its Darling distribution, where it was common in channel habitats, with abundances similar to *P. australiensis*. Channel habitats of both rivers were typified by these shrimps, the prawn *M. australiense* and a diversity of chironomids. At the time of sampling flows across all mesohabitats were minimal, therefore, other factors are likely to contribute to differences in invertebrate assemblage composition.

Microhabitats varied amongst the mesohabitats. In lower Murray billabongs snags and unvegetated littoral areas were abundant, backwaters contained a greater diversity of submerged and emergent vegetation and snags, while microhabitats within the channel included the above as well as unvegetated sand and silt substrata. On the Darling River, weir pool habitats differed from all other habitats; they contained a greater diversity of microhabitats, including submerged vegetation. In the channel habitats snags and unvegetated littoral regions were common, while in billabongs unvegetated littoral with silt substrata predominated. The distribution of microhabitats may have a stronger influence on mesohabitat dissimilarities than differences in flow.

The assemblages of specific microhabitats often reflect varying degrees of structural complexity (cf. Boulton and Lloyd, 1991), with species diversity and abundance greater on complex surfaces (cf. Minshall, 1984; Cyr and Downing, 1988). A major portion of microhabitat biomass in large rivers occurs as snags, which cover a broad range of complexity from smooth surface, cylindrical shapes to highly grooved and dissected forms (O'Connor, 1992). Using both artificial and natural snags O'Connor (1993) found grooved and complex surfaces supported more species than smooth surfaces.

The distribution of snag samples on the ordination plots suggest samples were collected from a diversity of forms, with degree of complexity perhaps contributing to assemblage composition. Unvegetated open littoral regions are perhaps the least complex of all microhabitats, they also contained distinct assemblages. It is impossible from this study, however, to determine how structural complexity is

influencing faunal composition of microhabitats. A high degree of complexity may increase the surface area available for food resources or enhance shelter (cf. Cyr and Downing, 1988).

Assemblage differences, therefore, were detected at all three spatial scales; between rivers (macrohabitats), billabongs, backwaters and channel (mesohabitats) and between vegetation, snags and substrata (microhabitats). The initial separation of macrohabitats and mesohabitats, with finer divisions relating to microhabitat, has been observed in other systems. In the Buffalo River, southern Africa, mesohabitats were a major factor structuring assemblages in the middle and lower reaches (Palmer *et al.,* 1991). Using TWINSPAN the first separation related to macrohabitat or reach, with middle and lower reaches separating from upper reaches. The second division reflected mesohabitat, backwater sites separated from riffle sites; subsequent divisions related to microhabitat, vegetation separated from unvegetated stony regions.

Difference in assemblage composition between microhabitats, perhaps reflecting structural complexity, may contribute to differences at the meso and macrohabitat level. The lower Murray has a broad and complex floodplain, with frequent lateral exchanges of water between the channel and floodplain. This supports a diverse array of lentic mesohabitats containing a wide range of structurally complex microhabitats, including snags, submerged and emergent vegetation. In contrast, the Darling is dominated by channel habitats, and the lateral exchanges between these and the shallow billabongs on the high-level floodplain are less frequent. The common microhabitats are snag and open littoral substrata. Such spatial patterns, however, will only occur while water levels are confined to the various mesohabitats. When levels rise, and floodplain regions become inundated, the assemblage composition of the various mesohabitats would change.

Although temporal patterns were not considered in this study, the importance of temporal changes (flood pulse) for invertebrate assemblages may be estimated through an examination of feeding group representation. If temporal changes in water levels are significant, then we may expect an abundance of collector-gatherers in all habitats, reliant on allochthonous organic matter inputs from the floodplain.

The distribution of FFG's amongst the habitats emphasises the significance of organic matter as a food source in large rivers. Collectors dominated assemblages in all habitats, predators occurred in small numbers, while scrapers were rare occurring

predominantly in billabongs. The RCC (Vannote *et al.,* 1980) suggested that the common benthic collectors in large rivers would be filterers, with FPOM the most abundant food source. Predators would occur in small numbers in all habitats from headwaters to lowland reaches, while scrapers would dominate assemblages in middle reaches and be rare in lowland sections. The rationale for these suggestions relates to differences in organic litter input (cf. Section 3.1).

Using gut contents as the basis for feeding group selection Palmer *et al.* (1993a, 1993b) examined feeding group representation in the lower reaches of the Buffalo River in southern Africa. They found small detrital fragments and silt to be the most common component of the gut contents, with diatoms and leaf fragments forming rare additions to the diets of larger instars. Collectors also dominated the macroinvertebrate communities at Chowilla on the lower Murray, however, most were generalist gatherers rather than filterers (Boulton and Lloyd, 1991). Benke *et al.* (1984) found collector-gatherers and collector-filterers (*Hydropsyche* spp. and *Simulium* spp.) contributed most to invertebrate productivity in the Satilla River (Georgia, USA).

It is difficult to separate the collectors in the Murray and Darling assemblages into narrower groups, such as collector-filterer, collector-gatherer or shredder (cf. Cummins and Klug, 1979), as little is known of specific diets. Few of the taxa, however, would be regarded as predominantly collector-filterers (e.g. the chironomid *Kiefferulus martini*), most are generalist collector-gatherers. In both rivers the abundant taxa (e.g. *P. australiensis*, *C. mccullochi*, *M australiense*, *Micronecta* spp., *Dicrotendipes* sp., *Chironomus* spp.) were collector-gatherers, suggesting the utilisation of a broad range of particulate organic matter.

This pattern of feeding group representation does not reflect the organic matter processes suggested in the RCC. In large rivers lateral interactions between floodplain and main-channel habitats are stronger than upstream-downstream linkages (cf. Chapter 2). Habitats in the littoral zone of large rivers receive coarse organic matter directly from the riparian zone through leaf and branch fall. A large proportion of organic matter input, however, will be derived from the surrounding floodplain and include CPOM as well as FPOM and DOC (Cuffney, 1988; Grubaugh and Anderson, 1989; Lieberman and Burke, 1993). Thus, in the Murray and Darling, an abundance of generalist collectors (e.g. gatherers) would dominate assemblages in large floodplain rivers.

River geomorphology obviously influences invertebrate assemblage composition through the diversity of mesohabitats and microhabitats it supports. Likewise, flow regulation may also modify assemblage composition by favouring the development of specific microhabitats and isolating mesohabitats. Unlike the Darling River, the lower River Murray is a highly regulated system, however, due to differing floodplain morphology it was impossible to fully replicate the mesohabitats within the two systems. Thus, this study does not allow an examination of the effects of flow regulation on spatial patterns. Regulation may influence the diversity of submerged and emergent vegetation within the littoral zone (cf. Walker *et al.*, 1994) and this would be reflected in the spatial patterns of invertebrate assemblages. A more detailed examination of the impact of flow regulation on spatial patterns in the main-channel of the lower Murray is provided in Chapter 4.

Chapter 4

Longitudinal Patterns of Macroinvertebrate Assemblages between Low-Level Weirs.

4.1 INTRODUCTION

Many theoretical and empirical studies of the ecology of small streams support the notion of a strong relationship between environmental variation (or environmental gradients) and macroinvertebrate community composition (cf. Faith and Norris, 1989). Longitudinal, or downstream, changes in abiotic parameters such as temperature, current velocity, organic matter input and substrata type (Naiman *et al.*, 1987; Statzner *et al.*, 1988; Haag and Thorp, 1991) have been used to explain downstream shifts in the structure of benthic communities in lotic systems (cf. RCC: Vannote *et al.*, 1980). In regulated streams, longitudinal patterns can be disrupted by impoundments creating discontinuities in abiotic parameters whare are reflected in biotic changes (cf. Stanford *et al.*, 1988). These ideas were explored in the Serial Discontinuity Concept (SDC), suggested by Ward and Stanford (1983), where regulated systems essentially become alternating sections of lentic and lotic environments (Chapter 2).

Regulation may introduce gradients in food resources for macroinvertebrates. Below large dams, such as those on the Blue, Gunnison and upper Colorado rivers (Colorado), shifts in the composition of benthic periphyton assemblages and substrate detritus have been recorded (cf. Hauer *et al.*, 1989; Rader and Ward, 1989; Voelz and Ward, 1990). Immediately below the dam, periphyton comprises filamentous chlorophytes and diatoms, with the detritus dominated by decaying algal material and plankton from the upstream reservoir. Further downstream, benthic periphyton is dominated by diatoms, while the detritus comprises a diverse range of organic matter. Below the low-level weirs on the lower Murray, the trophic gradient is reversed. Thin periphytic biofilms, dominated by diatoms, are common in the lower pool sections immediately downstream of weirs, whereas filamentous algae (*Spirogyra* sp.) are abundant in the shallow impounded water immediately upstream (cf. Chapter 6).

The River Murray is a highly regulated system where the combined influence of upstream storages and low-level weirs has decreased lateral movement of the littoral zone and imposed a system of alternating lentic and lotic environments in a longitudinal gradient on the main channel (Chapter 1). This is particularly the case in the lower Murray, which is regulated by 10 low-level weirs (Walker and Thoms, 1993). The short distance between the weirs (22-98 km), combined with extreme low gradients, means the river above Blanchetown consists entirely of pool environments.

Sparks *et al.* (1990) divided the pools of the regulated upper Mississippi into two sections: an "upstream zone", that retains characteristics of the natural river, and a "downstream zone", where floodplain features are permanently inundated. In the lower Murray, each pool can be divided into lower, middle and upper sections. The *lower pool* (Figure 4.1) is the reach immediately downstream of a weir. Water levels in lower pools are variable (Figure 4.2a) owing to managed levels in the immediate upstream pool (cf. Section 1.2.3; Walker *et al.,* 1992). Lower pools are typically erosion zones, where the channel cross-section has increased since weir construction (Thoms and Walker, 1993). Increased erosion has perhaps enhanced the diversity of microhabitats; eroding benches are often unvegetated and there are large sand bars. Areas of emergent *Phragmites australis* and *Cyperus gymnocaulos* occur with some plants, including *Myriophyllum verrucosum,* growing preferentially in lower pool regions (Walker *et al.,* 1994).

Water level changes in the *middle pool* section (Figure 4.1) become more stable with distance downstream (Figure 4.2b). The edge of the channel in these sections is lined with a nearly pure stand of common reeds (*P. australis).* There are occasional snags from fallen trees on sharp bends and stands of the spiny sedge *C. gymnocaulos* on depositing banks.

The *upper pool* is the section immediately behind the weir (Figure 4.1). Water levels are kept stable (Figure 4.2c) by manipulation of stoplogs and Boulé panels, within the weir structure (cf. Section 1.2.3). The impounded water has drowned large stands of river redgum (*Eucalyptus camaldulensis*), so submerged woody debris is a common microhabitat. The upper pool sections of Pools 2 and 3 are active deposition zones, as channel cross-sections have decreased since weir construction (Thoms and Walker, 1993). A number of macrophytes show an apparent preference for upper pools, including the ribbonweed *Vallisneria spiralis* and cumbungi *Typha* spp. (Walker *et al.,* 1994).

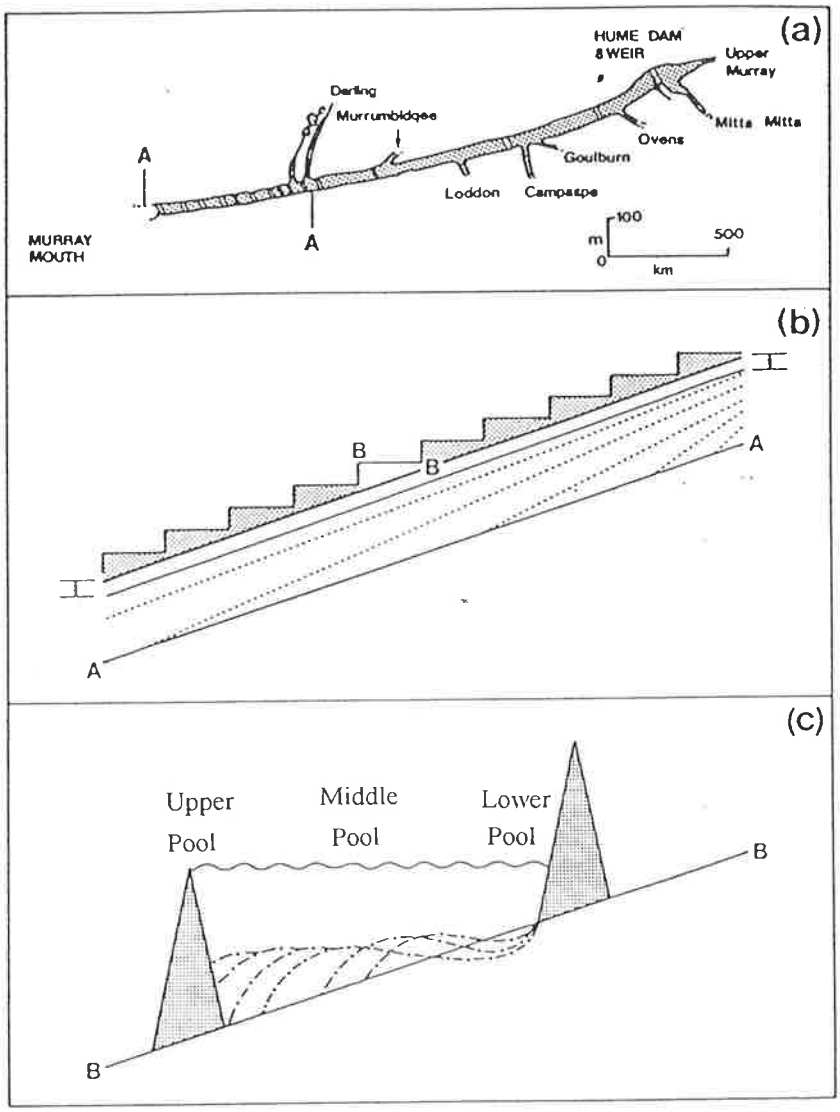


Figure 4.1 Schematic diagram of the regulated lower River Murray. (a) The long profile of the River Murray, (b) the channel profile of the lowland section, (c) relative position of the water level between two weirs on the lower river, showing upper, lower and middle pool regions. After Thoms and Walker (1992).

Aquatic and semi-aquatic plants are conspicuous in all sections of the littoral zone of the main channel of the lower Murray and at the spring-summer water level the distribution of these plants tends towards three vertical 'zones' (cf. Walker *et al.*, 1992; Figure 4.3):

- *Upper littoral*: Equivalent to the uppermost 0.5 m or the euphotic zone. In the lower pool this zone may be subject to daily fluctuations in water level. The vegetation includes semi-aquatic (e.g. sedges) and emergent species (e.g. reeds).
- *Middle littoral*: Extends from around 0.5 to 2 m. In the lower pool this zone is only exposed during extreme fluctuations. Vegetation includes submerged aquatics.
- *Lower littoral*: Extends from 2 to 4 m and is usually free of macrophytes due to light limitation.

Snags occur in all zones.

This chapter describes longitudinal changes in macroinvertebrate assemblage structure and species dominance in the common littoral zone microhabitats of Pools 2 and 3, main channel, lower Murray. The FFG composition of assemblages in different pool sections is used to explore trophic discontinuities induced by the weirs.

We may expect distinct assemblages in lower, middle and upper pools, given the differences in water level fluctuations and microhabitat composition. The FFG composition of assemblages should reflect a shift in food resources from collector-filterers in lower pool sections, where FPOM and DOC from the impounded water upstream would be abundant, to generalist collector-gatherers in middle pools. Upper pools should show an increase in the abundance of scrapers, in response to an increase in biomass of benthic algae.

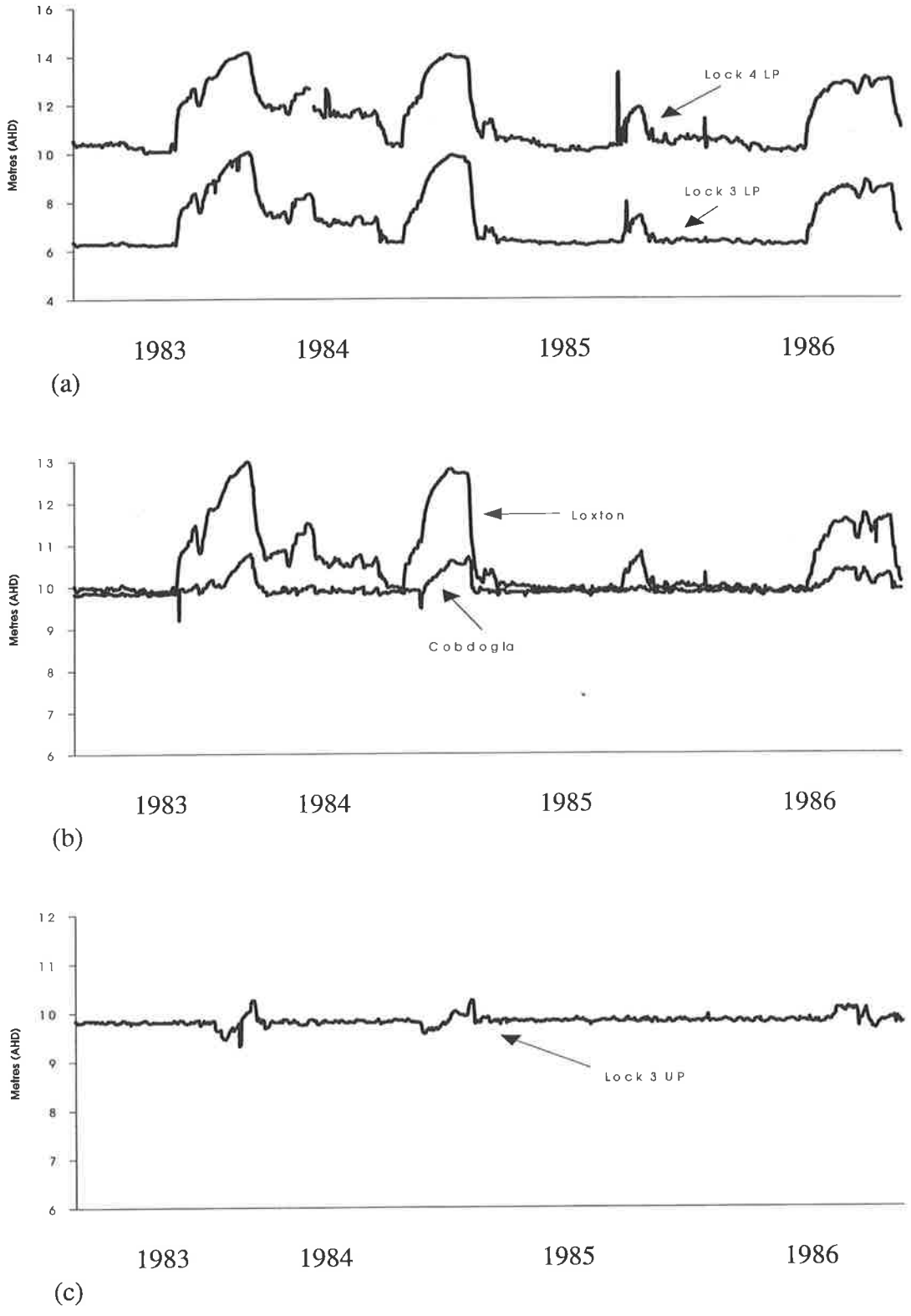


Figure 4.2 A progression along the lower Murray highlighting the differences in water level variations between pool types. (a) Lower Pool regions of Pool 3 and Pool 2, (b) Middle Pool regions at Loxton and Cobdogla, (c) Upper Pool region immediately above Lock 3.

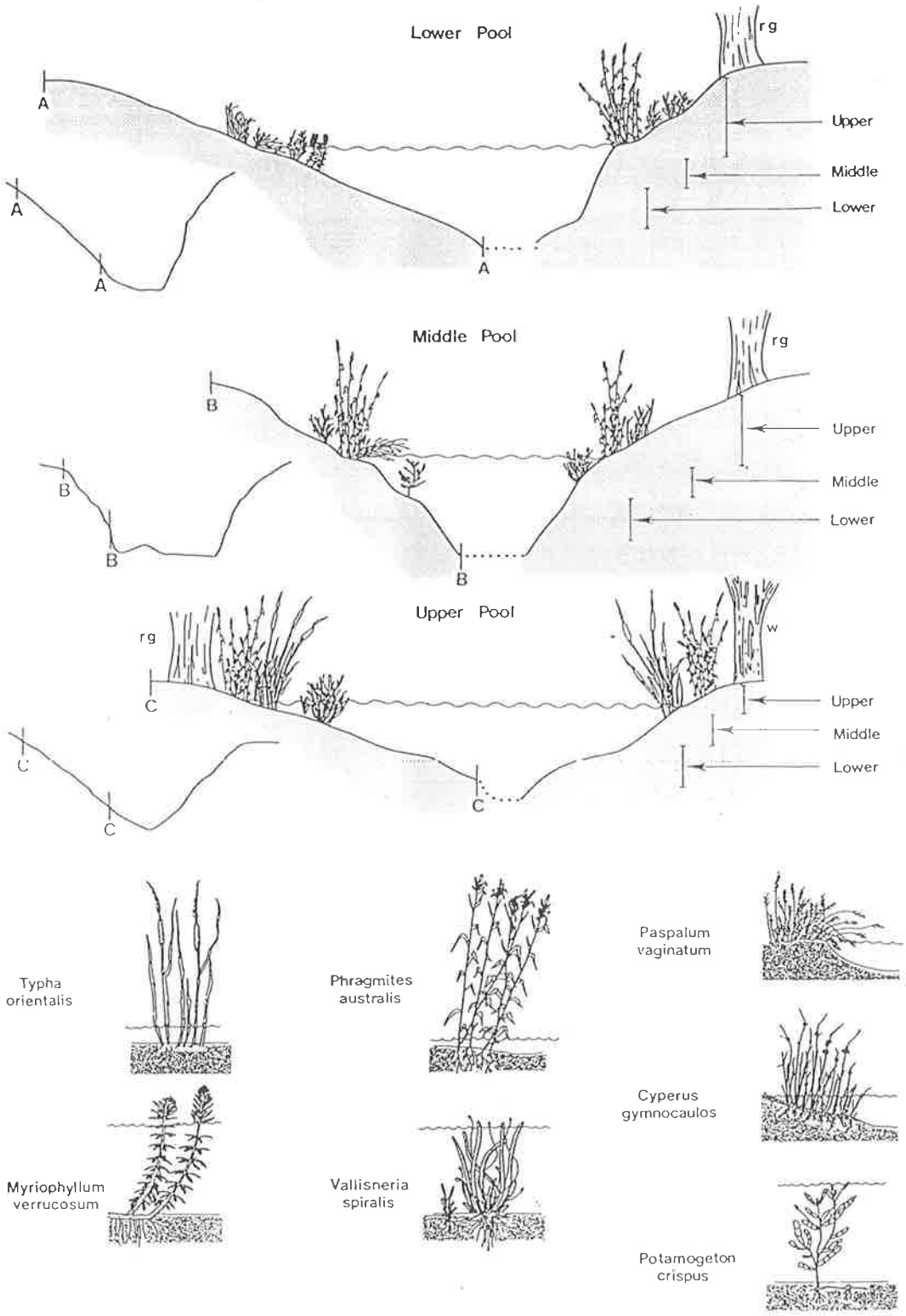


Figure 4.3 Typical zonations of aquatic and semi-aquatic plants in the lower, middle and upper pools of the River Murray between Lock 4 and Lock 2. At each site a typical profile is depicted (left), and zonations are shown for erosional and depositional banks. From Walker *et al.*, (1992).

4.2 STUDY AREA

The study area for this chapter included sites along the 154 river-km reach of the main channel of the lower River Murray occupied by Pools 2 and 3, governed by Locks 2 (Waikerie), 3 (Overland Corner) and 4 (Bookpurnong) (Figure 4.4). The weirs and pools are of similar dimensions and were constructed at about the same time (Table 4.1). The processes associated with channel change in response to flow regulation have been well documented for these pools (cf. Thoms and Walker, 1989; 1992; 1993), as has the longitudinal distribution of the aquatic and semi-aquatic plants in the littoral zone (cf. Walker *et al.*, 1992, 1994). Overland Corner (below Lock 3) was also the main site for an investigation into the ecology of snags in the lower Murray (Lloyd *et al.*, 1990).

The river between Lock 4 and Lock 2 (Pools 2 and 3) straddles two distinct landform sections of the lower Murray. Pool 3 lies in the *Valley* section, while Pool 2 lies within the *Gorge* section which begins at Overland Corner (Lock 3). The Valley section of the lower Murray (cf. Pressey *et al.*, 1986) extends 906 river-km from the Darling confluence to Overland Corner (Figure 4.4). The floodplain in this section is 5-10 km wide and the river meanders freely with a wavelength of about 4 km (cf. Walker and Thoms, 1993). The Gorge section begins at Overland Corner where the Murray enters a 30 m limestone gorge and the floodplain is constrained to 2-3 km. The morphological diversity of wetlands in the Gorge section is much less than in the Valley section (Figure 4.5): the backwater areas along Pool 2 account for 36% of the total water surface area associated with the river and its floodplain (1713 ha), whereas those along Pool 3 account for 62% of the total (3795 ha) (Walker and Thoms, 1993; Walker *et al.*, 1994; see also Chapter 3).

Samples were collected from 12 sites (Table 4.2); sites were classified according to pool section: lower, middle and upper pools (cf. Section 4.1). These are essentially 'sub-meso' habitats (cf. Chapter 2) although in reality clear distinctions between the sections do not exist as there is a gradient extending from immediately below one weir to above the subsequent weir, in environmental factors and water level changes (cf. Section 1.2.3).

Table 4.1 Physical data for Weirs and Pools 2, 3 and 4 on the lower River Murray. Weir lengths include the lock chambers; upper pool levels are relative to the Australian height datum. From Thoms and Walker (1993).

	Pool 2	Pool 3	Pool 4
Year Completed	1928	1925	1929
Distance from mouth (river-km)	362	431	516
Storage capacity (Mm^3)	40	43	31
Weir length (m)	138.4	123.1	124.7
No. of sluice bays	15	13	13
No. of pass bays	5	5	5
Weir height (m)	6.09	6.14	6.86
Upper pool level (m)	6.10	9.80	13.2

Table 4.2 Number, abbreviation and description of sites sampled in Pool 3 and Pool 2 on the lower River Murray, February, 1990.

No.	Abbreviation	Site Name	Lock	Pool Section
1	KILP	Katarapko Island	4	Lower
2	PVLP	Palm Villa	4	Lower
3	KPMC	Kapunda Island	4	Middle
4	PRMC	Pyap Reach	4	Middle
5	GMMC	Gerard Mission	4	Middle
6	NIMC	Nynes Island	4	Middle
7	TIUP	Thurk Island	4	Upper
8	LLUP	Loch Luna	4	Upper
9	BILP	Ball Island	3	Lower
10	OCLP	Overland Corner	3	Lower
11	DPMC	Devlin Pound	3	Middle
12	YGMC	Yarra Glen	3	Middle

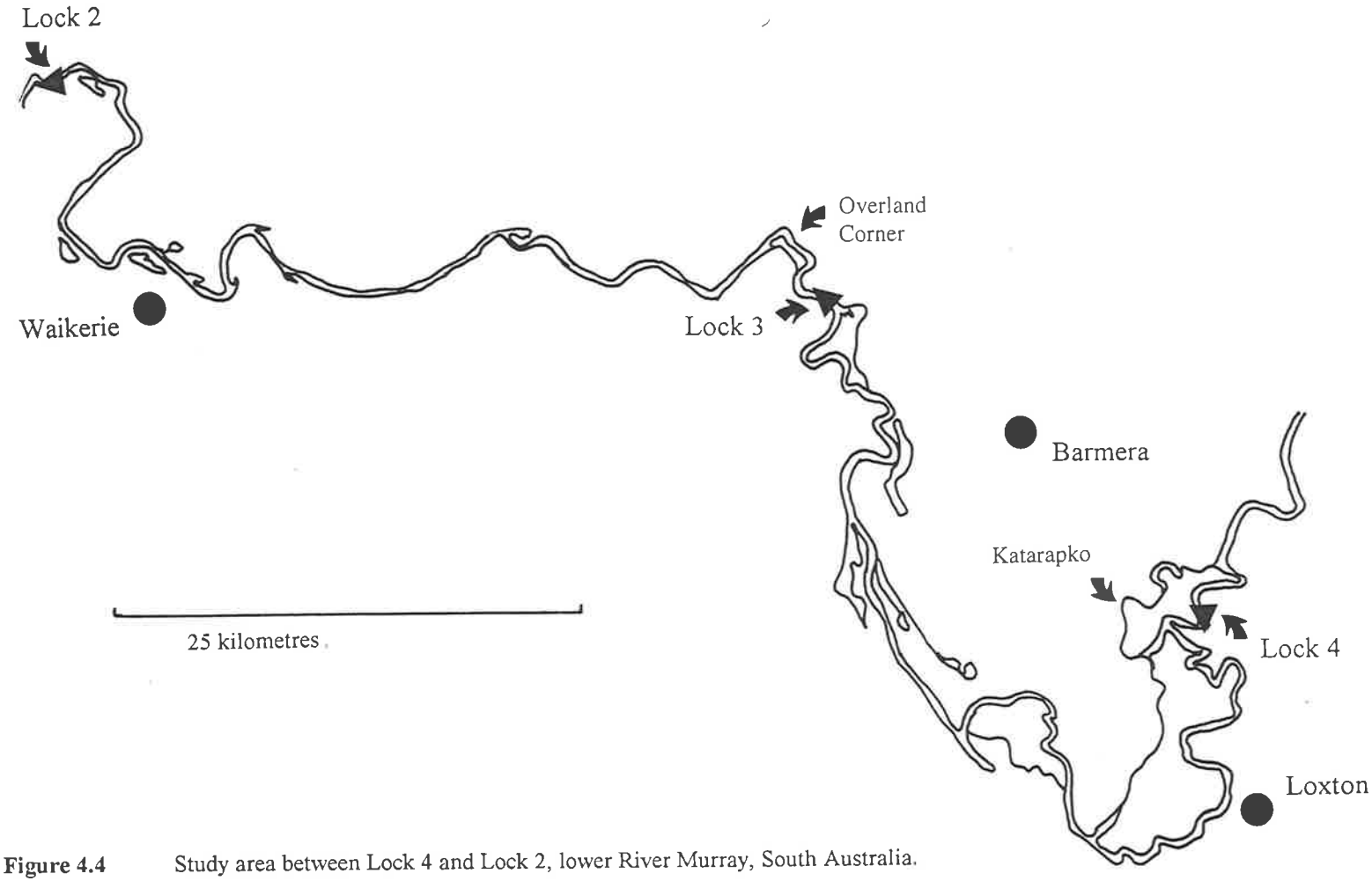


Figure 4.4 Study area between Lock 4 and Lock 2, lower River Murray, South Australia.

The following microhabitats were recognised for the main channel of the lower Murray:

- *Phragmites australis* (common reed), occurs in near monospecific stands in the uppermost 0.5 m along the edge of upper and middle pools and in clumps in lower pools,
- *Typha* spp. (cumbungi). Both *T. orientalis* and *T. domingensis* occur along the lower Murray but in this survey were not distinguished. *Typha* spp. also occur in the uppermost 0.5 m of the littoral zone and tends to prefer upper pool regions (cf. Walker *et al.,* 1994). They may also be found in small clumps in middle and lower pools,
- *Juncus* sp. (rush) occurs in discrete clumps in the uppermost 0.5 m. It mainly inhabits middle pools, but is also occasionally found in upper and lower pools,
- *Paspalum vaginatum* (saltwater couch) is an ubiquitous semi-aquatic grass occurring along the main channel in all pool types,
- *Cyperus gymnocaulos* (spiny sedge) a small emergent semi-aquatic species growing in the uppermost 0.5 m on depositional benches in middle and lower pools,
- *Vallisneria spiralis* (ribbonweed), a submerged aquatiç occurring in the 'middle littoral' between 0.5 m and 2 m. *V. spiralis* forms large beds in the upper pool region where extensive areas of shallow stable water occur. Small beds also occur in middle and lower pools in stable protected areas behind snags or clumps of larger emergent species,
- Snags (submerged woody debris) occur at all depths along the length of the main channel,
- Unvegetated littoral , silt substrata,
- Unvegetated littoral, sand substrata.

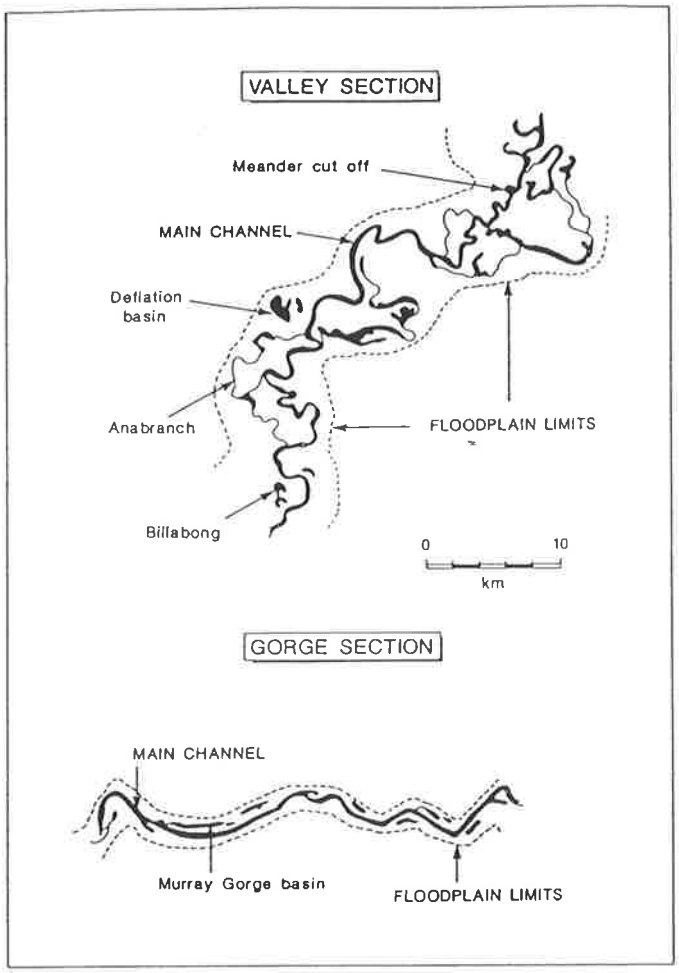


Figure 4.5 Wetland forms associated with the Valley and Gorge sections of the lower River Murray. From Walker and Thoms (1993).

4.3 METHODS

4.3.1 Field Methods

Replicate samples were collected from 12 sites on the main channel of the lower River Murray between Lock 4 and Lock 2 (Figure 4.6). At each site samples were collected from the three most abundant microhabitats (as described above). At nearly all sites the two most abundant microhabitats were "emergent vegetation" and "snags", the third microhabitat varied. Benthic, nektonic and epiphytic invertebrates were collected by sweeping a pond net (500 μm mesh) for 20 seconds while moving over the microhabitat. Samples were preserved in 70 percent ethanol and returned to the laboratory. At each site values for water temperature, dissolved oxygen, conductivity, turbidity and water depth were measured. Substratum type was recorded as clay or silt. A ranked value from 0 (absent) to 5 (very abundant) for the amount of fine organic matter (FPOM) and coarse organic matter (CPOM) in the sweep net, as well as the degree of shading from riparian vegetation, was recorded for every sample from each microhabitat (Chapter 3).

Laboratory processing of samples and assigning of taxa to functional feeding groups (FFG's) were as described in Section 3.3.2.

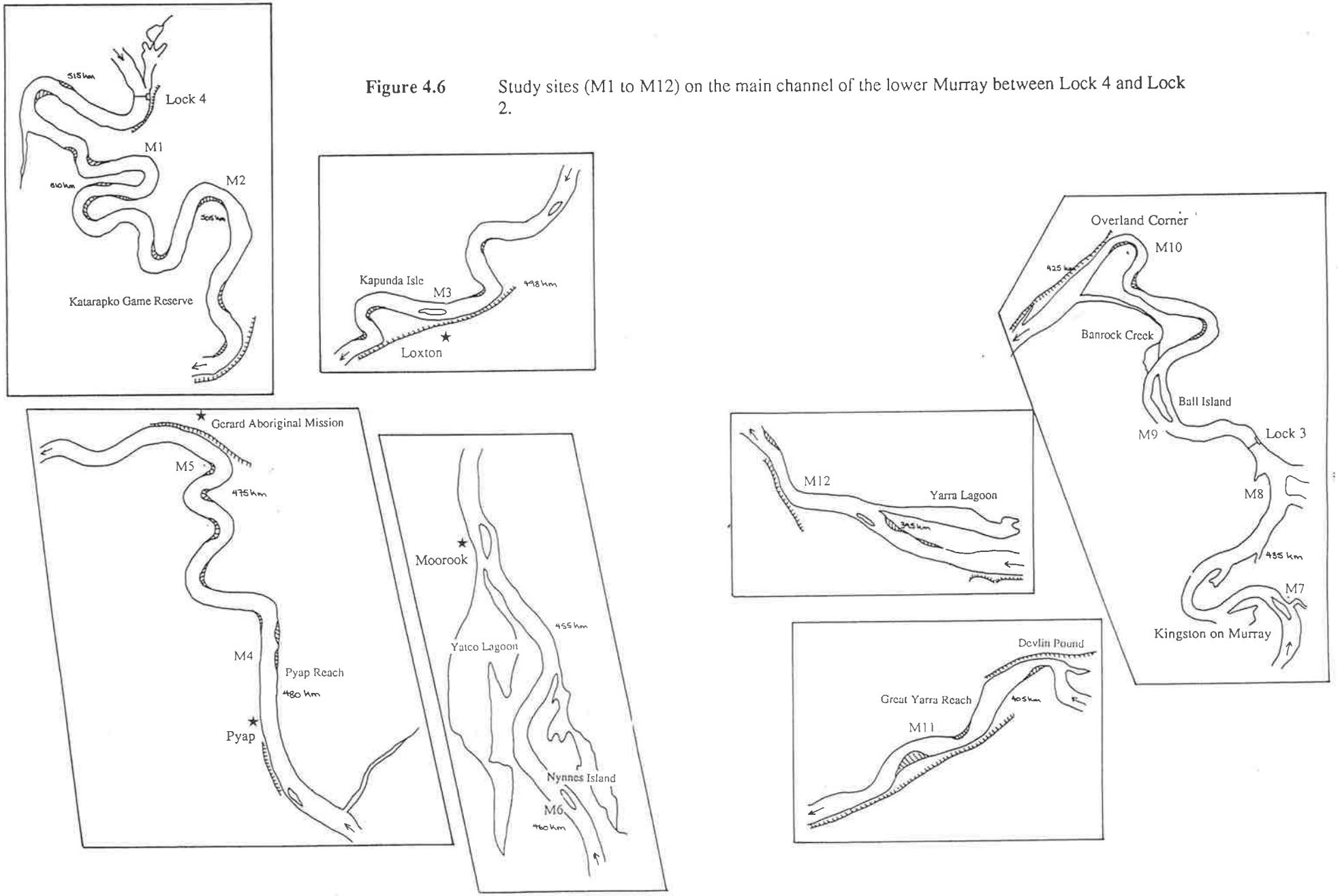


Figure 4.6 Study sites (M1 to M12) on the main channel of the lower Murray between Lock 4 and Lock 2.

4.3.2 Data Analysis

Kruskal-Wallis non-parametric one-way ANOVAs (SYSTAT v5.0; Wilkinson, 1990) were used to explore differences in richness, total abundance and the frequencies of three FFG's (collector, predator and scraper) between sites, pool sections and microhabitats. The significance level was Bonferroni adjusted (Neter *et al.,* 1985) to p=0.01 and differences located using Tukey's HSD procedure (see Section 3.2.3).

TWINSPAN (Hill *et al.,* 1975; Hill, 1979), on $\log_{10}(x+1)$ transformed data, was used to identify assemblages characteristic of pool sections and microhabitats. Based on the range of abundances in the dataset, pseudospecies cut levels equivalent to 0, 2, 5, 10, 20, 50, 100, 200 and 750 were used, with default values for all other settings. The ordered two-way tables produced by TWINSPAN were condensed using Boesch's Fidelity Index (F_{ij}) (see Section 3.3.2) to demonstrate sample group preference or avoidance by a species group. Ordination of the macroinvertebrate data was conducted using SSH in the PATN software package (see Section 3.2.3).

Longitudinal gradients in the distribution of the six dominant taxa, the shrimps *P. australiensis*, *C. mccullochi,* the prawn *M. australiense*, and the chironomids *Cladotanytarsus* sp., *Tanytarsus* sp. and *Cricotopus* spp., were examined by plotting their mean abundance at each site progressively downstream. Tukey's Honestly Significant Difference (HSD) tests were used to suggest differences in mean abundance of each of the six species between sites.

The Margalef Index, Menhinick's Index and the Berger-Parker Index were used to describe the richness and evenness of the main channel assemblage (Section 3.3).

4.4 RESULTS

Environmental Conditions

Environmental conditions in the study reach (Table 4.3) were typical for the main channel of the lower Murray in late summer (cf. Mackay *et al.,* 1988). Salinities slowly increased downstream between Lock 4 and Lock 2. The Murray intercepts saline groundwater throughout its length in South Australia, with a significant proportion of the total inflow occurring near Woolpunda in Pool 3 (Close, 1990).

Most sites were highly oxygenated with Secchi depths of around 20 cm and temperatures of 24-25°C.

Table 4.3 Environmental conditions in the littoral zone of each site in Pool 3 and Pool 2, lower Murray, February 1990.

	Site	Salinity (mg/L)	Oxygen (% saturation)	Secchi depth (cm)	Temperature (^{0}C)
1	KILP	346	95	23	24
2	PVLP	356	96	23	24
3	KPMC	378	98	25	24
4	PRMC	370	100	22	25
5	GMMC	362	100	25	25
6	NIMC	366	98	23	25
7	TIUP	375	97	22	24
8	LLUP	363	94	19	25
9	BILP	364	100	19	25
10	OCLP	368	99	17	24
11	DPMC	399	98	19	24
12	YGMC	388	97	23	25

Community Composition

A total of 29,000 individuals from 60 taxa (Appendix D) was collected in 108 samples. Insects comprised 80 percent of the taxa but only 14 percent of the individuals (Figure 4.7). Of the Insecta the Diptera comprised the most taxa (27) with the Hemiptera (8) and Coleoptera (6) less dominant. Within the Diptera the most abundant family was the Chironomidae (90%) compared with Ephemeroptera (4.5%) and Hemiptera (3.5%) (Figure 4.8). The Coleoptera, Odonata and Trichoptera were relatively rare, and together contributed less than two percent of the total abundance.

The Crustacea were the most abundant group, comprising only 10 percent of taxa but 85 percent of individuals (cf. Figure 4.7). The aytid shrimps *Paratya australiensis* (81%) and *Caridina mccullochi* (4.6%) were dominant, with the large paleomonid prawn *Macrobrachium australiense* comprising 13% of the total abundance. Of the entire assemblage the shrimps and *M. australiense* were still the most abundant taxa,

along with the chironomids *Cladotanytarsus* sp. and *Cricotopus* spp. Six taxa occurred only once.

Table 4.4 gives the mean (SE) number of taxa and individuals for each site. The median number of taxa did not differ between sites (Kruskal-Wallis $H = 25.11$, $p<0.05$) whereas the number of individuals did vary significantly between sites ($H = 40.51$, $p<0.001$). When sites were grouped according to pool section differences existed in the number of taxa ($H = 11.64$, $p<0.01$) but not in the number of individuals ($H = 1.64$, $p>0.05$). Middle and upper pool samples had a greater number of taxa than did lower pool samples. Significant differences also existed between pool sections for predator and scraper FFG's but not for collectors (Table 4.5; Figure 4.9). More predatory and scraper taxa occurred in upper pools than in either middle or lower pools (Table 4.5). No scrapers were found in samples collected from lower pools.

The number of taxa and number of individuals also differed between microhabitats ($H = 26.23$, 46.15, respectively, $p<0.001$). The least number of individuals was collected on snags and unvegetated sand substrata (Table 4.7; Figure 4.10). Significant differences also existed between microhabitats for all FFG's (cf. Table 4.5). There were no differences in either the number of taxa or the number of individuals for the different emergent vegetation microhabitats (*P. australis*, *Typha* spp., *Juncus* sp., *C. gymnocaulos, Paspalum* sp.). For multivariate analyses these microhabitats were combined as 'emergent vegetation'.

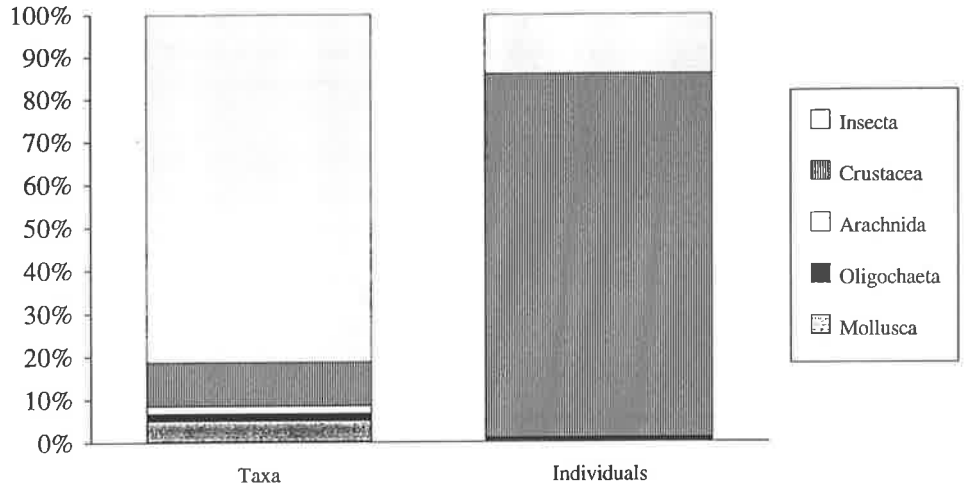


Figure 4.7 Percent representation of the major invertebrate groups in the samples collected between Lock 4 and Lock 2, lower River Murray, February 1990.

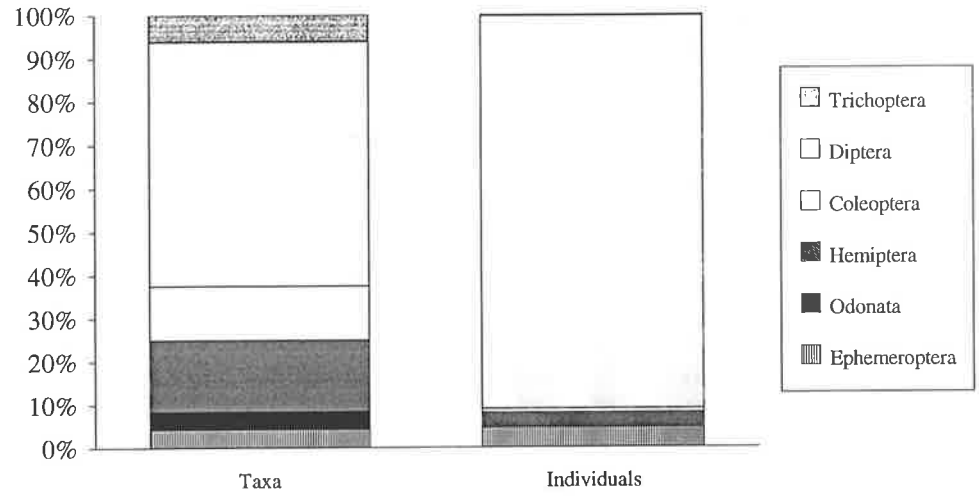


Figure 4.8 Percent representation of the major Insect orders in the samples collected between Lock 4 and Lock 2, lower River Murray, February 1990.

Table 4.4 The mean number (SE) of (a) taxa and (b) individuals in total and for three functional feeding groups at each site in Pool 3 and Pool 2, lower River Murray, in February 1990. (n) = number of samples

(a)

Site	(n)	Total	Collectors	Predators	Scrapers
KILP 1	9	9.4 *(1.1)*	8.7 *(0.9)*	0.8 *(0.3)*	0
PVLP 2	9	7.4 *(1.1)*	7.2 *(0.9)*	0.2 *(0.1)*	0
KPMC 3	9	9.9 *(1.1)*	9.0 *(0.7)*	0.7 *(0.3)*	0.1 *(0.1)*
PRMC 4	9	9.3 *(0.5)*	8.5 *(0.5)*	0.7 *(0.3)*	0.1 *(0.1)*
GMMC 5	9	9.8 *(0.7)*	9.0 *(0.7)*	0.7 *(0.2)*	0.1 *(0.1)*
NIMC 6	9	11.2 *(0.7)*	10.4 *(0.7)*	0.4 *(0.2)*	0.1 *(0.1)*
TIUP 7	9	8.7 *(0.9)*	7.1 *(0.6)*	1.0 *(0.2)*	0.5 *(0.2)*
LLUP 8	9	12.8 *(1.1)*	9.9 *(0.8)*	2.7 *(0.7)*	0.2 *(0.1)*
BILP 9	9	7.5 *(1.0)*	7.0 *(0.9)*	0.6 *(0.2)*	0
OCLP 10	9	7.3 *(0.9)*	6.8 *(0.7)*	0.6 *(0.2)*	0
DPMC 11	9	10.0 *(0.7)*	8.9 *(0.7)*	1.0 *(0.2)*	0.1 *(0.1)*
YGMC 12	9	10.0 *(0.9)*	8.8 *(0.8)*	1.1 *(0.2)*	0.1 *(0.1)*

(b)

Site	(n)	Total	Collectors	Predators	Scrapers
KILP 1	9	224.3 *(35.9)*	223.3 *(35.8)*	1.0 *(0.5)*	0
PVLP 2	9	113.7 *(22.5)*	113.4 *(22.5)*	0.2 *(0.1)*	0
KPMC 3	9	92.1 *(24.2)*	90.0 *(23.8)*	0.8 *(0.3)*	0.3 *(0.3)*
PRMC 4	9	258.2 *(50.2)*	257.2 *(50.3)*	0.9 *(0.4)*	0.1 *(0.1)*
GMMC 5	9	272.4 *(50.6)*	271.5 *(50.7)*	0.8 *(0.3)*	0.1 *(0.1)*
NIMC 6	9	249.7 *(57.5)*	248.8 *(57.3)*	0.4 *(0.2)*	0.3 *(0.2)*
TIUP 7	9	248.3 *(47.2)*	246.0 *(47.4)*	1.7 *(0.5)*	0.7 *(0.3)*
LLUP 8	9	275.3 *(63.1)*	268.0 *(63.7)*	7.1 *(2.6)*	0.2 *(0.1)*
BILP 9	9	291.3 *(50.2)*	290.4 *(50.5)*	0.9 *(0.4)*	0
OCLP 10	9	320.3 *(70.5)*	319.5 *(70.1)*	0.8 *(0.4)*	0
DPMC 11	9	324.9 *(37.1)*	323.5 *(36.9)*	1.2 *(0.3)*	0.1 *(0.1)*
YGMC 12	9	551.7 *(82.4)*	550.0 *(82.5)*	1.3 *(0.2)*	0.3 *(0.3)*

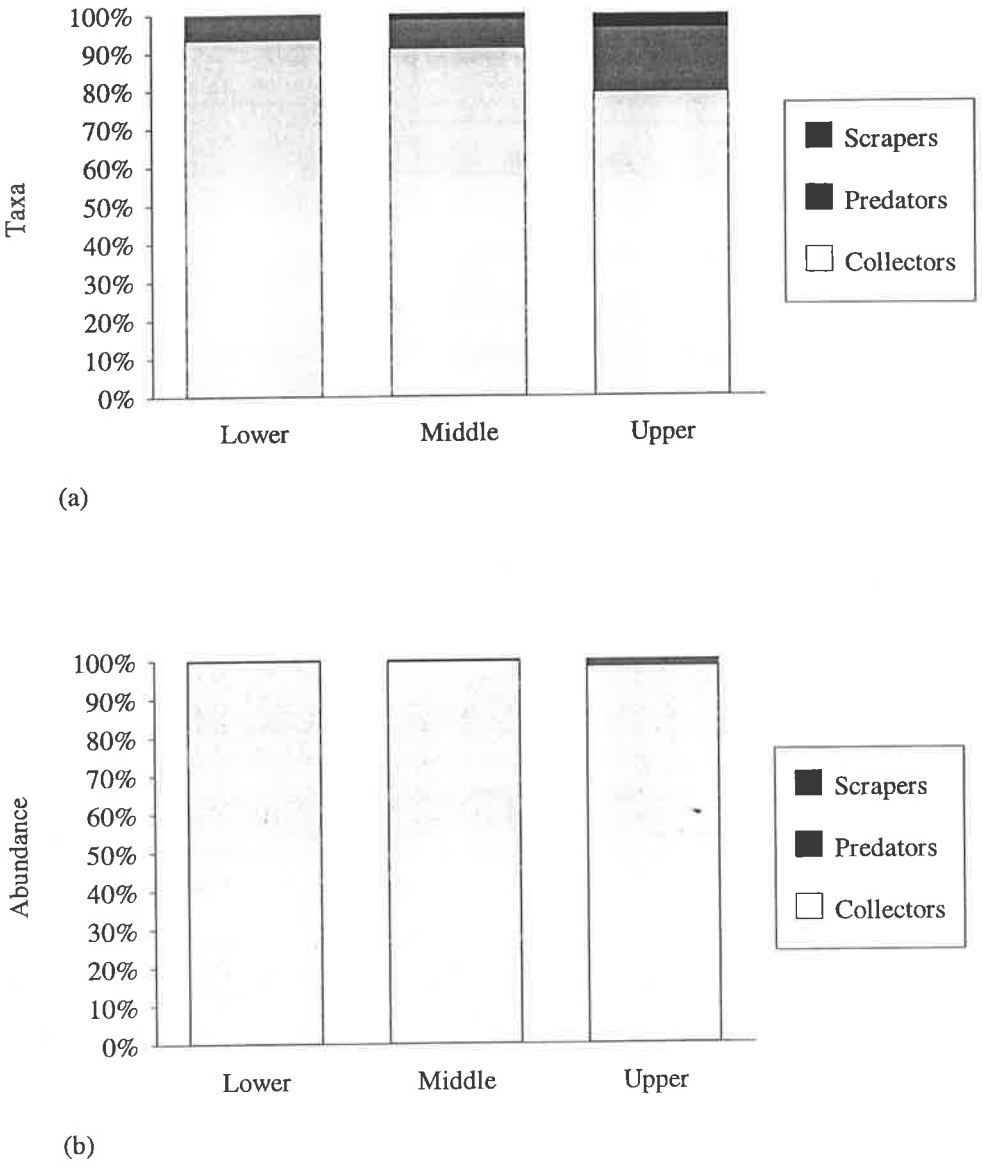


Figure 4.9 Proportion of (a) Taxa and (b) Individuals of the three FFG's (collector, predator and scraper) in each pool type between Lock 4 and Lock 2, lower River Murray, February 1990.

Table 4.5 Values for Kruskal-Wallis H statistic for differences in the median number of taxa and median number of individuals in each FFG for pool section and microhabitat. A Bonferroni corrected significance level of p=0.01 is used.

	Taxa	Individuals
Pool Section		
Collector	H=8.31, p<0.01	H=1.52, p>0.01
Predator	H=12.14, p<0.01	H=14.61, p<0.001
Scraper	H=12.57, p<0.01	H=12.23, p<0.01
Microhabitat		
Collector	H=21.18, p<0.01	H=46.73, p<0.001
Predator	H=24.14, p<0.01	H=20.78, p<0.01
Scraper	H=33.2, p<0.001	H=32.66, p<0.001

Table 4.6 The mean number (SE) of (a) taxa and (b) individuals in total and for three functional feeding groups for each pool section sampled in Pool 3 and Pool 2, lower Murray, in February 1990. (n) = number of samples.

(a)

	(n)	Total	Collectors	Predators	Scrapers
Lower Pool	36	7.9 *(0.5)*	7.4 *(0.4)*	0.5 *(0.1)*	0
Middle Pool	54	10.1 *(0.3)*	9.1 *(0.3)*	0.7 *(0.1)*	0.1 *(0.1)*
Upper Pool	18	10.7 *(0.8)*	8.5 *(0.6)*	1.8 *(0.4)*	0.4 *(0.1)*

(b)

	(n)	Total	Collectors	Predators	Scrapers
Lower Pool	36	237.4 *(26.7)*	236.7 *(26.6)*	0.7 *(0.2)*	0
Middle Pool	54	291.5 *(22.9)*	290.3 *(27.9)*	0.9 *(0.1)*	0.2 *(0.1)*
Upper Pool	18	261.8 *(38.3)*	257.0 *(38.6)*	4.4 *(1.4)*	0.4 *(0.2)*

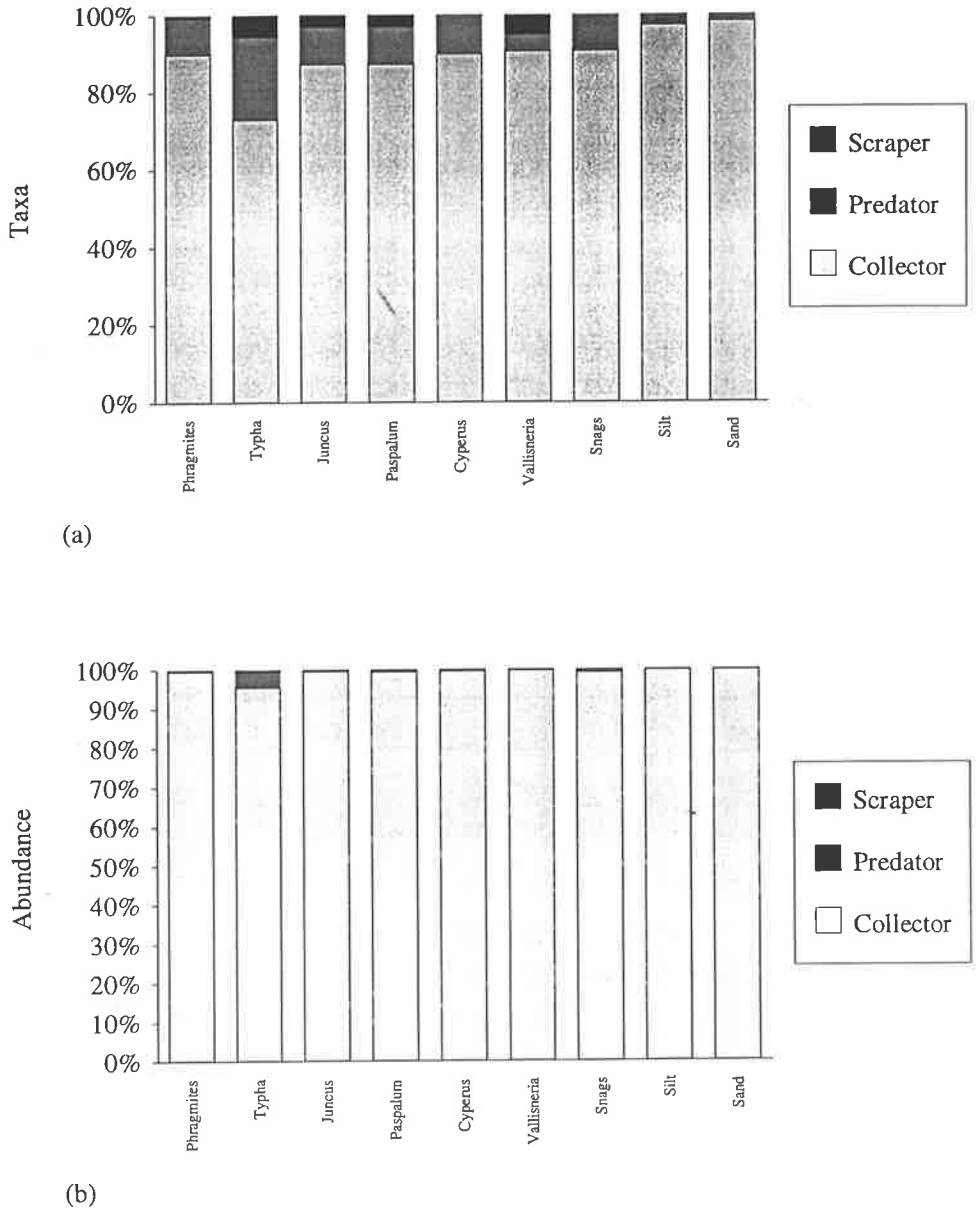


Figure 4.10 Proportion of (a) Taxa and (b) Indivduals of the three FFG's (collectot, predator and scraper) for each microhabitat sampled in the littoral zone between Lock 4 and Lock 2, lower River Murray, February 1990.

Table 4.7 The mean number (SE) of (a) taxa and (b) individuals in total and for three functional feeding groups for each microhabitat sampled in Pool 3 and Pool 2, lower Murray, in February 1990. (n) = number of samples.

(a)

	(n)	Total	Collectors	Predators	Scrapers
Phragmites	27	9.4 *(0.5)*	8.4 *(0.4)*	0.9 *(0.2)*	0.1 *(0.1)*
Typha spp.	6	11.7 *(0.9)*	8.5 *(0.6)*	2.5 *(0.7)*	0.7 *(0.2)*
Juncus sp.	3	10.3 *(0.3)*	9.0 *(0)*	1.0 *(0)*	0.3 *(0.3)*
Paspalum	3	10.3 *(1.3)*	9.0 *(1.5)*	1.0 *(0)*	0.3 *(0.3)*
Cyperus	15	11.0 *(0.6)*	9.9 *(0.5)*	1.1 *(0.2)*	0
Vallisneria	15	9.1 *(0.5)*	8.2 *(0.4)*	0.4 *(0.1)*	0.5 *(0.2)*
Snags	27	9.0 *(0.7)*	8.1 *(0.6)*	0.8 *(0.3)*	0
Silt Substrata	3	11.7 *(0.7)*	11.3 *(0.9)*	0.3 *(0.3)*	0
Sand Substrata	9	6.1 *(0.5)*	6.0 *(0.5)*	0.1 *(0.1)*	0

(b)

	(n)	Total	Collectors	Predators	Scrapers
Phragmites	27	251.4 *(41.7)*	250.2 *(41.7)*	1.0 *(0.2)*	0.1 *(0.1)*
Typha spp.	6	142.0 *(18.2)*	135.5 *(18.7)*	5.7 *(2.4)*	0.8 *(0.3)*
Juncus sp.	3	303.3 *(44.5)*	299.0 *(44.7)*	1.0 *(0)*	0.3 *(0.3)*
Paspalum	3	457.3 *(85.7)*	454.6 *(86.2)*	1.7 *(0.3)*	1 *(1)*
Cyperus	15	336.3 *(48.4)*	334.7 *(48.2)*	1.6 *(0.4)*	0
Vallisneria	15	434.5 *(31.7)*	433.1 *(31.6)*	0.8 *(0.5)*	0.5 *(0.2)*
Snags	27	213.8 *(27.6)*	212.2 *(27.5)*	1.6 *(0.8)*	0
Silt Substrata	3	337.0 *(7.5)*	336.3 *(7.8)*	0.7 *(0.7)*	0
Sand Substrata	9	82.4 *(18.1)*	82.2 *(18.1)*	0.2 *(0.2)*	0

When the Margalef (D_{Mg}), Menhinick (D_{Mn}) and Berger-Parker (d) indices are calculated for the main channel assemblage (Table 4.8), the unevenness of the assemblage is depicted in a high value for N_{max} compared with total N and low values for the three indices. The plot of the number of species in the eight abundance classes also highlights the unevenness (Figure 4.11). Most taxa are rare with only a few abundant.

Table 4.8 Diversity indices calculated from total abundance data for all samples collected in Pool 3 and Pool 2 on the lower River Murray, February 1990.

Description		Value
No. of Species	S	60
No. Individuals	N	29001
N in most abundant species	N_{max}	20101
Margalef Index	D_{Mg}	5.74
Menhenick's Index	D_{Mn}	0.35
Berger-Parker Index	d	0.69
	$1/d$	1.44

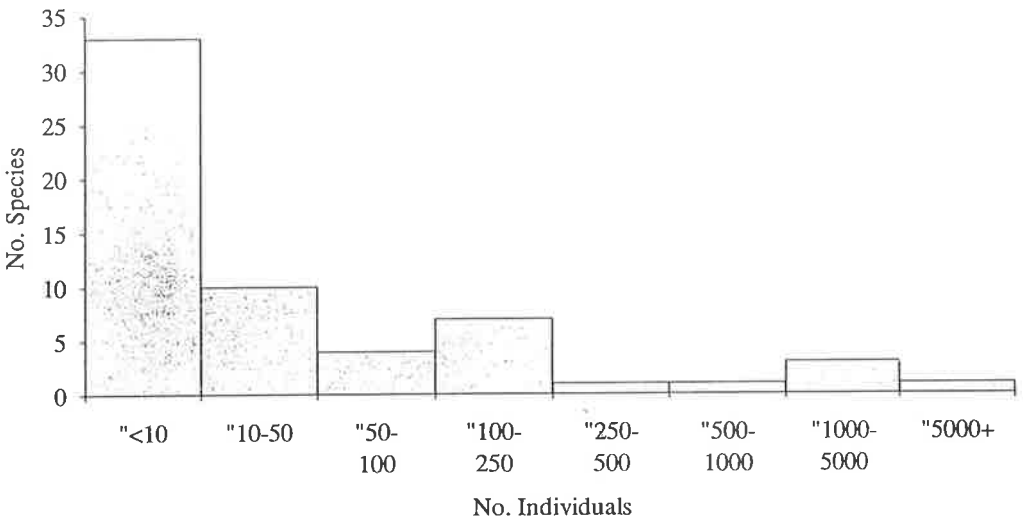


Figure 4.11 The number of species in eight abundance classes for habitats in Pool 3 and Pool 2, lower River Murray, February 1990.

Multivariate Analysis of Samples

TWINSPAN (log-transformed data) yielded seven groups (A-G) at the fourth level of division (Figure 4.12). The first division separated samples from unvegetated littoral areas with a sand substratum (Group G) from all other samples (A-F), the indicator species was the shrimp *Paratya australiensis* (Table 4.9). This is expected as samples from this microhabitat had significantly fewer taxa and individuals (cf. Table 4.7). Subsequently, samples from the sand microhabitat were removed and the data reanalysed.

The second TWINSPAN, on 99 samples, yielded nine groups (A-I) at the fourth level of division. The first division separated a majority of middle pool samples (A-D) from lower and upper pool samples (E-I) (Figure 4.13; Table 4.10). Indicator species for middle pool samples were the chironomids *Tanytarsus* sp., *Cladotanytarsus* sp. and *Cricotopus* spp. as well as the ceratopogonid *Forcipomyia* sp. The lower and upper pool samples were characterised by the shrimp *C. mccullochi*.

The group of middle pool samples (A-D) separated at the second division into Group A, comprising samples from snag and the sedge *C. gymnocaulos* (Table 4.10), with the indicator species *Cladotanytarsus* sp., and Groups B to D characterised by *Forcipoymia* sp. The latter groups (B to D) separated further into Groups B and C, containing samples from snag and emergent vegetation with indicator species *Austroargathona picta*, *Cladotanytarsus* sp. and *M. australiense*. Nearly all samples in Group D were from emergent vegetation and snag microhabitats in the middle pool of Pool 2 (cf. Table 4.9; Table 4.11).

Samples in Groups E to I were also best described according to microhabitat. Groups E and F contained all samples from *V. spiralis* and were characterised by the crustaceans *A. picta*, *P. autraliensis* and *C. mccullochi* and the ephemeropteran *Cloeon* sp. Most of the samples in Group G were from lower pool sites (cf. Table 4.10) and snag microhabitats. Groups H and I contained samples from emergent vegetation including *Typha* spp. The composition of the TWINSPAN groups reflected sample depth, CPOM and FPOM (Table 4.12).

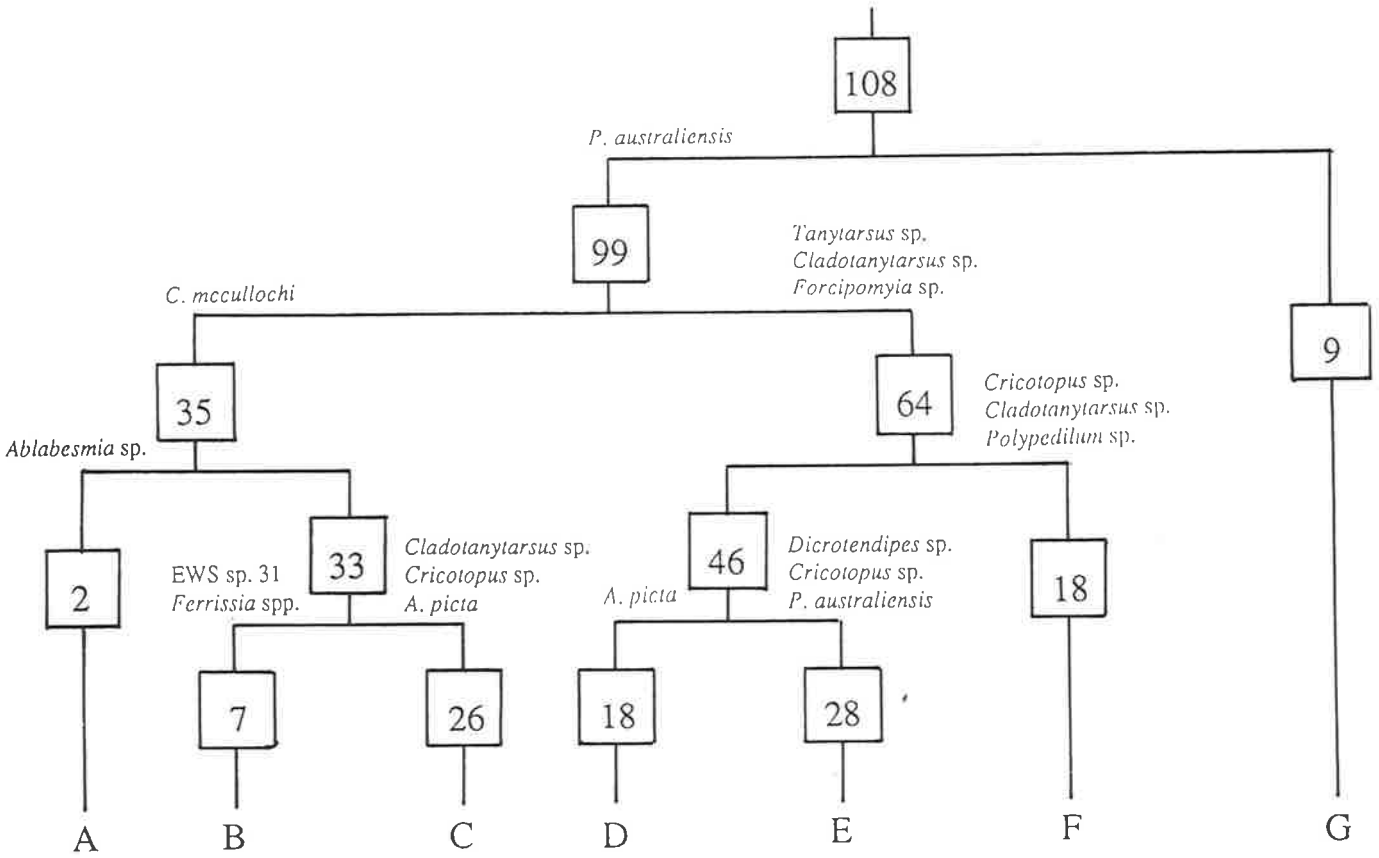


Figure 4.12 TWINSPAN dendogram of samples collected from all sites between Lock 4 and Lock 2, lower River Murray, in February 1990. Indicator species are listed above the relevant divisions. Entities in sample groups A-G are listed in Table 4.9

Table 4.9 Samples according to microhabitat and pool section ("UP" = upper pool, "MP" = middle pool; "LP" = lower pool) in the seven sample groups (A-G) yielded by TWINSPAN of all samples collected in Pool 3 and Pool 2, lower River Murray in February 1990.

Group	Sample Composition
A	Seven Emergent Vegetation, four Snag, three Silt (7MP, 4LP, 3UP)
B	Twelve Snag, eleven Emergent Vegetation (6LP, 15MP, 2UP)
C	Seven Emergent Vegetation, three Snag (10MP)
D	Thirteen Emergent Vegetation, fifteen Submerged Vegetation (10LP, 10MP, 8UP)
E	Thirteen Emergent Vegetation, seven Snag (10LP, 7MP, 3UP)
F	Two Emergent Vegetation (2UP)
G	Nine Sand (9LP)

Table 4.10 Samples according to pool type in the nine sample groups (A-I) yielded by TWINSPAN of all samples remaining after removing those collected from open littoral sand microhabitats in Pool 3 and Pool 2, lower River Murray in February 1990.

Group	Sample Composition
A	Four Lower pool, seven Middle pool and three Upper pool
B	Four Lower pool, six Middle pool and two Upper pool
C	Two Lower pool and ten Middle pool
D	Ten Middle pool
E	Six Lower pool, six Middle pool and three Upper pool
F	Four Lower pool, four Middle pool and five Upper pool
G	Ten Lower pool, five Middle pool and one Upper pool
H	Two Middle pool and two Upper pool
I	Two Upper pool

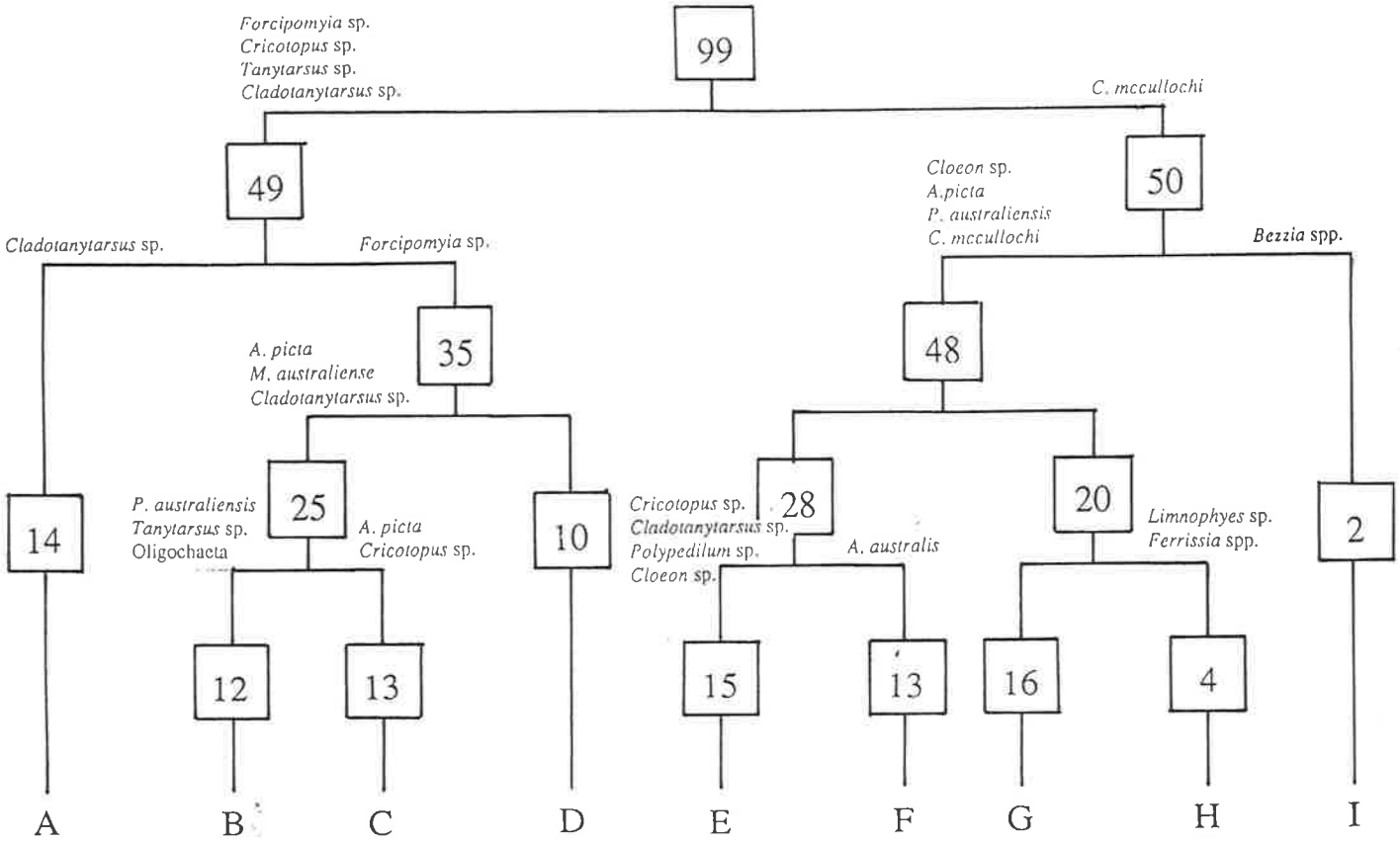


Figure 4.13 TWINSPAN dendogram of the 99 samples remaining after removal of the nine samples from the sand substrate microhabitat, from sites between Lock 4 and Lock 2, lower River Murray, in February 1990. Indicator species are listed above the relevant divisions. Entities in sample groups A-I are listed in Table 4.10 and Table 4.11

Table 4.11 Samples according to microhabitat in the nine sample groups (A-I) yielded by TWINSPAN of all samples remaining after removing those collected from open littoral sand microhabitats in Pool 3 and Pool 2, lower River Murray in February 1990.

Group	Sample Composition
A	Six *Cyperus* sp., one *Phragmites australis*, three Silt and four Snag
B	Two *Cyperus* sp. and seven Snag
C	Seven *P. australis* and five Snag
D	Four *P. australis*, three *Cyperus* sp. and three Snag
E	Five *Cyperus* sp., two *P. australis* and eight *Vallisneria spiralis*
F	Four *Cyperus* sp., two *Typha* spp. and seven *V. spiralis*
G	One *Cyperus* sp., seven *P. australis* and seven Snag
H	Two *P. australis* and two *Typha* spp.
I	Two *Typha* spp.

Table 4.12 Spearman Rank correlation coefficients (r_S) between environmental variables and the samples in the nine groups (A-I) yielded by the TWINSPAN of all samples remaining after removal of open littoral sand microhabitat samples collected from the littoral zone of the lower River Murray in Pool 3 and Pool 2, February 1990.

Variable	r_S	Significance
CPOM	-0.210	$p<0.05$
FPOM	-0.238	$p<0.05$
Shade	0.045	n.s.
Salinity	-0.032	n.s.
Oxygen	0.098	n.s.
Temperature	0.183	n.s.
Secchi Depth	-0.151	n.s.
Sample Depth	0.244	$p<0.05$

Multivariate ordination of the sample data supported the distinctiveness of the sand samples. Figure 4.14 shows the distribution of samples on the first and second axes of the SSH plot, the outlier sand samples, are evident when labelled according to microhabitat (Figure 4.15). There were significant associations between Axis 1 and depth (Table 4.13), while Axis 2 showed correlations with FPOM, shade and salinity (Table 4.13). Sand samples were subsequently removed and the data reanalysed.

In this second SSH the solution in four dimensions had the lowest stress and this solution is presented here. Figure 4.16 shows the distribution of samples on the first three axes of the second SSH plot. There were significant associations between Axis 1 and Secchi depth, between Axis 2 and sample depth, while Axis 3 showed correlations with shade (Table 4.14). The samples did not separate according to the pool from which they were collected (Figure 4.17), samples from Pool 3 and Pool 2 were superimposed on the SSH plot. When labelled according to pool section (Figure 4.18) most upper pool samples fall high on Axis 1, low on Axis 2 and high on Axis 3. Samples from lower pool regions form a more constricted cluster in the centre of Axes 1 and 2 and high on Axis 3. When combined, samples from upper and lower pools form a diffuse separate group with high scores on Axis 3, which appears to reflect pool section. Samples collected from middle pool sites were dispersed along all axes and did not form clusters.

There is some clustering of samples according to microhabitats (Figure 4.19). Samples collected from *V. spiralis* form a distinct cluster with low scores on Axis 2 while most of the snag and silt samples have high scores on Axis 2. Samples from emergent vegetation do not form distinct clusters but there is a shift along Axis 2 from detritus based microhabitats, such as open littoral silt substrata and snag, to submerged vegetation. Axis 2 reflects FPOM, site salinity and depth, these physical variables may also be reflective of different microhabitats. Silt and snag samples have a larger proportion of FPOM and tend to occur at shallow depths compared with samples collected from *V. spiralis,* which inhabits deeper water and tends to have less FPOM.

When the groups produced by the TWINSPAN are mapped onto the SSH plot (Figure 4.20) there is an apparent gradient between pool sections. TWINSPAN sample groups A to D, from middle pool regions, form a relatively coherent group low on Axis 1 and high on Axes 2 and 3. The combined group of upper and lower pool samples (E to I) tend to fall on the higher portion of Axis 1 and the lower regions of Axes 2 and 3, overlapping slightly groups A to D.

Table 4.13 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first and second axes of the SSH of faunal data from all samples collected in Pool 3 and Pool 2, lower River Murray in February 1990.

CPOM	1.00									
FPOM	0.339	1.00								
Shade	0.268	0.366	1.00							
Salinity	0.166	-0.031	0.149	1.00						
Oxygen	-0.032	0.035	0.218	0.416	1.00					
Temp	-0.005	0.084	0.339	0.037	0.334	1.00				
Secchi	0.024	0.092	0.192	-0.171	-0.067	-0.131	1.00			
Depth	0.235	0.054	0.207	0.261	-0.150	0.078	-0.002	1.00		
A1	**-0.070**	**0.092**	**-0.088**	**-0.069**	**-0.084**	**-0.215**	**0.177**	**-0.510**	**1.00**	
A2	**-0.049**	**0.304**	**0.301**	**0.281**	**0.098**	**0.117**	**-0.024**	**0.145**	**0.031**	**1.00**

Table 4.14 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first three axes of the SSH of faunal data from samples remaining after removal of open littoral sand microhabitat samples collected in Pool 3 and Pool 2, lower River Murray in February 1990.

CPOM	1.00										
FPOM	0.171	1.00									
Shade	0.096	0.255	1.00								
Salinity	0.072	-0.102	0.078	1.00							
Oxygen	-0.126	0.007	0.203	0.353	1.00						
Temp	-0.188	-0.060	0.263	-0.031	0.320	1.00					
Secchi	0.098	0.165	0.260	-0.184	-0.052	-0.106	1.00				
Depth	-0.001	-0.186	0.036	0.192	-0.254	-0.094	0.079	1.00			
A1	**-0.154**	**-0.073**	**0.201**	**-0.003**	**0.148**	**-0.058**	**0.262**	**0.237**	**1.00**		
A2	**0.171**	**0.257**	**0.107**	**0.246**	**0.123**	**-0.071**	**-0.029**	**-0.262**	**-0.178**	**1.00**	
A3	**0.044**	**-0.079**	**-0.306**	**-0.292**	**0.000**	**-0.112**	**0.216**	**-0.137**	**0.076**	**-0.091**	**1.00**

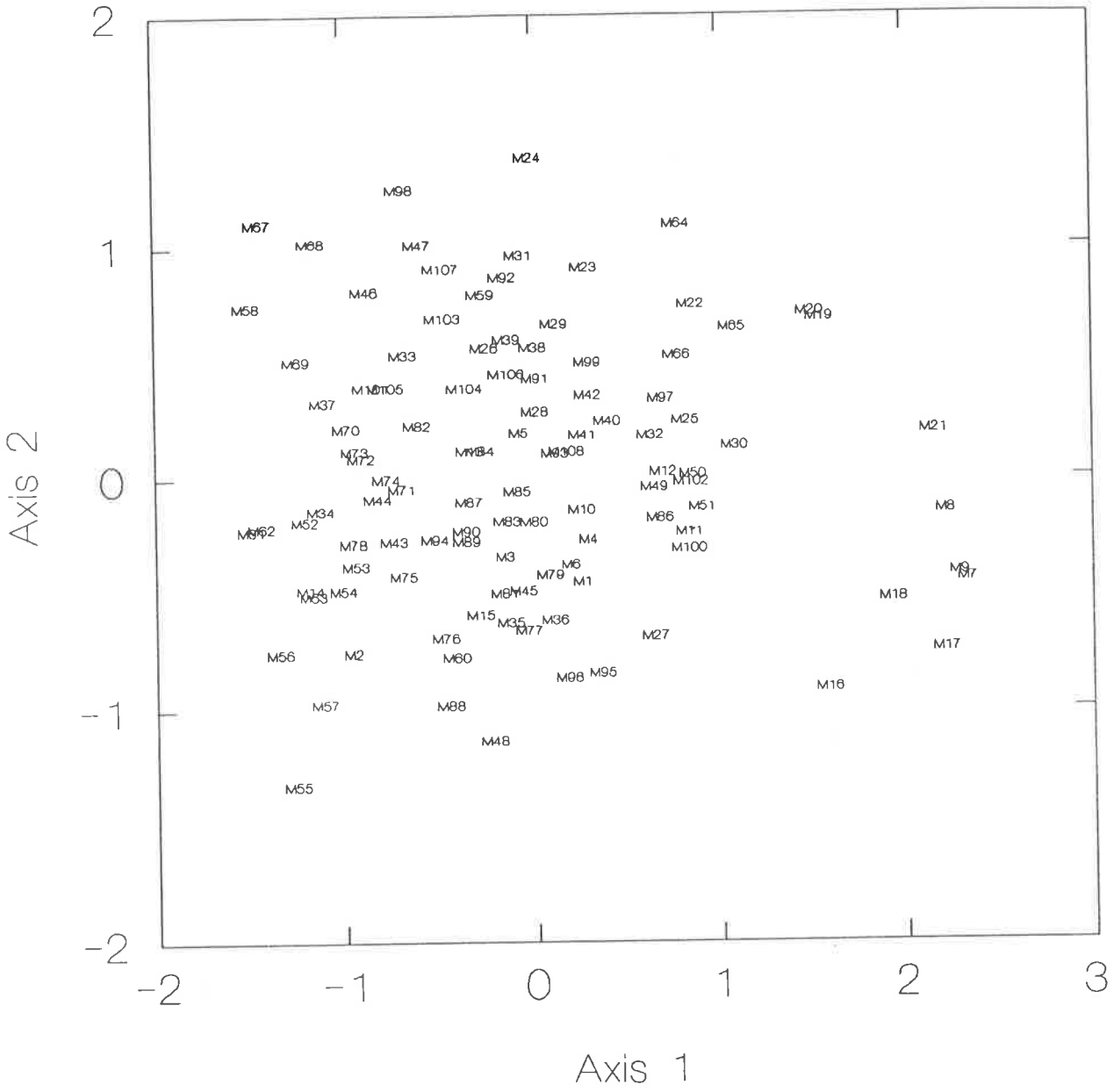
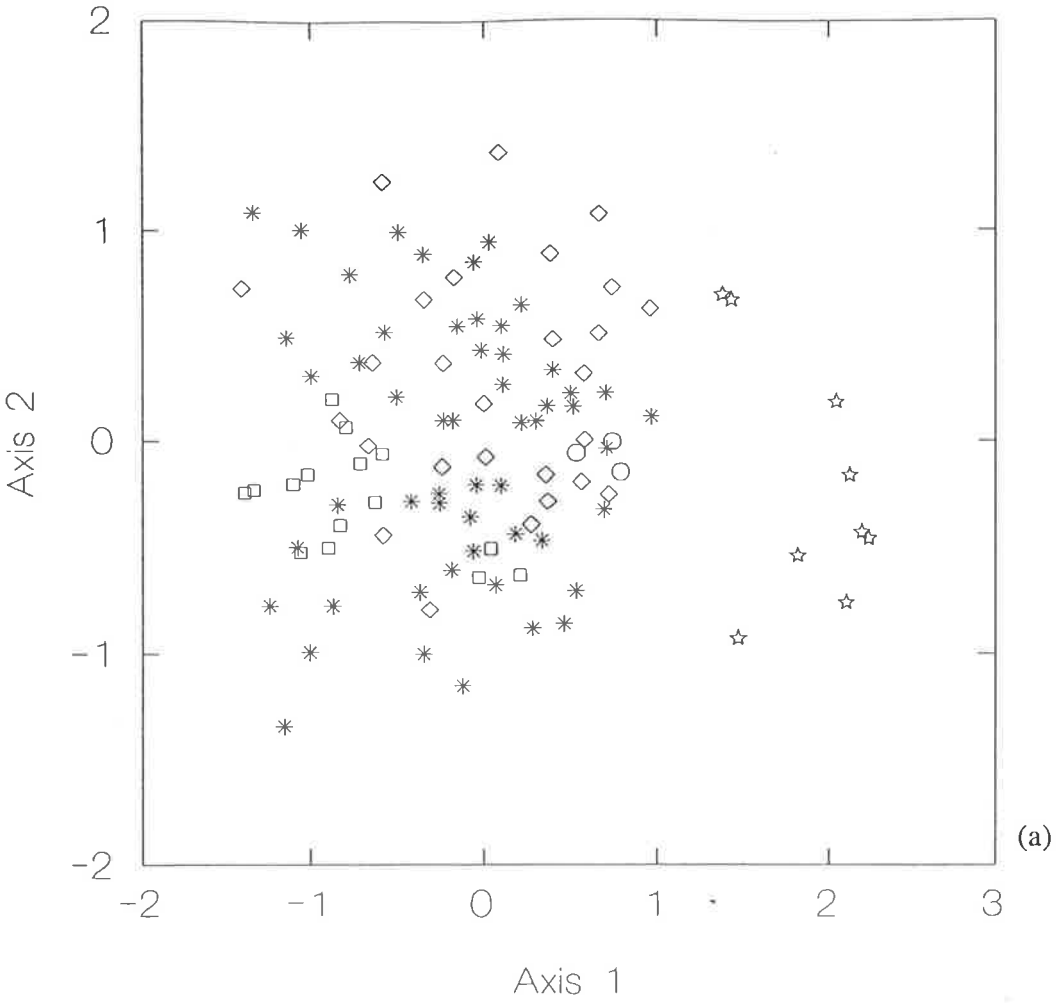


Figure 4.14 Distribution of samples on the first and second axes of the SSH plot of all samples collected from the littoral zone between Lock 4 and Lock 2, lower River Murray (February 1990).

Figure 4.15 SSH plot of all samples from the littoral zone between Lock 4 and Lock 2, lower River Murray (February 1990). Samples in plot (a) are labelled according to microhabitat; ✡ = open littoral sand substrata, 'diamonds' = snag, 'squares' = submerged vegetation, 'circles' = open littoral silt substrata and 'asterisk' = emergent vegetation. Plot (b) highlights the group of open littoral sand substrata samples.


2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
3
Axis 1
(a)

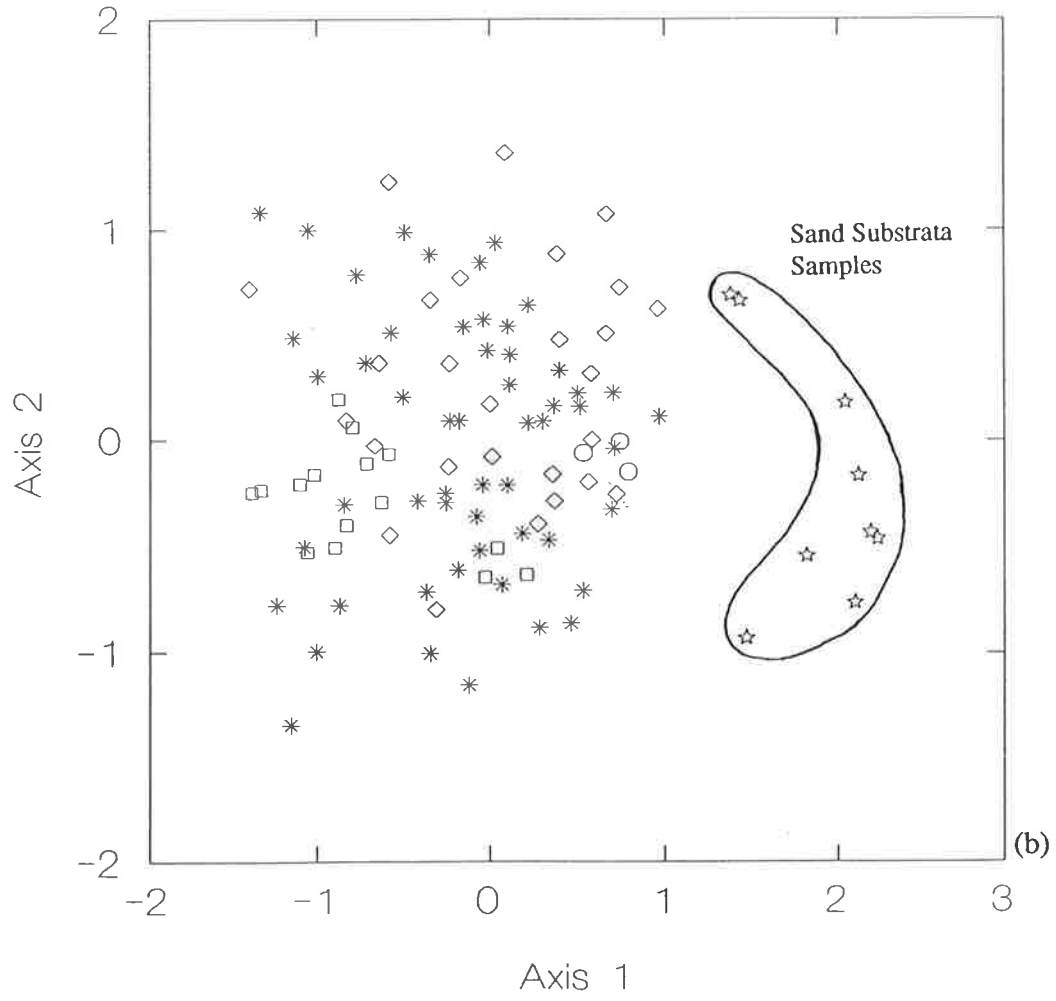
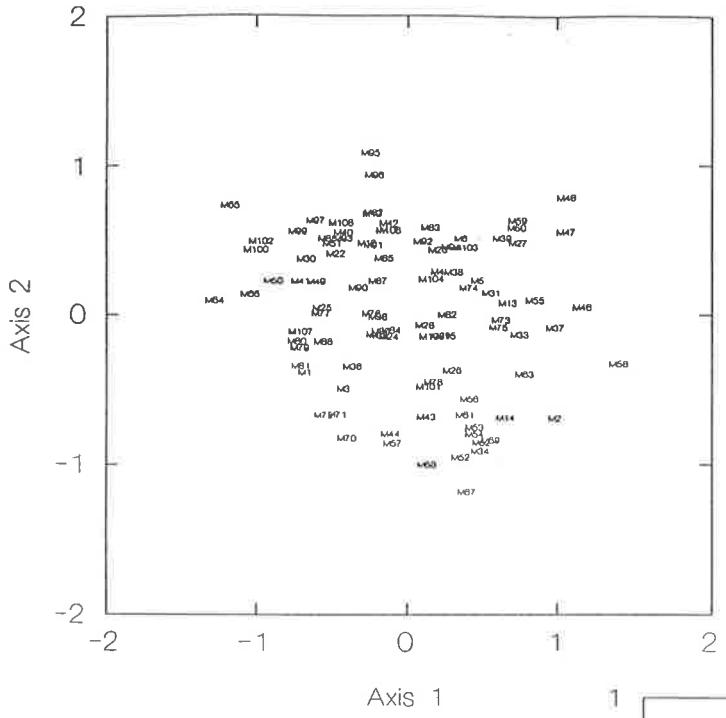
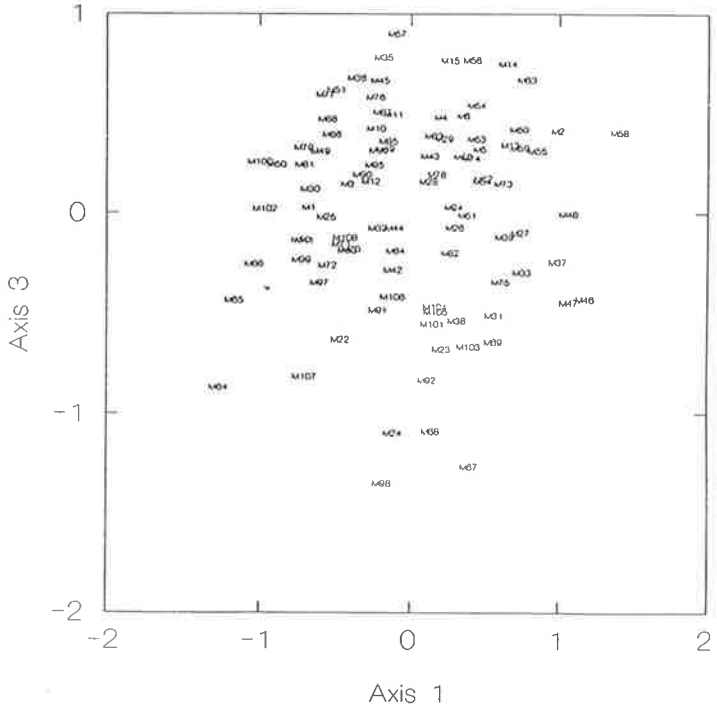

2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
3
Axis 1
Sand Substrata
Samples
(b)

Figure 4.16 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after the removal of the nine sand substrata samples, from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990.


Axis 2
Axis 1


Axis 3
Axis 1

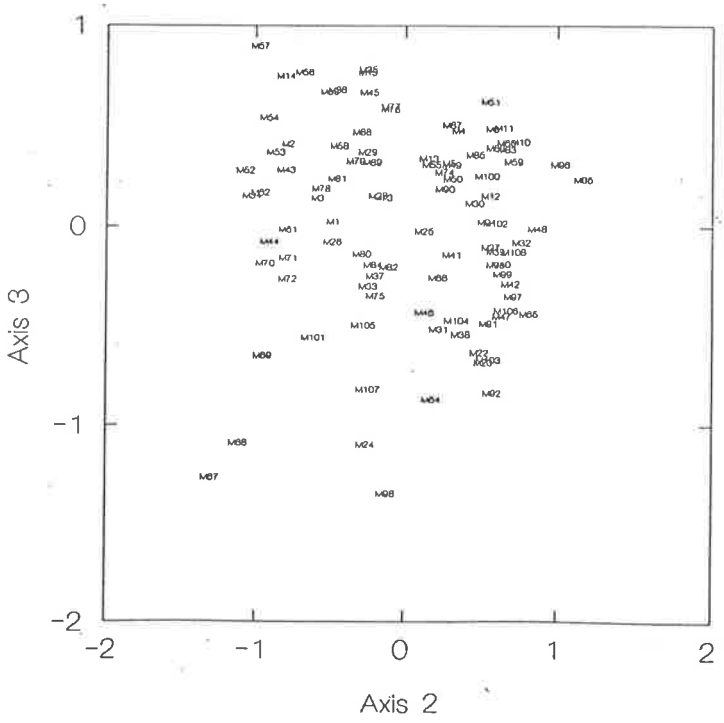
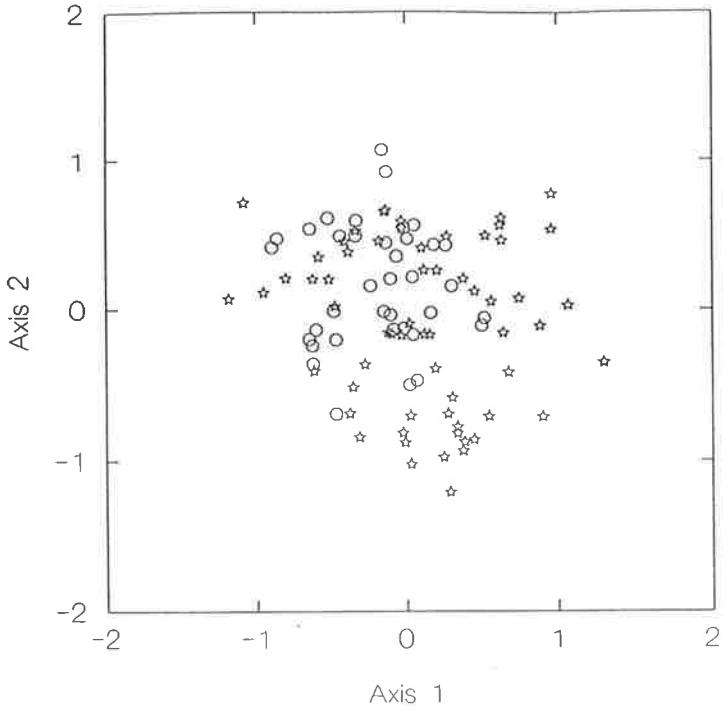
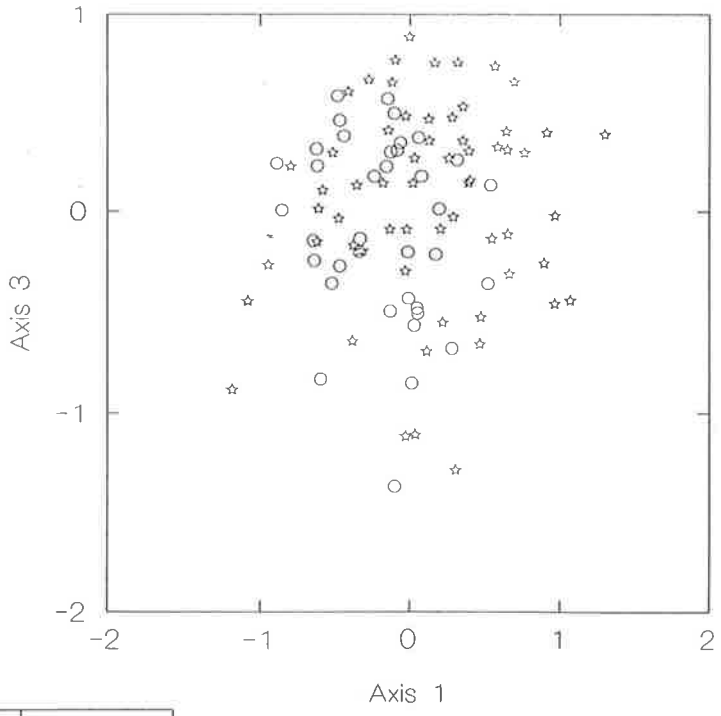

Axis 3
Axis 2

Figure 4.17 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the Lock from which they were collected where 'stars' = Lock 3 and 'circles' = Lock 2.


2
1
0
-1
-2
Axis 2
-2
-1
0
1
2
Axis 1


1
0
-1
-2
Axis 3
-2
-1
0
1
2
Axis 1

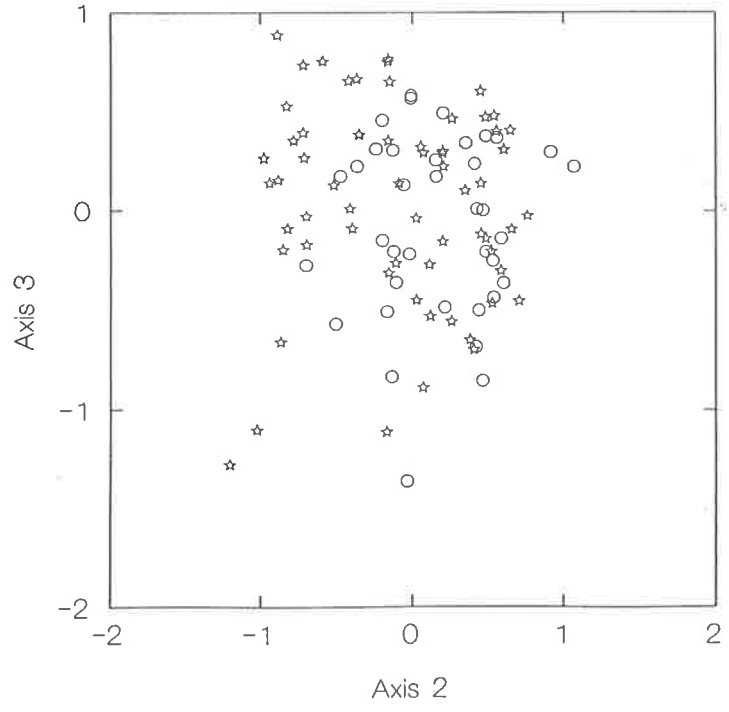
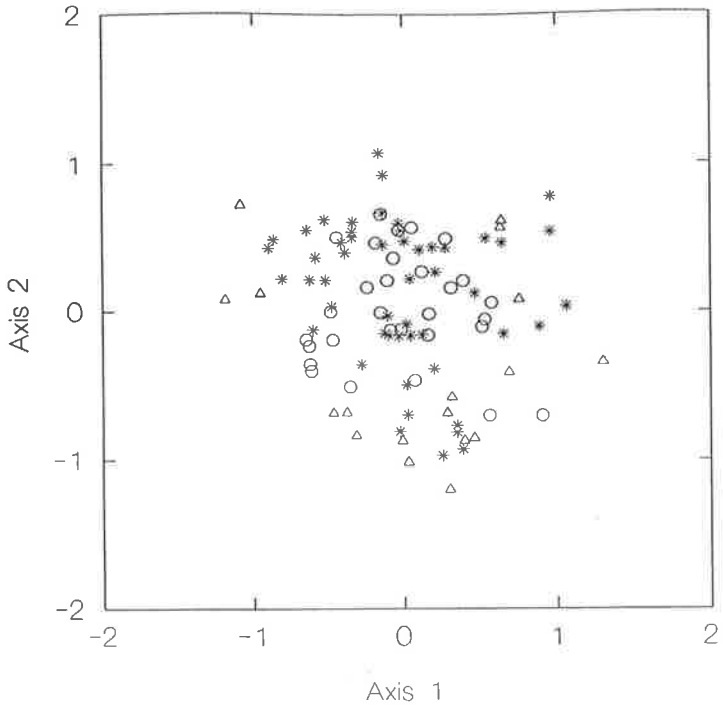
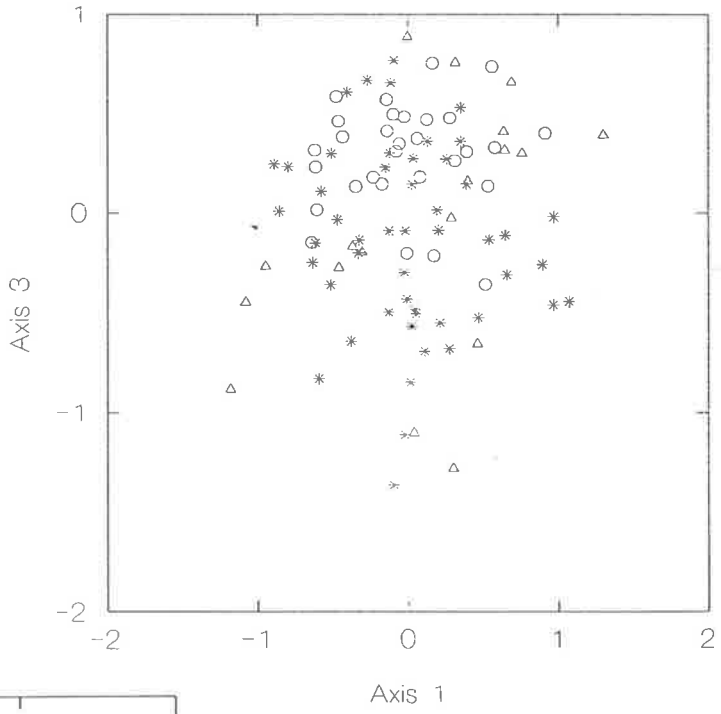

1
0
-1
-2
Axis 3
-2
-1
0
1
2
Axis 2

Figure 4.18 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the Pool type from which they were collected where 'triangles' = Upper pool regions, 'asterisk' = Middle pool regions and 'circle' = Lower pool regions.


Axis 2
Axis 1
2
1
0
-1
-2
-2
-1
0
1
2


Axis 3
Axis 1
1
0
-1
-2
-2
-1
0
1
2

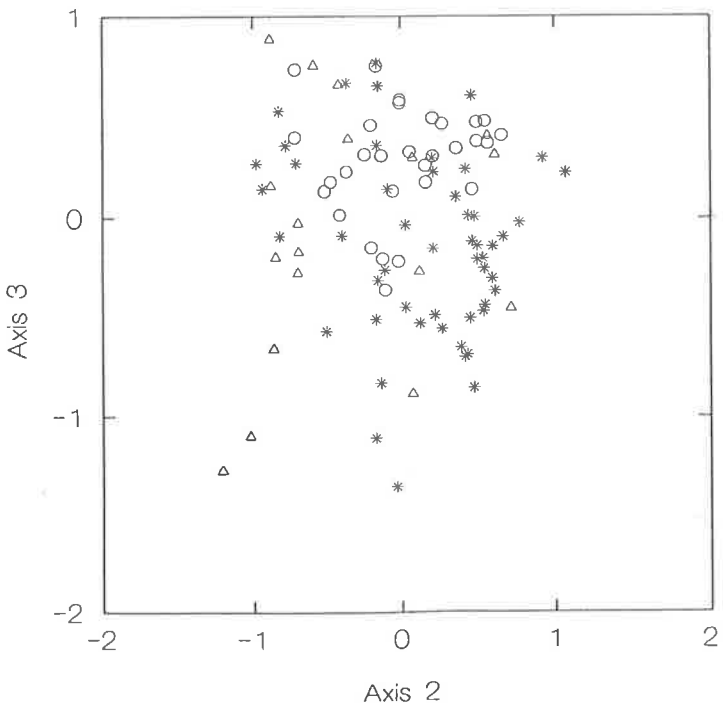
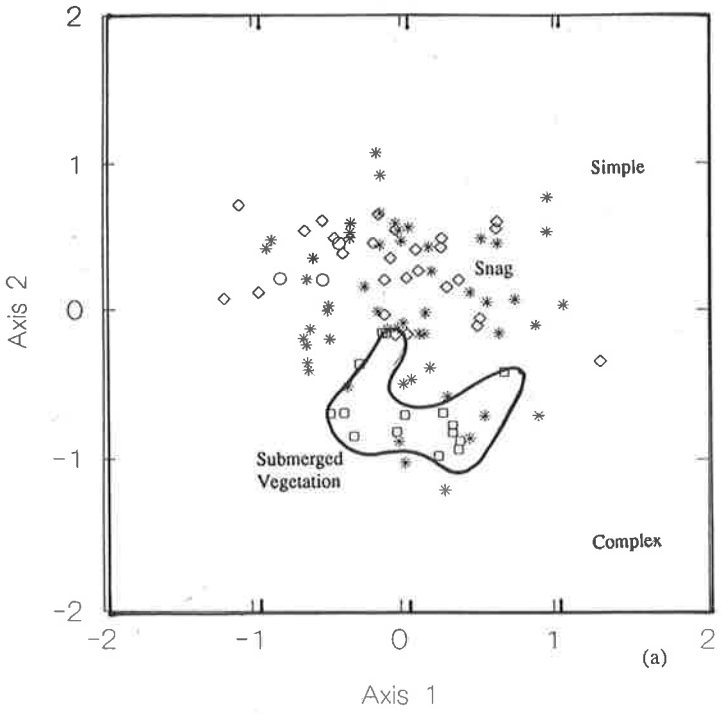
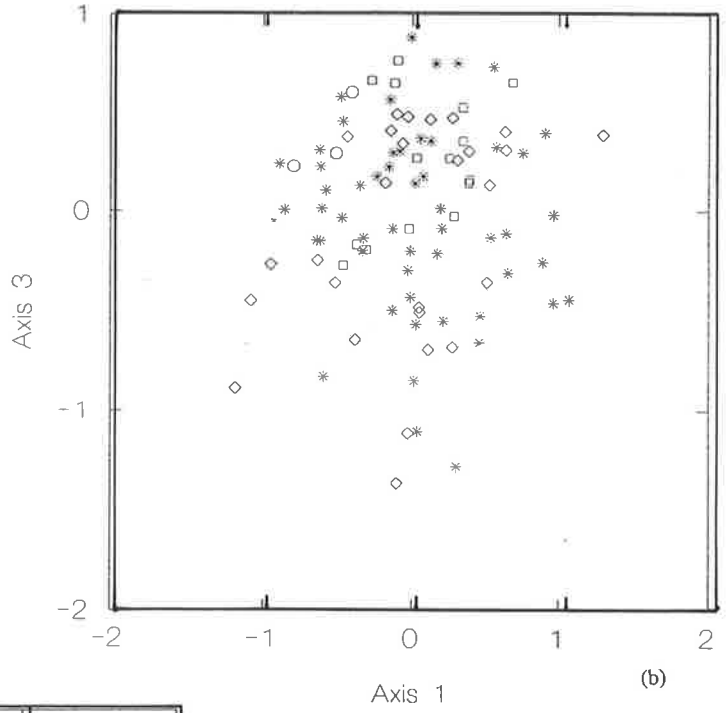

Axis 3
Axis 2
1
0
-1
-2
-2
-1
0
1
2

Figure 4.19 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the microhabitat from which they were collected where 'diamond' =snag, 'square' = submerged vegetation, 'circle' = open littoral silt substrata and 'asterisk' = emergent vegetation. The overlay highlights the grouping of the submerged vegetation samples and the relative position of the snag samples.


Simple
Snag
Submerged
Vegetation
Complex
Axis 2
Axis 1
(a)


Axis 3
Axis 1
(b)

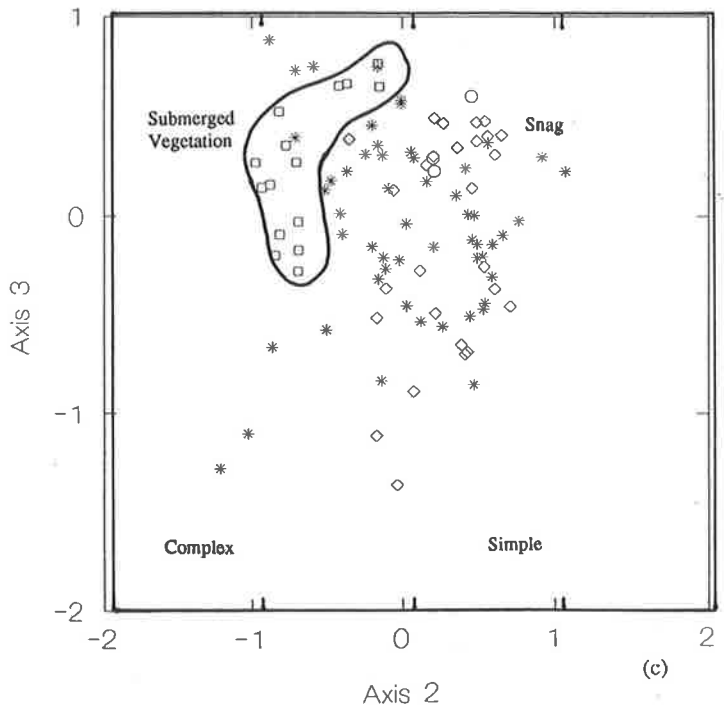
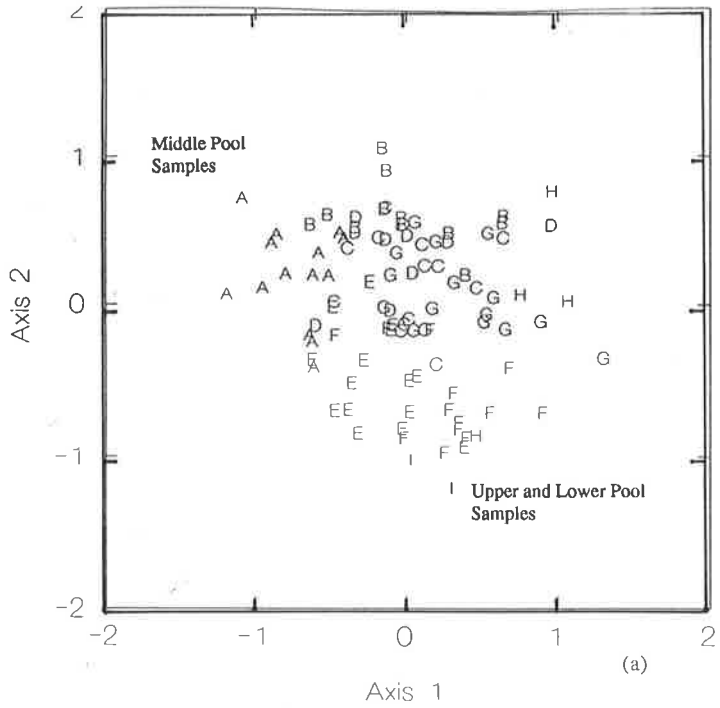
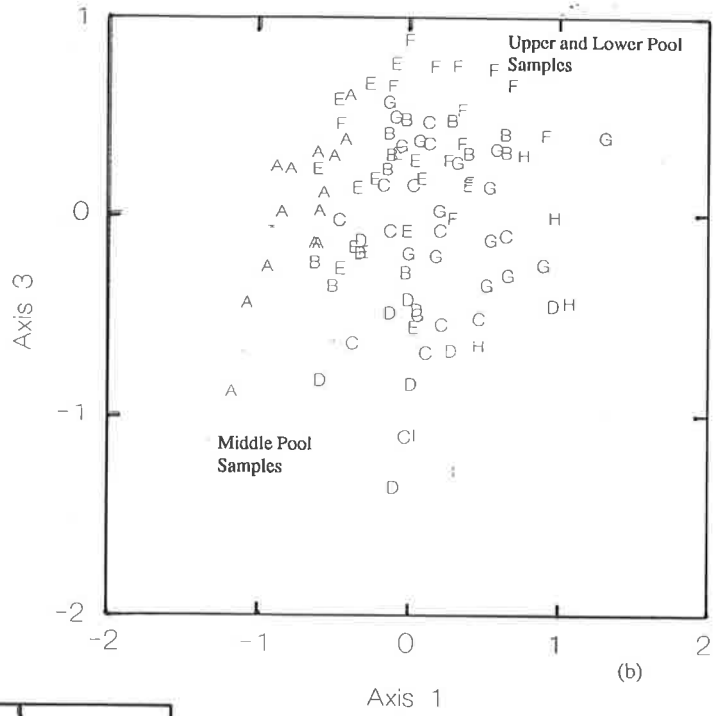

Submerged
Vegetation
Snag
Complex
Simple
Axis 3
Axis 2
(c)

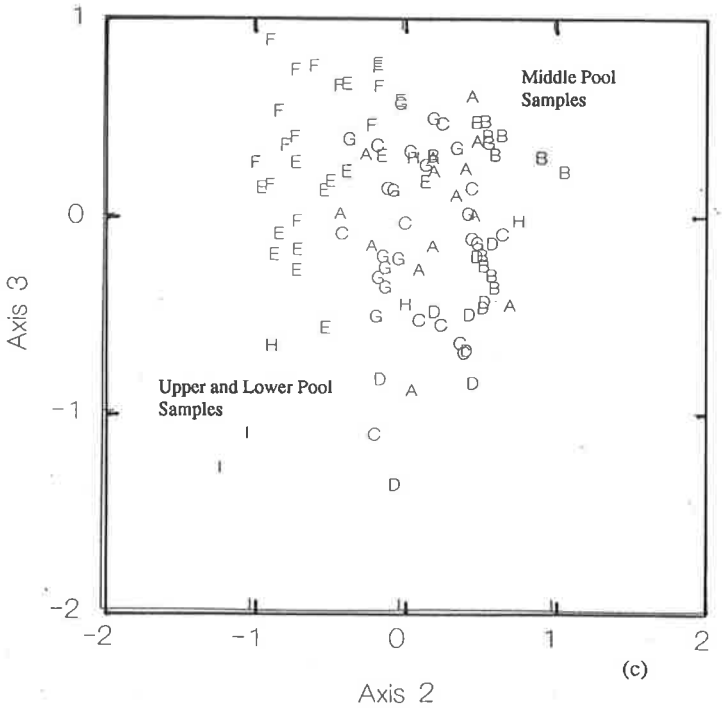
Figure 4.20 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Groups derived from TWINSPAN of the same data are superimposed (cf. Tables 4.9 and 4.10). The overlay highlights the gradient between middle pool samples and a combined group of upper and lower pool samples.


Middle Pool
Samples
Upper and Lower Pool
Samples
Axis 2
Axis 1
1
0
-1
-2
-2
-1
0
1
2

(a)


Upper and Lower Pool
Samples
Middle Pool
Samples
Axis 3
Axis 1
1
0
-1
-2
-2
-1
0
1
2

(b)


Middle Pool
Samples
Upper and Lower Pool
Samples
Axis 3
Axis 2
1
0
-1
-2
-2
-1
0
1
2

(c)

Multivariate Analysis of All Species

TWINSPAN of the species in samples produced seven groups (S1 to S7) (Table 4.15; Figure 4.21). The first division separated species groups S1 to S4 from groups S5 to S7. The division could not be explained in terms of the proportion of taxa belonging to the three FFG's within the species groups, but the groups appear to have some association with the relative abundance of the taxa. Species groups S1 and S2 contain taxa that are either rare or moderately abundant (Table 4.15). Groups S3 and S5 contain moderately abundant and common taxa with species group S5 containing the most abundant taxon, *P. australiensis*. Groups S6 and S7 contain taxa that are rare or only moderately abundant (Table 4.15).

Using the 'fidelity index' (Figure 4.22) species groups S1 and S2, containing relatively rare taxa, showed preferences for sample groups A to D, collected from middle pool sites. Species groups S3 to S5, containing highly abundant taxa, such as *P. australiensis* and *M. australiense,* exhibited preferences for nearly all samples groups, particularly A to G. This suggests that these species are ubiquitous, not showing obvious pool type or microhabitat preferences. Both groups showed avoidance of sample groups H and I, which contain samples from the emergent macrophyte *Typha* spp. in upper pool sections.

Species groups S6 and S7, also containing taxa of rare and moderate abundance (cf. Table 4.15), showed preferences for sample groups E to I, from upper and lower pool sections. These species groups included taxa such as the gastropods *Ferrissia* sp. and *Physa acuta,* the amphipod *Austrochiltonia australis* and the shrimp *C. mccullochi.* These taxa tend to be slightly more common in lentic habitats (cf. Boulton and Lloyd, 1991; Goonan *et al.,* 1992)

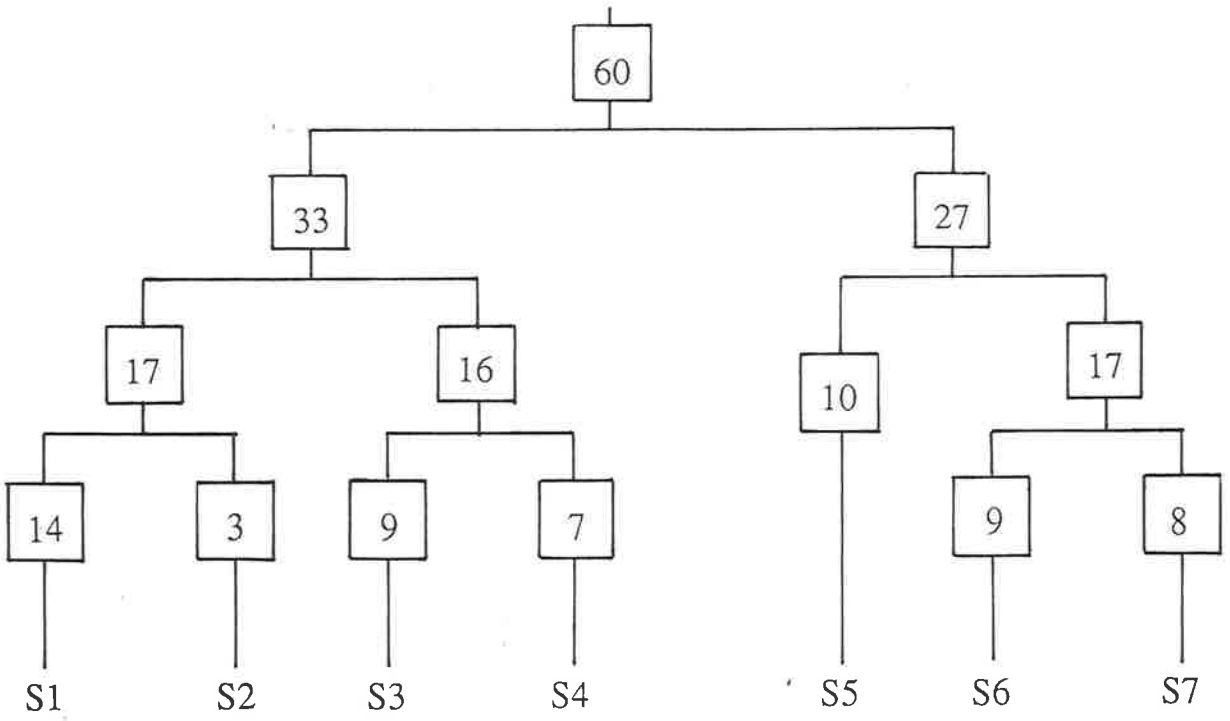


Figure 4.21 TWINSPAN dendogram of the species data from the 99 samples remaining after removal of the sand substrata samples, collected from the littoral zone between Lock 4 and Lock 2, lower River Murray in February 1990. Taxa in species groups S1 to S7 are listed in Table 4.15

Table 4.15 Species and their FFG and relative abundance for the seven species groups (S1 to S7) yielded by TWINSPAN of all samples remaining after removal of open littoral sand microhabitat (99 samples) collected from the littoral zone of the lower River Murray in Pool 3 and Pool 2, February 1990.

	Species	FFG	Abundance
Group S1	*Forcipomyia* sp.	Collector	Common
	Stenochironomus sp.	Collector	Rare
	Triplectides australis	Collector	Rare
	Dicrotendipes conjunctus	Collector	Rare
	Ochtheridae sp.	Collector	Rare
	Psychodidae sp.	Collector	Rare
	Tanytarsus fuscithorax	Collector	Moderate
	Cricotopus sp. (Black)	Collector	Rare
	Allodessus sp.	Predator	Rare
	Coxelmis sp. (larvae)	Predator	Rare
	Ecnomus sp.	Predator	Rare
	Nosostica solida	Predator	Rare
	Procladius sp.	Predator	Rare
	Pentaneura sp.	Predator	Rare
Group S2	*Parakiefferiella* sp.	Collector	Moderate
	Limnophyes sp.	Collector	Moderate
	Empididae sp.	Predator	Rare
Group S3	*Micronecta* spp.	Collector	Common
	Oligochaeta spp.	Collector	Common
	Cricotopus spp.	Collector	Abundant
	Sphaerium sp.	Collector	Common
	Cladotanytarsus sp.	Collector	Abundant
	Tanytarsus spp.	Collector	Common
	Dicrotendipes sp.	Collector	Moderate
	Gerridae sp.	Predator	Rare
	Muscidae sp.	Predator	Rare
Group S4	*Tasmanocoenis arcuata*	Collector	Moderate
	Cryptochironomus sp.	Collector	Common
	Polypedilum sp.	Collector	Moderate
	Tipulidae spp.	Predator	Rare
	Ablabesmyia sp.	Predator	Moderate
	Bezzia sp.	Predator	Rare
	Anisops sp.	Predator	Rare

Group S5	*Paratya australiensis*	Collector	Abundant
	Macrobrachium australiense	Collector	Abundant
	Austroargathona picta	Collector	Common
	Paratanytarsus sp.	Collector	Moderate
	Mesovelia sp. 1	Predator	Rare
	Parachironomus sp.	Predator	Moderate
	Hydrophilidae (larvae) sp. 1	Predator	Moderate
	Antiporus femoralis	Predator	Rare
	Peza ops	Predator	Rare
	Enochrus sp.	Scraper	Rare
Group S6	*Austrochiltonia australis*	Collector	Moderate
	Cherax destructor	Collector	Moderate
	Cloeon sp.	Collector	Common
	Caridina mccullochi	Collector	Abundant
	Chironomus cloacalis	Collector	Moderate
	Triplectides elongatus	Collector	Rare
	Temnocephala sp.	Predator	Rare
	Tiny Zygoptera	Predator	Rare
	Ferrissia spp.	Scraper	Moderate
Group S7	*Sigara* sp.	Collector	Rare
	Kiefferulus sp.	Collector	Rare
	EWS sp. 31	Collector	Moderate
	Mesovelia sp. 2	Predator	Rare
	Naucoris sp.	Predator	Rare
	Muscidae sp. 2	Predator	Moderate
	Ochthebius sp.	Scraper	Rare
	Physa acuta.	Scraper	Rare

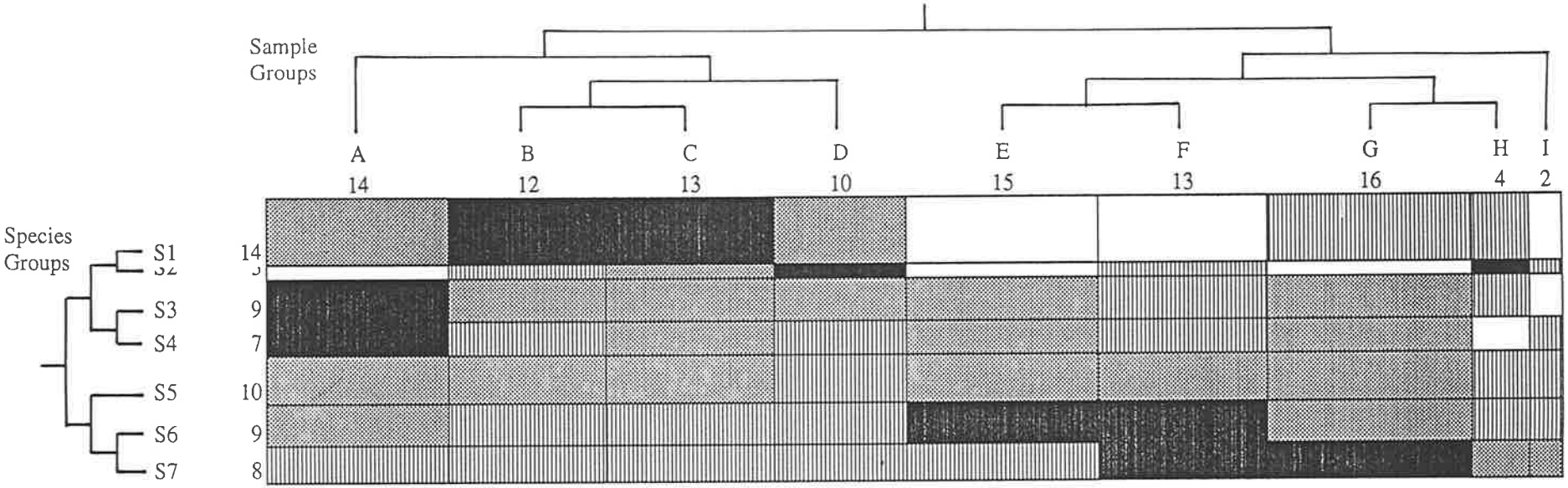


Figure 4.22 Two-way table of species group fidelities (Fij) to sample groups. Both species groups (S1-S7) and sample groups (A-I) are derived from the TWINSPAN of the faunal data in the 99 samples remaining after removal of those from the sand substrata microhabitat. Samples are from between Lock 4 and Lock 2, lower River Murray, February 1990. The numbers of elements in each group are near the label. Values of $F_{ij} > 2.0$ (full-shading) or $F_{ij} > 1.0$ (cross-hatching) indicate 'preference' while values of $F_{ij} < 1.0$ (vertical lines) or F_{ij} (no shading) indicate 'avoidance'.

Ordination of the species data demonstrates the difference in abundant and rare taxa. Figure 4.23 gives the distribution of the species on Axis 1 and Axis 2 of the SSH plot. When the relative abundance of each taxon is superimposed (Figure 4.24) the highly abundant species cluster in the centre of the plot with rare taxa having higher positive and lower negative scores on both axes. If the FFG of each taxon is mapped onto the ordination (Figure 4.25) the collector taxa are most abundant, occurring in the centre of the plot with rarer predators and scrapers around the perimeter.

When the groups produced by TWINSPAN of the species data are mapped onto the SSH plot (Figure 4.26), those species groups containing rare or moderately abundant taxa (S1, S2, S6 and S7) occur on the outer regions, while groups containing more abundant species (S3 to S5) cluster in the centre.

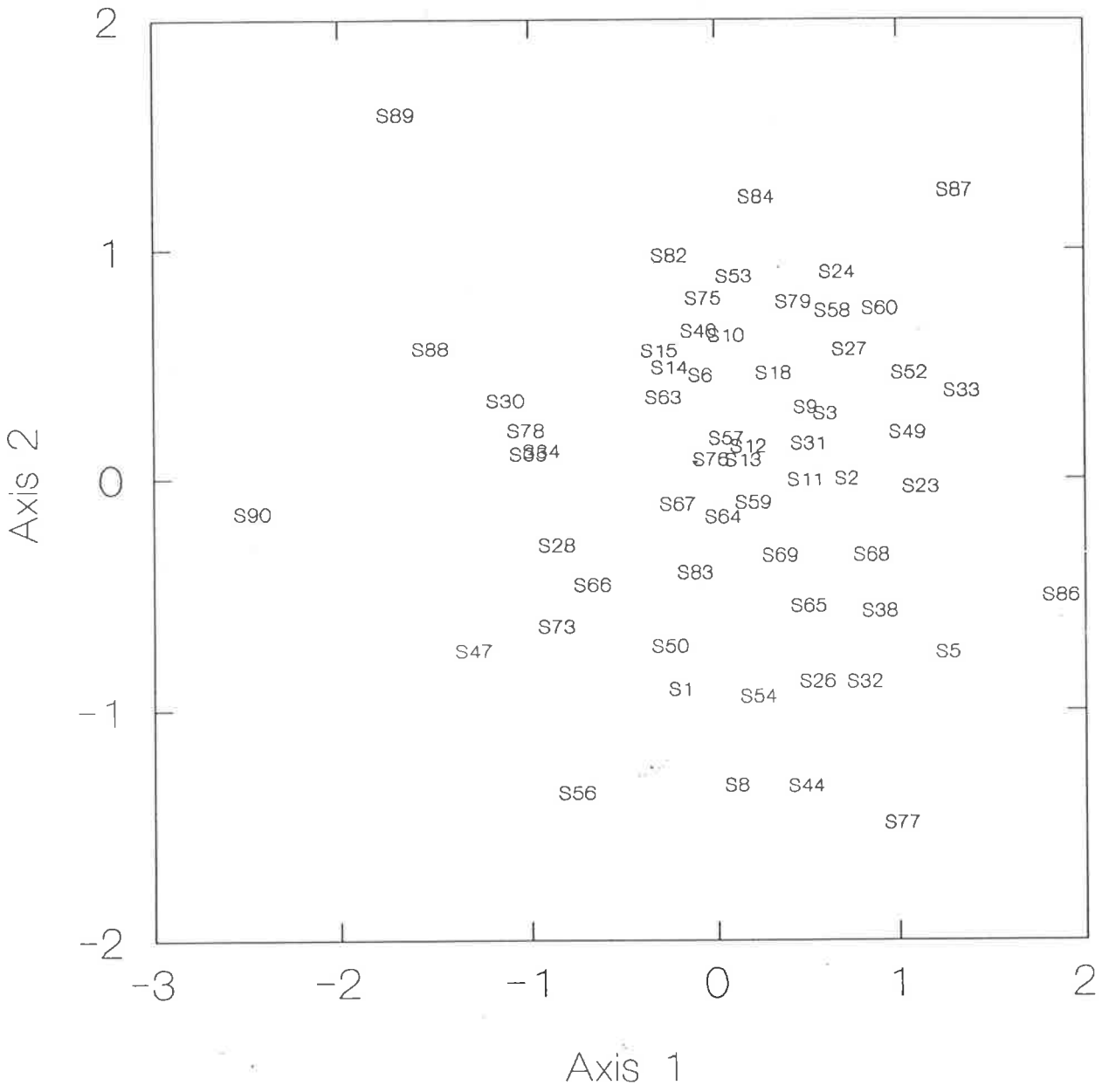
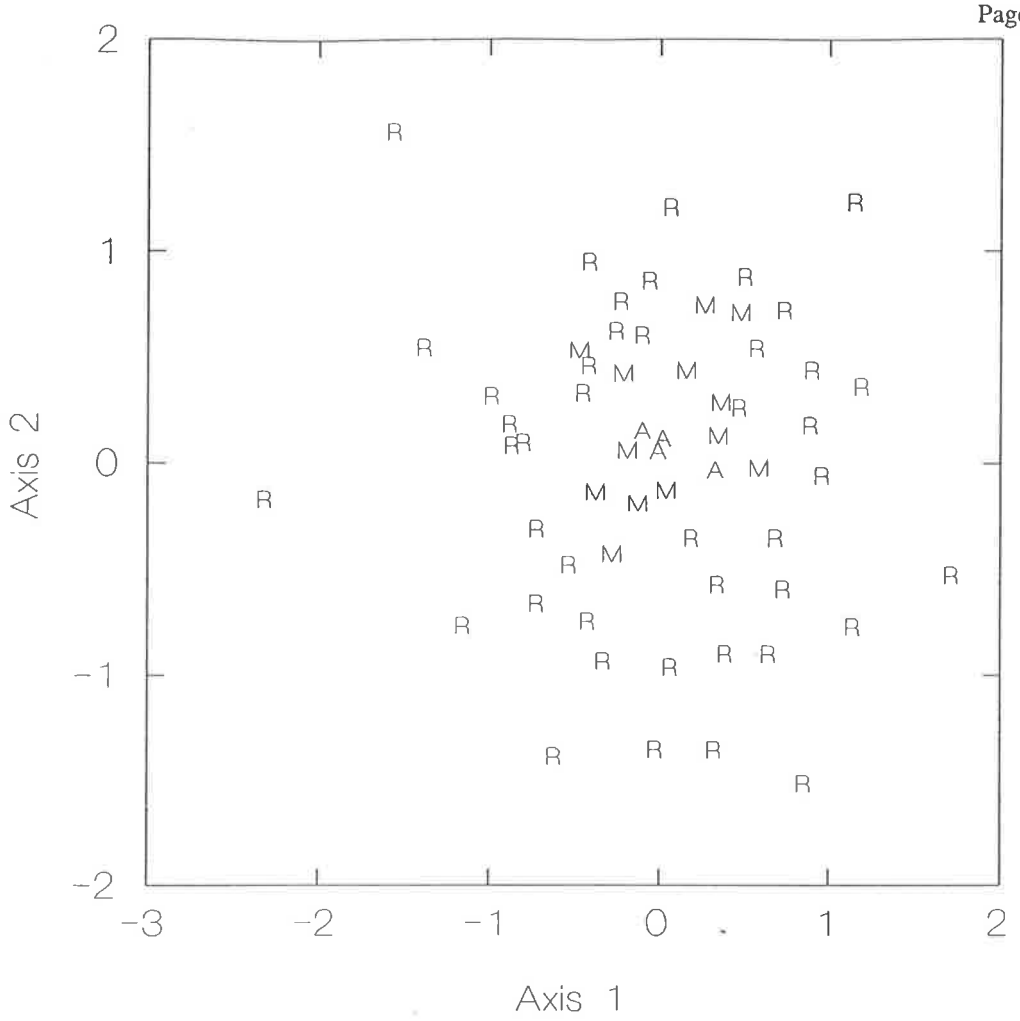


Figure 4.23 Distribution of the species on the first and second axes of the SSH ordination of species in sample data from the 99 samples (sand substrata microhabitat removed) collected between Lock 4 and Lock 2, lower River Murray, in February 1990.

Figure 4.24 SSH plot of the species in sample data from the 99 samples (sand substrata microhabitat removed) collected between Lock 4 and Lock 2, lower River Murray, in February 1990. Species are labelled according to their relative abundanee (a), 'A' = abundant, 'M' = moderate abundance, 'R' = rare (see Table 4.15), with suggested groupings highlighted (b).


2
1
0
-1
-2
-3
-2
-1
0
1
2
Axis 2
Axis 1

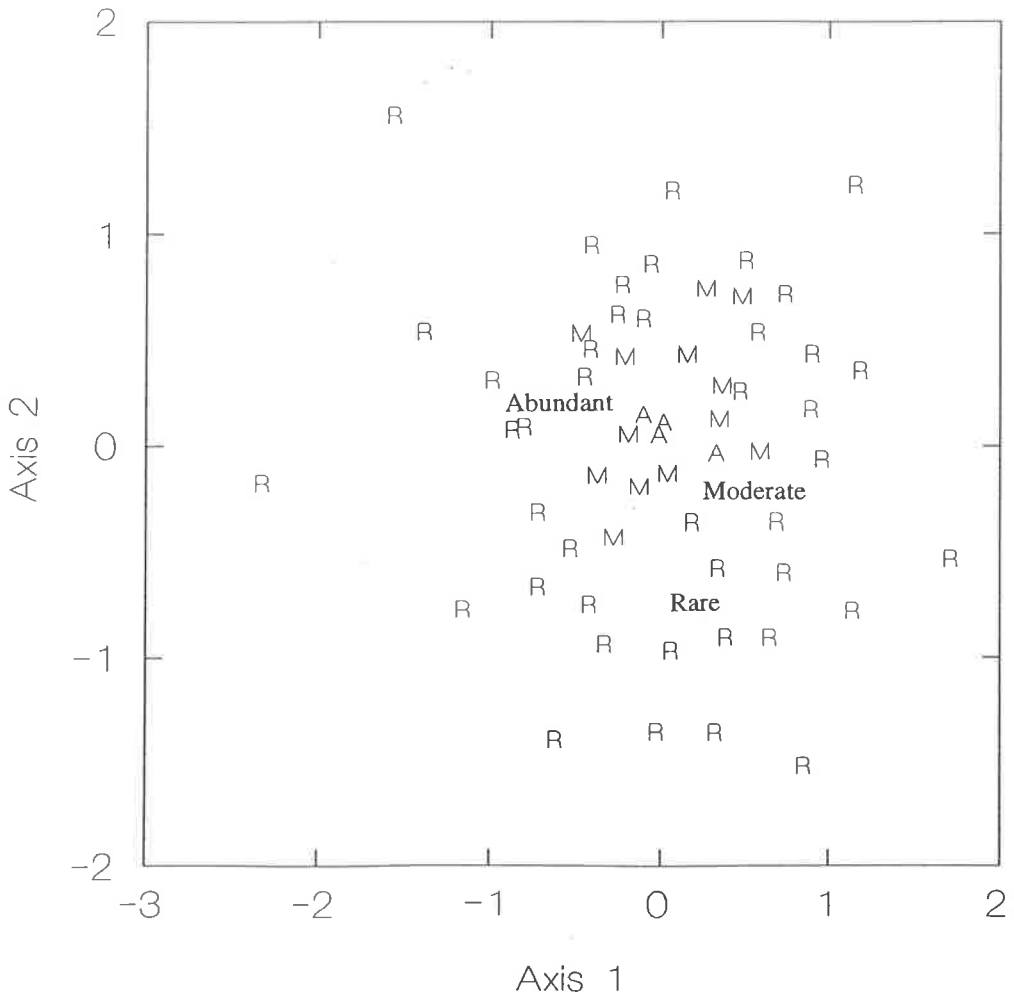
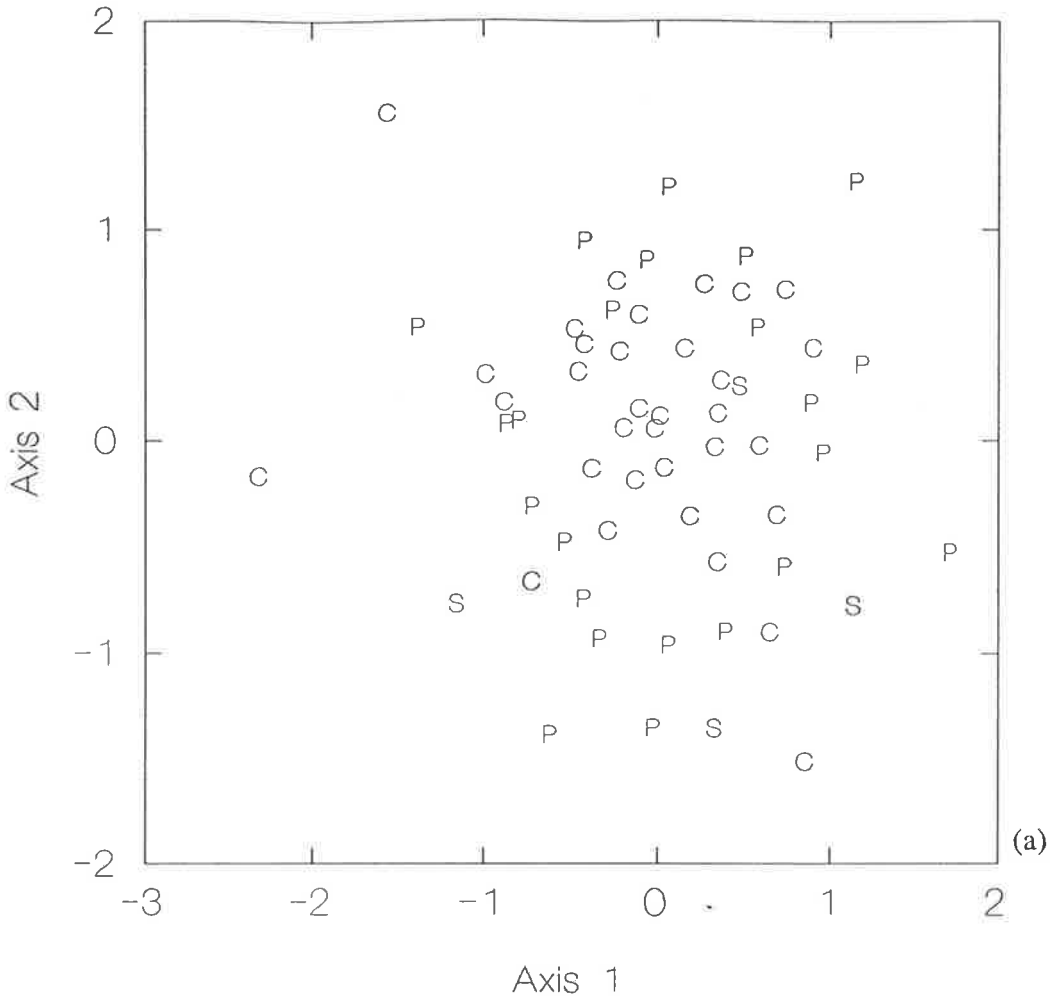

2
1
0
-1
-2
-3
-2
-1
0
1
2
Axis 2
Axis 1
Abundant
Moderate
Rare

Figure 4.25 SSH plot of the species in sample data from the 99 samples (sand substrata microhabitat removed) collected between Lock 4 and Lock 2, lower River Murray, in February 1990. Species are labelled according to their respective FFG (a), 'C' = collector, 'P' = predator, 'S' = scraper, with suggested groupings highlighted (b).


Axis 2
Axis 1
(a)

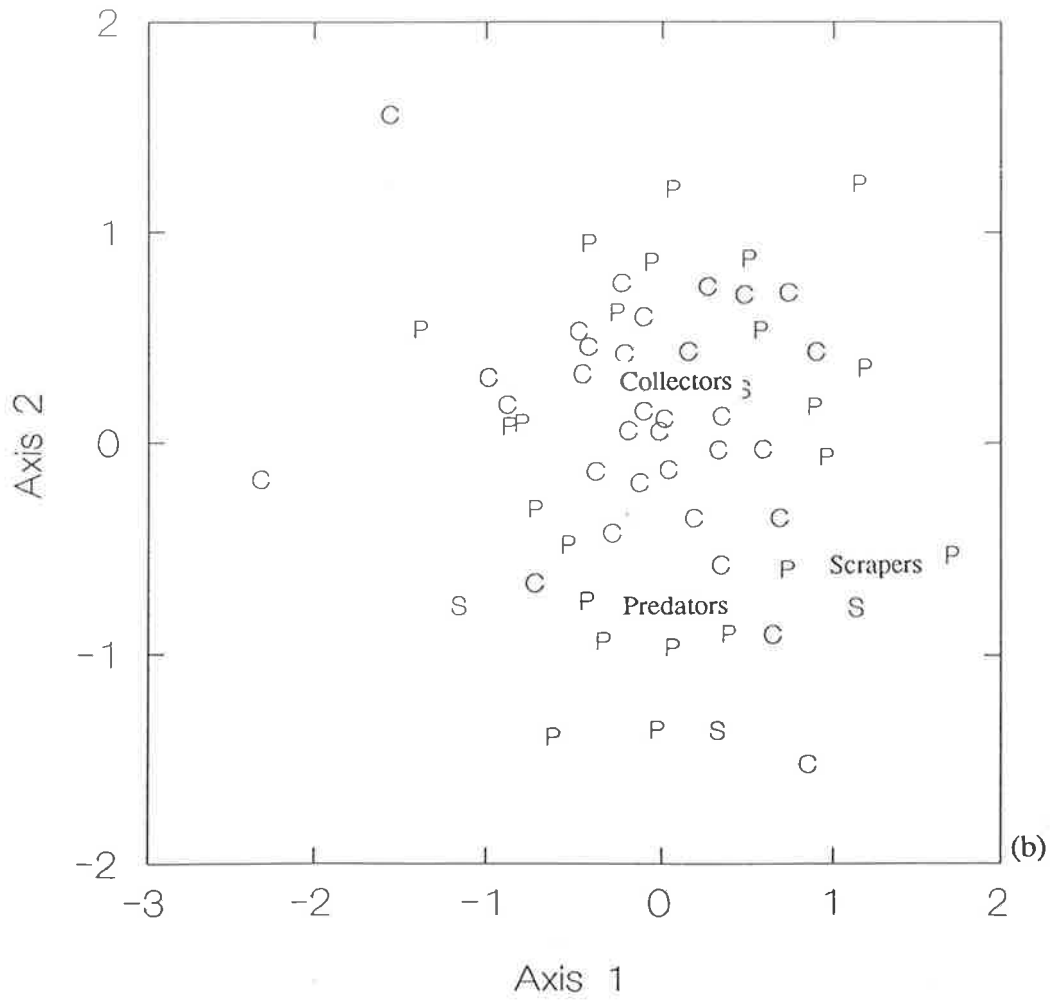
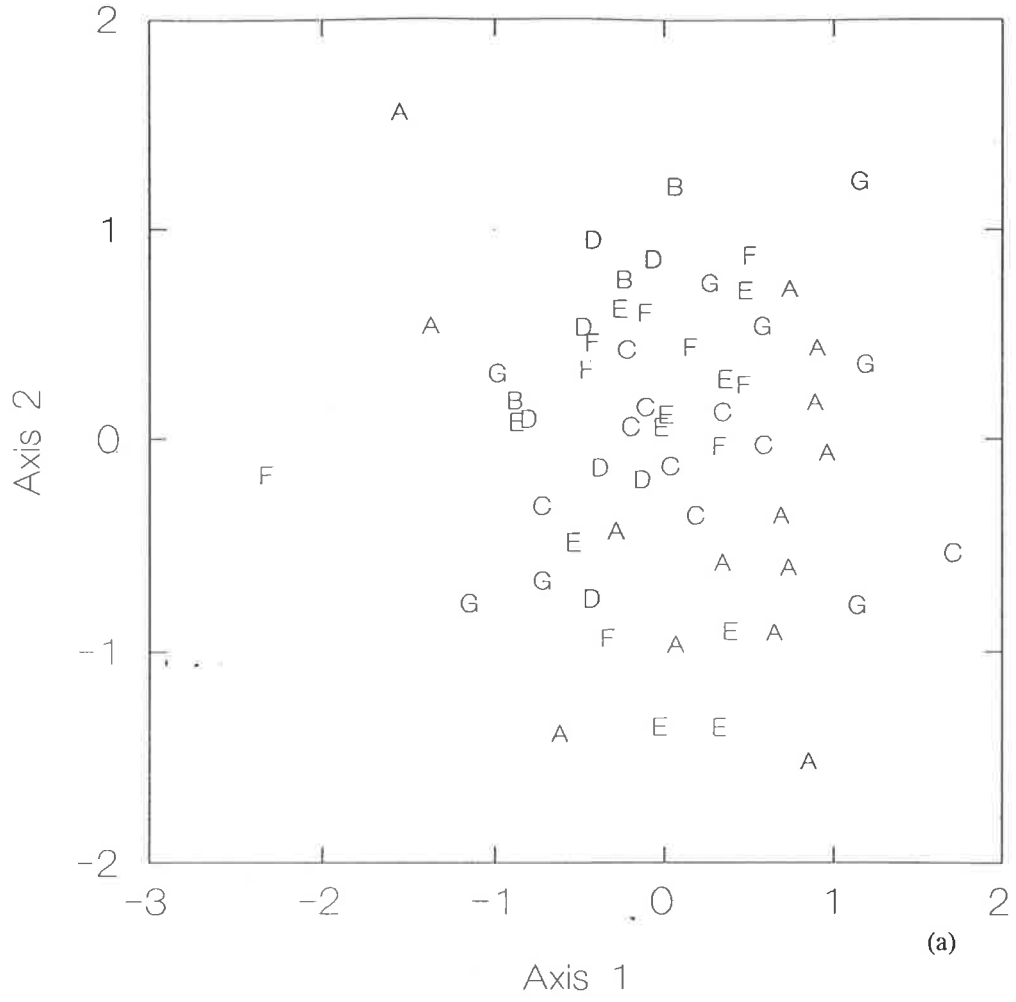
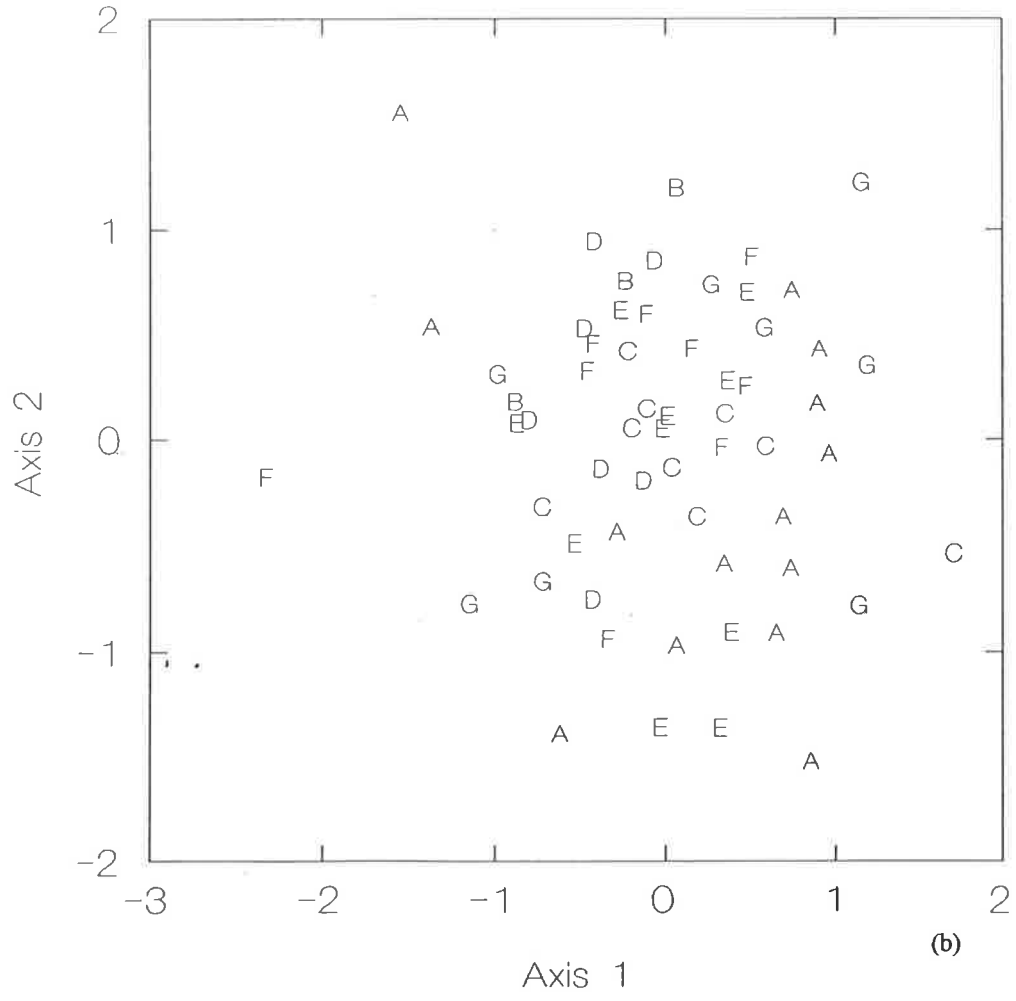

Collectors
Scrapers
Predators
Axis 2
Axis 1
(b)

Figure 4.26 SSH plot of the species in sample data from the 99 samples (sand substrata microhabitat removed) collected between Lock 4 and Lock 2, lower River Murray, in February 1990. Species groups derived from TWINSPAN of the species in sample data are superimposed; (a) 'A' = S1, 'B' = S2, 'C' = S3, 'D' = S4, 'E' = S5, 'F' = S6, 'G' = S7, with suggested groupings highlighted (b).



(a)



(b)

Longitudinal Patterns in Dominant Taxa

Longitudinal patterns were examined by plotting the mean abundance at each site for the six dominant taxa in a downstream gradient (Figure 4.27). There are no striking patterns in gradient for any of the taxa. The shrimp *C. mccullochi* appears to be somewhat more abundant in lower and upper pool sections than in the middle pools. However, Tukey's HSD suggests no difference in abundance between any of the sites (Table 4.16), which may be attributed to the high within-site variability for this taxon.

Despite being highly abundant at all sites (cf. Figure 4.27), the dominant shrimp *P. australiensis* occurred in significantly greater numbers in samples from Site 12 (YGMC) (Table 4.16). The majority of *P. australiensis* in these samples were juveniles and it is unlikely that this represents an increase in abundance in a longitudinal gradient. When all other sites are considered there are no longitudinal patterns in abundance for this taxon. *Macrobrachium australiense* appears to be more abundant in middle pool sections, Site 4 (PRMC) to Site 6 (NIMC) (cf. Figure 4.27). Tukey's test, however, suggests the main difference is between Site 4 (PRMC) and the majority of other sites (Table 4.16). No longitudinal changes in abundance are evident.

Of the chironomids, abundances of *Tanytarsus* sp. and *Cricotopus* spp. display both within-site and between-site variability (cf. Figure 4.27). There are no suggested differences in abundance between sites (Table 4.16) and no longitudinal patterns between weirs. The abundance of *Cladotanytarsus* sp. at Site 6 (NIMC) is significantly greater than at all other sites (Table 4.16; Figure 4.27). This, however, is likely to be related to local factors and does not represent any longitudinal changes in distribution.

None of the taxa dominating the assemblages collected in this study display longitudinal patterns in their abundance. The between and within-site variability for these taxa is high, suggesting their abundance possibly reflects conditions at a local scale rather than any strong environmental gradient.

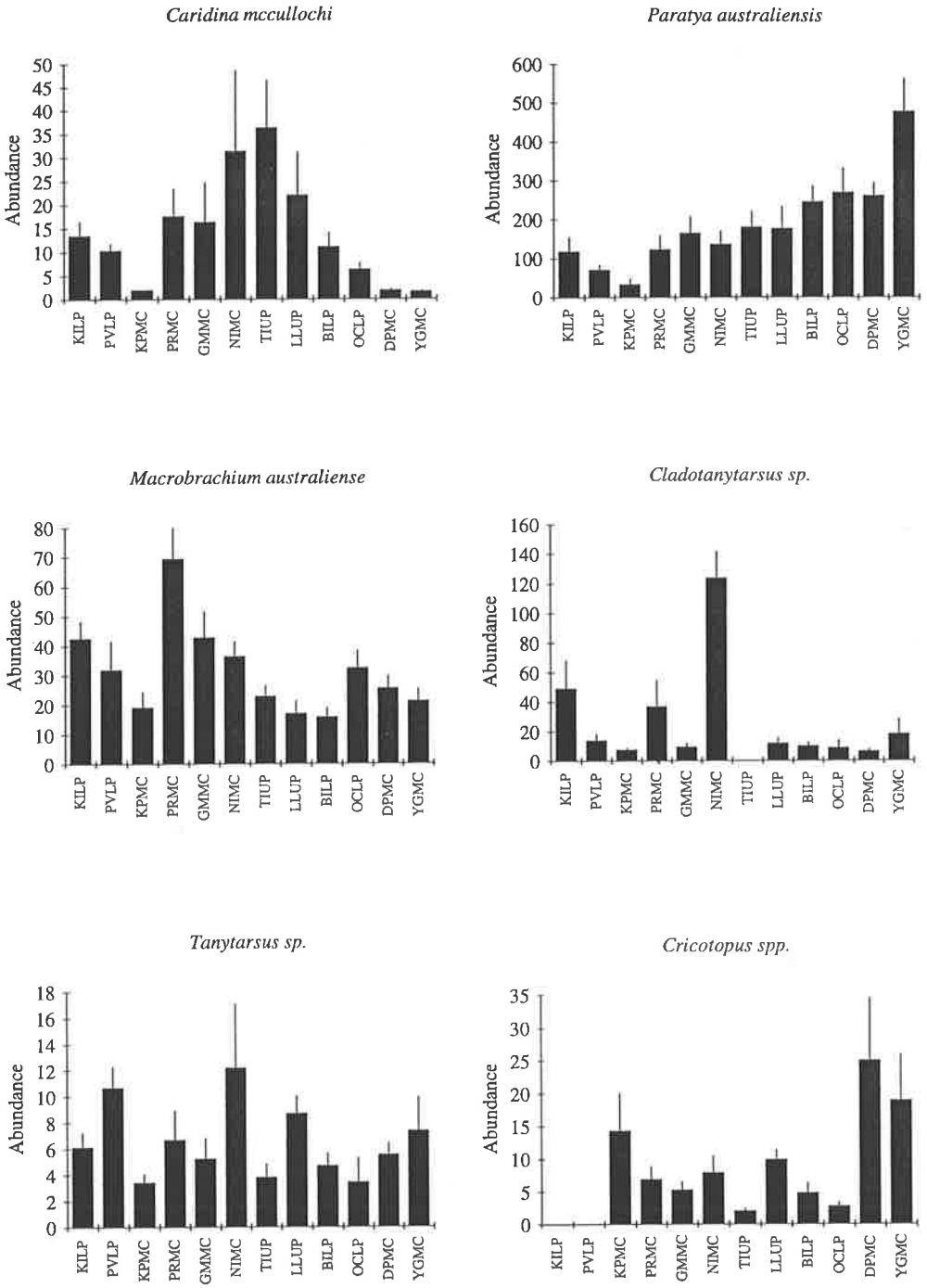


Figure 4.27 Mean abundance (SE) for each site of the six dominant taxa collected from the lower Murray, between Lock 4 and Lock 2, in February 1990. Abundances are plotted for each site downstream from KILP to YGMC.

Table 4.16 Results of Tukey HSD multiple comparisons between sites for the six most abundant taxa from the lower River Murray, February 1990. Lines join sites between which there are no significant differences.

Taxa	Tukey's HSD											
Paratya australiensis	12	10	11	1	2	5	6	7	8	9	3	4
Caridina mccullochi	1	2	3	4	5	6	7	8	9	10	11	12
Macrobrachium australiense	4	1	6	2	3	5	7	8	9	10	11	12
Cladotanytarsus sp.	1	2	3	4	5	8	9	10	11	12	7	6
Tanytarsus sp.	1	2	3	4	5	6	7	8	9	10	11	12
Cricotopus spp.	1	2	3	4	5	6	7	8	9	10	11	12

Assemblage Patterns of Rarer Taxa (Exclusion of *Paratya australiensis)*

The above examination of community composition and species assemblages for the littoral zone of the main channel in Pools 3 and 2 highlights the dominance of one species, the shrimp *Paratya australiensis*. This taxon is ubiquitous, being found in large numbers at all sites and microhabitats (cf. Figure 4.22). In many multivariate analyses it is the rare taxa, rather than dominant taxa, that are excluded (e.g. Walker *et al.,* 1994). The inclusion of rare taxa in multivariate analyses apparently increases the noisiness of the data and distorts relationships between community composition and measured physico-chemical environmental variables (see Faith and Norris, 1989).

Rare taxa, however may provide important information about habitats (cf. Nilsson, 1987; Nilsson *et al.,* 1988), particularly in modified systems such regulated rivers. The inclusion of these taxa may actually reveal additional environmental gradients and thus information important for conservation goals (Faith and Norris, 1989). The same may not be the case, however, for excessively dominant taxa. In this study the extraordinary dominance of *P. australiensis* may be masking patterns in assemblage composition between pool sections and microhabitats. If *P. australiensis* is excluded and the data reanalysed, patterns may become obvious.

TWINSPAN of the 99 samples in the second dataset (samples from the sand microhabitat removed), with *P. australiensis* excluded, yielded 11 groups (A-K) at the fourth level of division. The first division weakly separated a high proportion of the middle and lower pool samples (A-G) from the majority of upper pool samples (H-I) (Figure 4.28; Table 4.17). Indicators for upper pool samples were the

chironomids *Cladotanytarsus* sp., *Tanytarsus* sp. and *Cryptochironomus* sp., the ceratopogonid *Forcipoymia* sp. and *C. mccullochi*. A combination of pool type section and microhabitat best described the TWINSPAN groupings (Table 4.17 and Table 4.18). Significant correlations occurred between TWINSPAN groups and FPOM, site salinity and sample depth (Table 4.19).

The 69 predominantly middle pool samples further separated into sample groups A, B and C, characterised by the chironomids *Polypedilum* sp., *Cladotanytarsus* sp. and *Tanytarsus* sp., and groups D to G (Figure 4.28). Sample group A, with *Bezzia* spp. as the indicator, contained no middle pool samples but three snag samples from the upper pool of Pool 3, Site 8 (LLUP). Groups B and C comprised mainly middle and lower pool samples from emergent vegetation microhabitats. The 51 samples in groups D to G could be further separated into Groups D and E, comprising a majority of samples from snag and emergent vegetation microhabitats in middle pool sections, with indicator taxa *Cricotopus* spp. Sample groups F and G comprised a mix of both middle and lower pool samples, again from snag and emergent vegetation microhabitats, and were characterised by *Parachironomus* sp. *Cladotanytarsus* sp. *Tanytarsus* sp. and *M. australiense*.

The 30 samples on the positive side of the first division (cf. Figure 4.28) contained a high proportion of samples from emergent and submerged vegetation in upper pool sections (cf. Table 4.17 and Table 4.18). The samples separated on a second division into Groups H to J and group K. Group K, with indicators *Polypedilum* sp. *Cricotopus* spp. and *Cloeon* sp., contained samples from submerged and emergent vegetation in upper and lower pools. Sample group H contained three upper pool samples from *Typha* spp, with the amphipod *Austrochiltonia australis* as the indicator.

Table 4.17 Samples according to pool type in the eleven sample groups (A-K) yielded by TWINSPAN of all samples remaining after removal of open littoral sand microhabitat samples and exclusion of *Paratya australiensis,* collected from the littoral zone of the lower River Murray in Pool 3 and Pool 2, February 1990.

Group	Sample Composition
A	Three Upper pool
B	Nine Middle pool, one Lower pool
C	One Upper pool, four Lower pool
D	One Upper pool, three Middle pool
E	Sixteen Middle pool, three Lower pool
F	One Upper pool, eight Middle pool, six Lower pool
G	Six Middle pool, seven Lower pool
H	Three Upper pool
I	Three Upper pool, seven Middle pool, six Lower pool
J	One Upper pool, one Lower pool
K	Six Upper pool, one Middle pool, two Lower pool

Table 4.18 Samples according to microhabitat in the eleven sample groups (A-K) yielded by TWINSPAN of all samples remaining after removal of open littoral sand microhabitat samples and exclusion of *Paratya australiensis,* collected from the littoral zone of the lower River Murray in Pool 3 and Pool 2, February 1990.

Group	Sample Composition
A	Three Snag
B	Five Emergent vegetation, three Silt, two Snag
C	Four Emergent vegetation, one *Vallisneria spiralis*
D	Two Emergent vegetation, two Snag
E	Eleven Emergent vegetation, eight Snag
F	Nine Emergent vegetation, six Snag
G	Seven Emergent vegetation, four Snag, two *V. spiralis*
H	Three *Typha* spp.
I	Nine *V. spiralis*, six Emergent vegetation, one Snag
J	One Snag, one Emergent vegetation
K	Three *Typha* spp., three Emergent vegetation, three *V. spiralis*

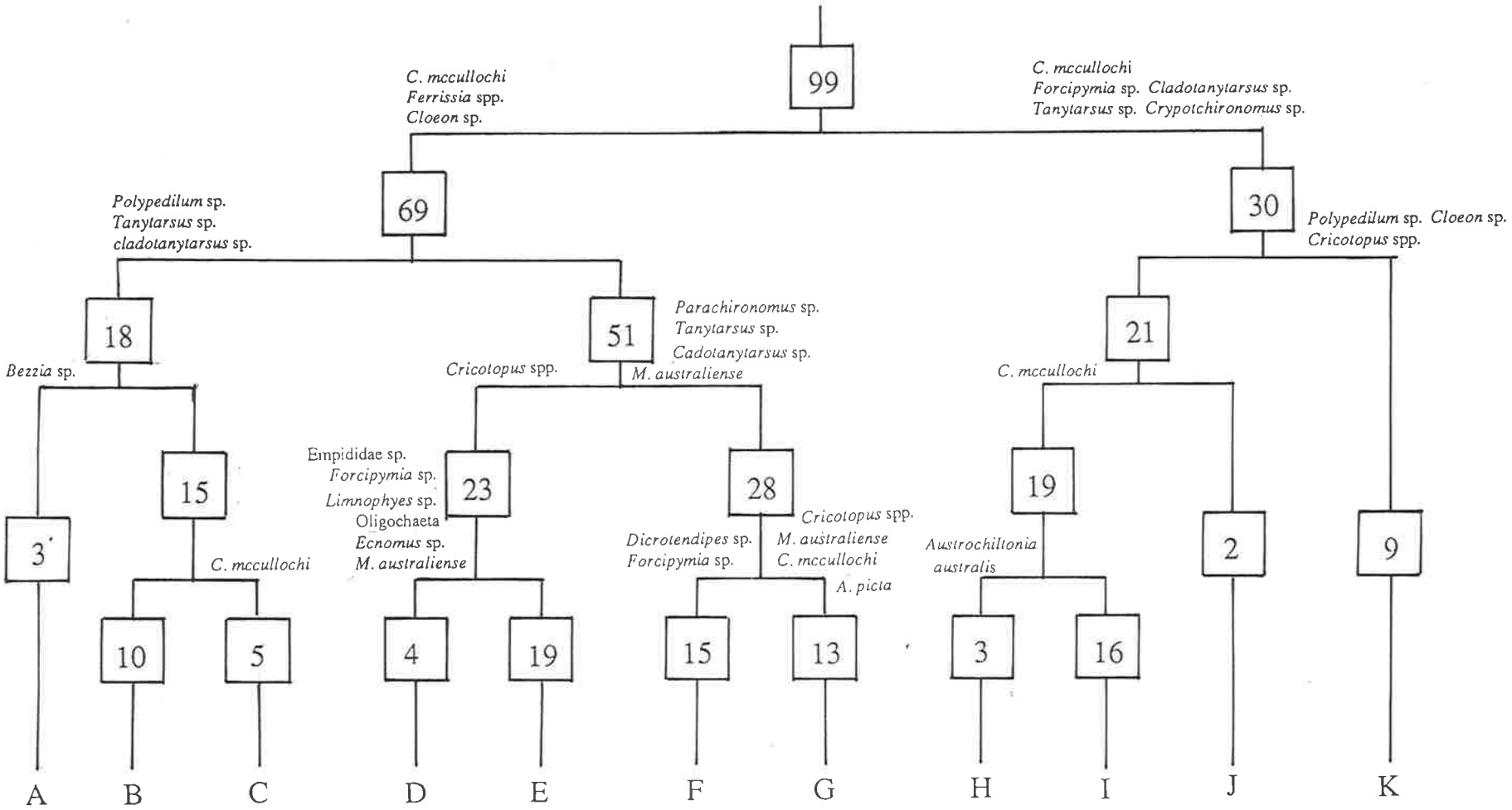


Figure 4.28 TWINSPAN dendogram of the 99 samples remaining after removal of the nine samples from the sand substrate microhabitat and the exclusion of *Paratya australiensis*, from sites between Lock 4 and Lock 2, lower River Murray, in February 1990. Indicator species are listed above the relevant divisions. Entities in sample groups A-K are listed in Table 4.17 and Table 4.18.

Table 4.19 Spearman Rank correlation coefficients (r_S) between environmental variables and the samples in the eleven groups (A-K) yielded by the TWINSPAN of all samples remaining after removal of open littoral sand microhabitat samples and exclusion of *Paratya australiensis* collected from the littoral zone of the lower River Murray in Pool 3 and Pool 2, February 1990.

Variable	r_S	Significance
CPOM	-0.067	n.s.
FPOM	-0.248	$p<0.05$
Shade	-0.112	n.s.
Salinity	-0.253	$p<0.05$
Oxygen	-0.186	n.s.
Temperature	-0.041	n.s.
Secchi Depth	-0.034	n.s.
Sample Depth	0.222	$p<0.05$

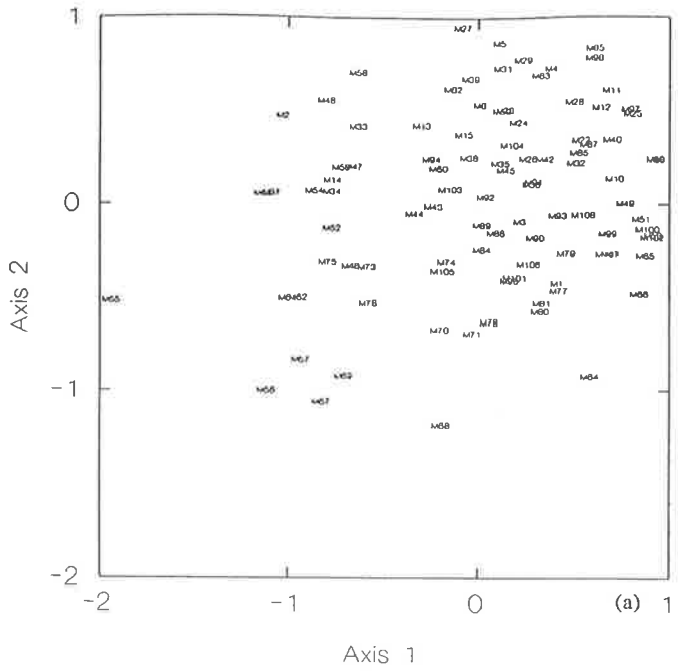
Multivariate ordination of this dataset (*Paratya australiensis* excluded) suggested a degree of assemblage difference between pool sections and microhabitats. Axis 1 of the SSH is now associated with sample depth and FPOM, Axis 2 correlates with FPOM, degree of riparian shading and site salinity. Axis 3 again correlates with FPOM, riparian shading and salinity (Table 4.20). The distribution of the samples on the first three axes of the SSH plot are depicted in Figure 4.29. The samples did not separate according to the pool from which they were collected (Figure 4.30), samples from both Pool 3 and Pool 2 were superimposed. When labelled with respect to pool section (Figure 4.31) upper pool samples had low scores on all three axes, middle pool samples had high scores, while lower pool samples had high scores on both Axis 1 and 2 and low scores on Axis 3.

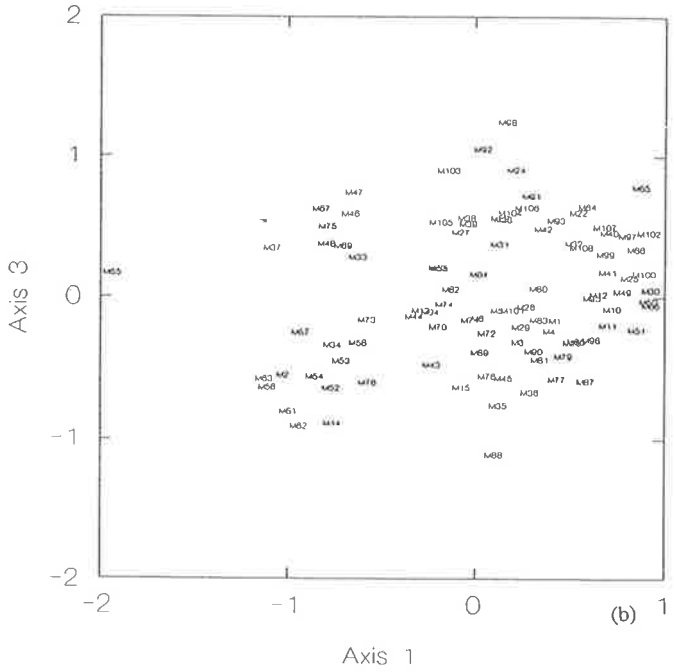
When labelled according to microhabitat (Figure 4.32) the cluster of submerged vegetation samples remained as did the gradient between vegetation microhabitats and detritus based microhabitats. With groups produced by TWINSPAN mapped onto the SSH plot the distinctiveness of the upper pool and submerged vegetation samples in TWINSPAN groups H to K becomes obvious (Figure 4.33). There is, however, a large degree of overlap of the TWINSPAN groups in the ordination space.

Table 4.20 Spearman Rank correlation coefficients between environmental variables and the sample scores on the first three axes of the SSH of faunal data from samples remaining after removal of open littoral sand microhabitat samples and exclusion of *Paratya australiensis* collected in Pool 3 and Pool 2, lower River Murray in February 1990.

CPOM	1.00										
FPOM	0.171	1.00									
Shade	0.096	0.255	1.00								
Salinity	0.072	-0.102	0.078	1.00							
Oxygen	-0.126	0.007	0.203	0.353	1.00						
Temp	-0.188	-0.060	0.263	-0.031	0.320	1.00					
Secchi	0.098	0.165	0.260	-0.184	-0.052	-0.106	1.00				
Depth	-0.001	-0.186	0.036	0.192	-0.254	-0.094	0.079	1.00			
A1	**0.126**	**0.331**	**-0.033**	**0.076**	**-0.043**	**0.031**	**-0.052**	**-0.383**	**1.00**		
A2	**0.055**	**0.288**	**0.208**	**0.078**	**0.222**	**-0.190**	**0.342**	**-0.157**	**0.178**	**1.00**	
A3	**0.069**	**0.219**	**0.358**	**0.345**	**0.007**	**0.010**	**-0.073**	**0.007**	**0.211**	**0.068**	**1.00**

Figure 4.29 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after the removal of the nine sand substrata samples and the exclusion of *Paratya australiensis*, from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990.


Axis 2
Axis 1
(a)


Axis 3
Axis 1
(b)

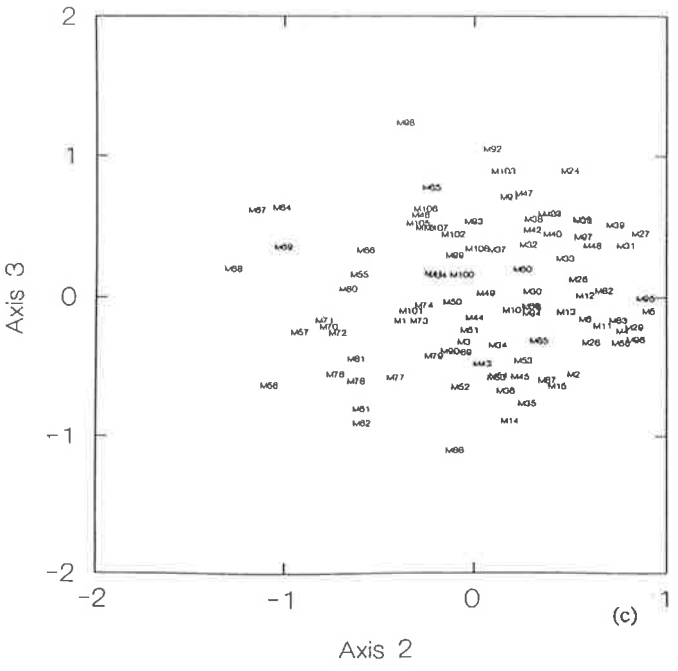
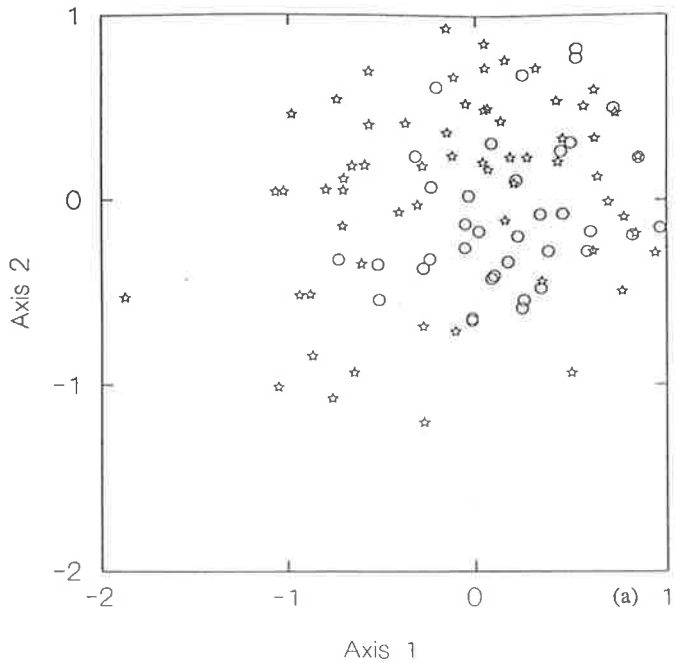
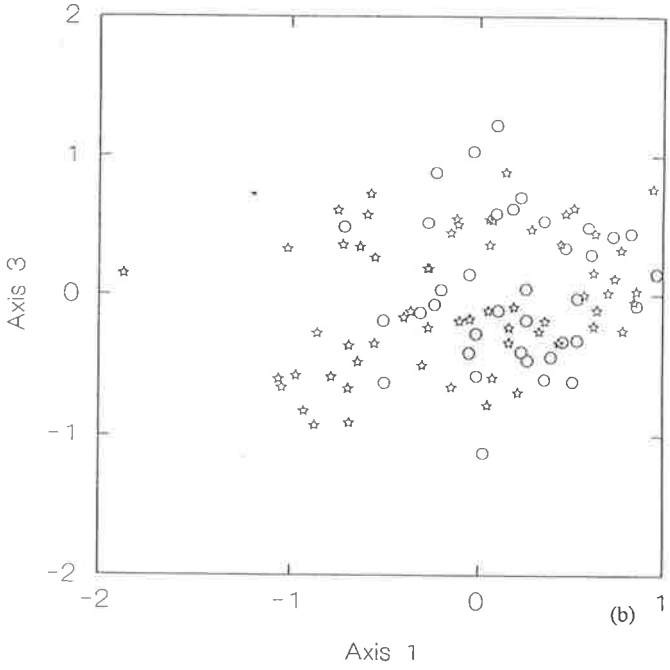

Axis 3
Axis 2
(c)

Figure 4.30 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples and the exclusion of *Paratya australiensis*, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the Lock from which they were collected where 'stars' = Lock 3 and 'circles' = Lock 2.


Axis 2
Axis 1
(a)


Axis 3
Axis 1
(b)

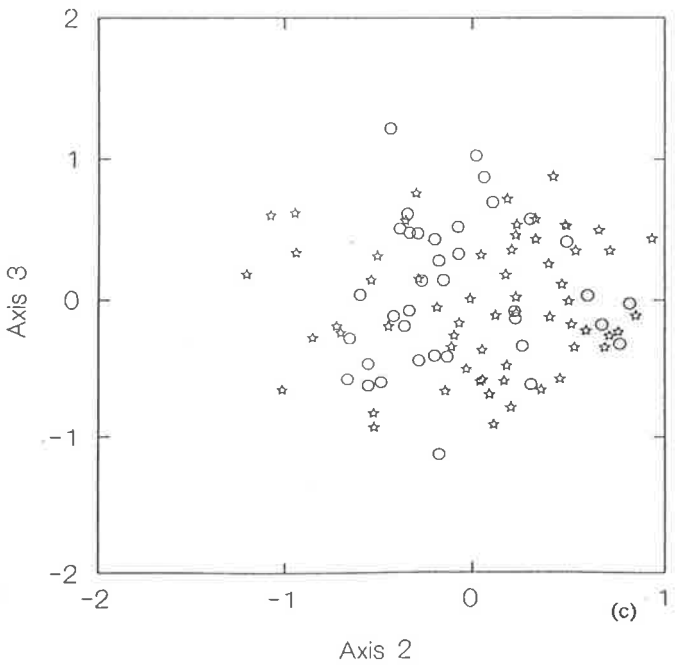
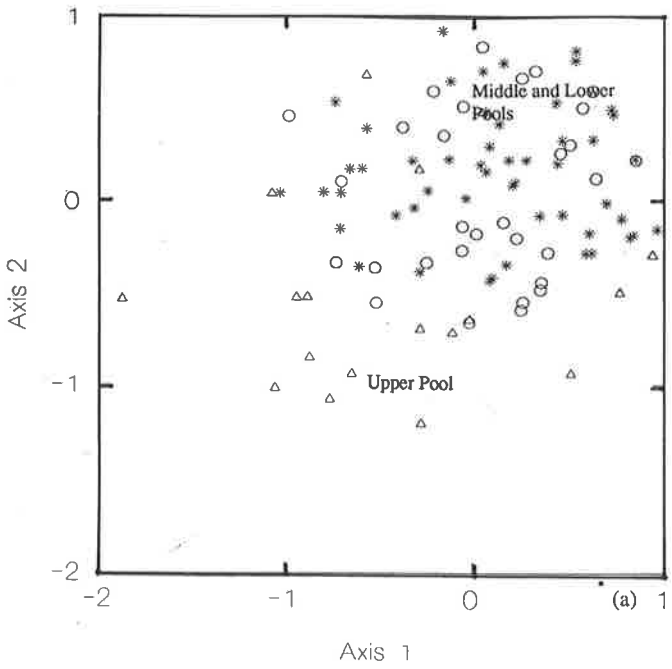
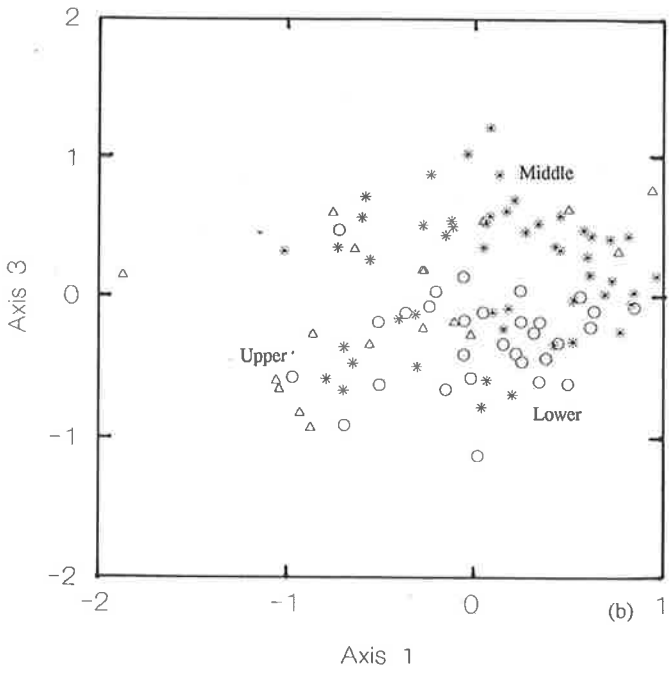

Axis 3
Axis 2
(c)

Figure 4.31 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples and the exclusion of *Paratya australiensis*, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the Pool type from which they were collected where 'triangles' = Upper pool regions, 'asterisk' = Middle pool regions and 'circle' = Lower pool regions. The overlay highlights the groupings of pool types.


Middle and Lower Pools
Upper Pool
Axis 2
Axis 1
(a)


Middle
Upper
Lower
Axis 3
Axis 1
(b)

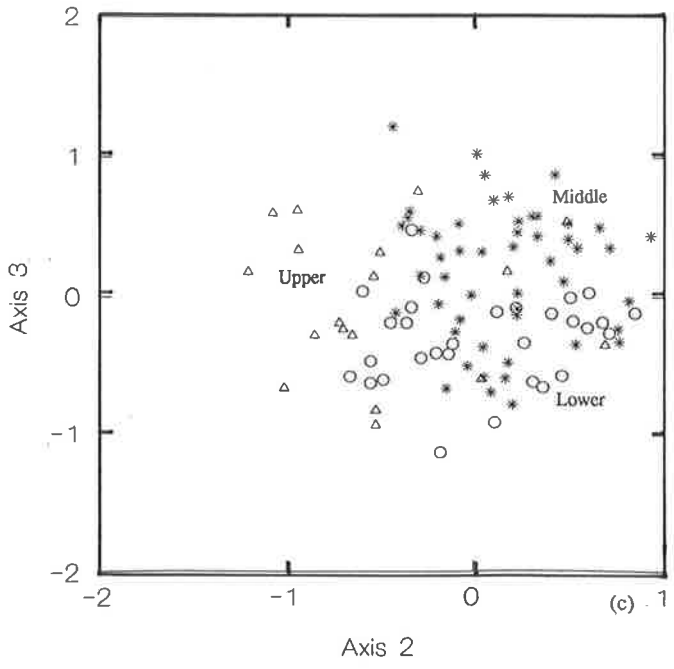
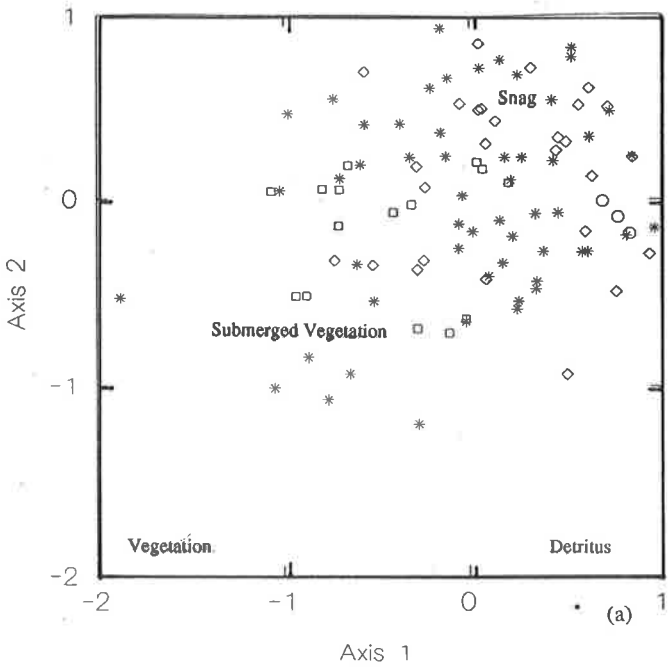
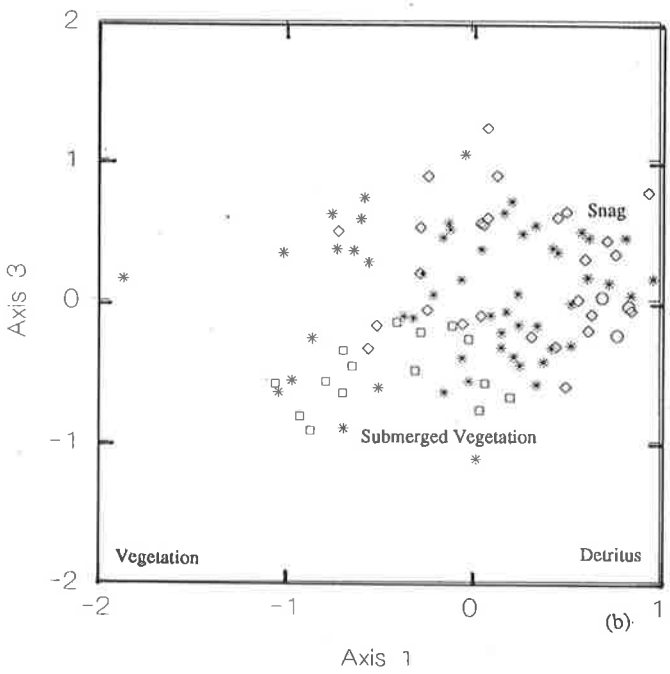

Middle
Upper
Lower
Axis 3
Axis 2
(c)

Figure 4.32 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples and the exclusion of *Paratya australiensis*, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Samples are labelled according to the microhabitat from which they were collected where 'diamond' =snag, 'square' = submerged vegetation, 'circle' = open littoral silt substrata and 'asterisk' = emergent vegetation. The overlay highlights the groupings of the various mesohabitats.


Snag
Submerged Vegetation
Vegetation
Detritus
Axis 2
Axis 1
(a)


Snag
Submerged Vegetation
Vegetation
Detritus
Axis 3
Axis 1
(b)

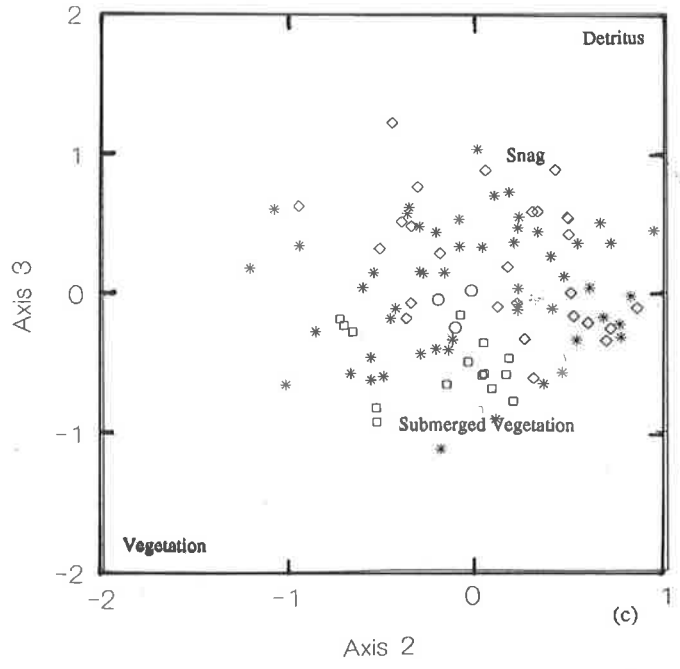
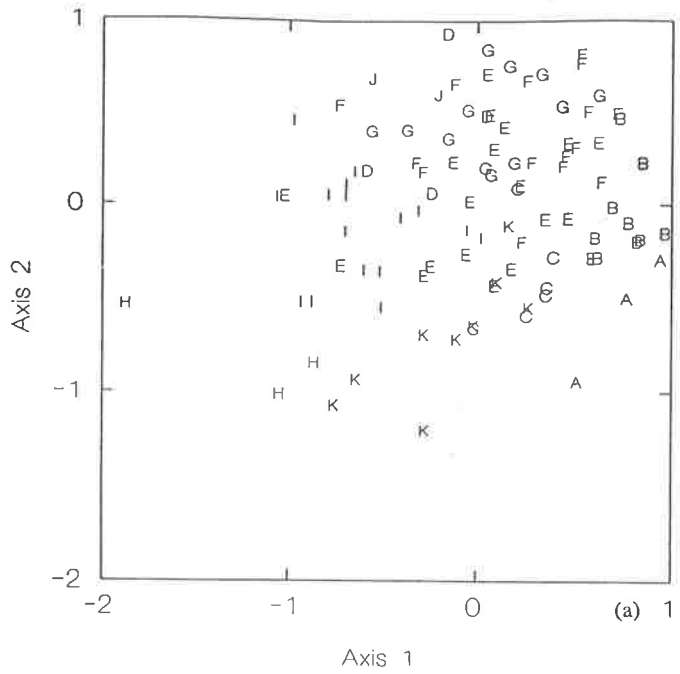
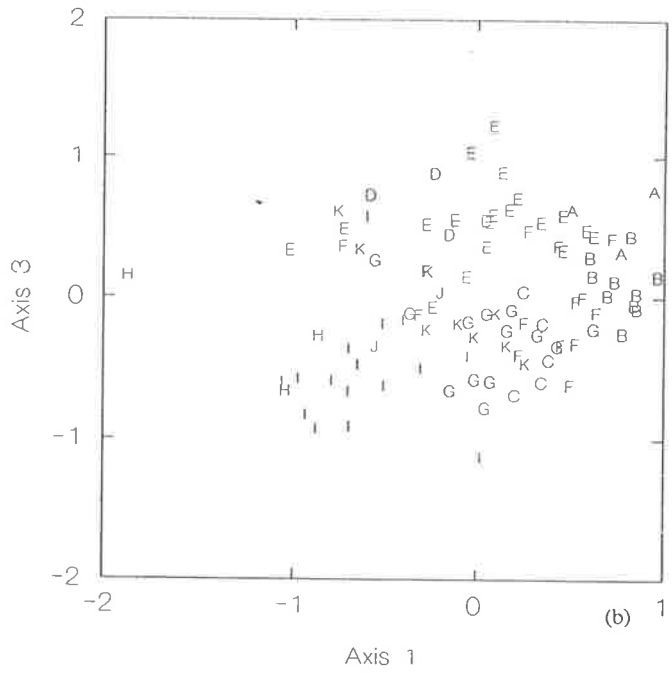
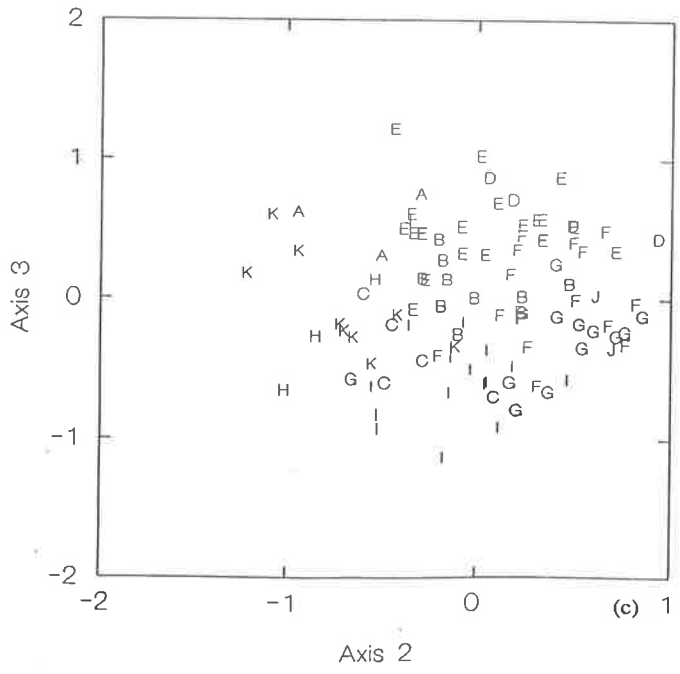

Detritus
Snag
Submerged Vegetation
Vegetation
Axis 3
Axis 2
(c)

Figure 4.33 Distribution of samples on axes (a) 1 vs 2, (b) 1 vs 3 and (c) 2 vs 3 of the SSH plot of the 99 samples remaining after removal of the nine sand substrata samples and the exclusion of *Paratya australiensis*, collected from the littoral zone of the lower River Murray between Lock 4 and Lock 2 in February 1990. Groups derived from TWINSPAN of the same data are superimposed (cf. Tables 4.17 and 4.18).


Axis 2
Axis 1
(a)


Axis 3
Axis 1
(b)


Axis 3
Axis 2
(c)

4.4 Discussion.

The main channel habitat of the lower River Murray supports a diverse array of taxa with 60 recorded in this survey. This compares with 62 taxa collected from the combined group of main channel and floodplain habitats (see Chapter 3), 104 taxa recorded from Murtho near Renmark in seasonal samples over a four year period (Bennison *et al.,* 1989) and 28 taxa collected from the main channel at Chowilla by Boulton and Lloyd (1991).

The overriding feature of the macroinvertebrate assemblage of the lower Murray is its 'unevenness'. This is caused almost entirely by the abundance of the shrimp *Paratya australiensis*, alone comprising 68 percent of the main channel macroinvertebrate fauna (cf. Appendix D). The dominance of this species has been observed in previous collections (cf. Walker, 1986; Boulton and Lloyd, 1991). Diversity indices demonstrate the uneven distribution of individuals amongst the species with low values obtained for the reciprocal Berger-Parker ($1/d$) and the Margalef (D_{Mg}) Index (cf. Magurran, 1988). The distribution of species among the eight abundance classes (cf. Figure 4.11) also highlights the large number of moderately rare taxa, with less than 50 individuals in total, and the few taxa dominating the abundance.

Although not as strong as observed in main channel habitats of Pools 3 and 2, an uneven distribution of individuals amongst taxa was also observed across all floodplain habitats on the lower Murray (Chapter 3). As discussed in Chapter 3, uneven assemblages appear to be a feature of other regulated rivers (cf. Rader and Ward, 1988; Munn and Brusven, 1991).

Despite the differing geomorphology of the two pools, Pool 3 lying within the Valley Section of the lower river and Pool 2 within the Gorge Section (cf. Figure 4.5), there were no detectable assemblage differences. This suggests that at least while the river is within its banks the extent of surrounding floodplain development has minimal influence on channel invertebrate assemblage composition. Differences, however, did occur in assemblage composition between pool sections and microhabitats.

Lower pools were generally depauperate in taxa compared with other sections while upper pool sites contained the most taxa. Given the apparent importance of microhabitat complexity for assemblage composition outlined in Chapter 3, the distribution of microhabitats in each pool may partly explain observed assemblage

differences. At nearly all sites the two most abundant microhabitats are emergent vegetation, mostly *P. australis,* and snags; the third microhabitat varies with pool section. Upper pool sites offer a diverse array of "third" microhabitats, particularly structurally complex forms such as submerged and emergent vegetation. Thus, when all microhabitats in upper pool sites are combined to describe the pool section, upper pool assemblages are possibly distinct, owing to the large number of different microhabitats. Likewise, the nature of channel change associated with flow regulation in lower pools (cf. Thoms and Walker 1993) has enhanced the process of deposition and erosion. In lower pools there is also a diverse array of "third' microhabitats; these tend to be structurally less complex compared with upper pool sites, mostly comprising unvegetated open littoral regions. The microhabitat poor regions of the main channel are middle pools where snags and monospecific stands of *P. australis* dominate the littoral zone (cf. Walker *et al.,* 1994), and location of "third" microhabitats is difficult.

Thus, discontinuities exist in microhabitat composition between pool sections. The rare taxa, showing a preference for upper pool sites, were indicative of submerged and emergent aquatic vegetation, while the rare group preferring lower pool sites were associated with open littoral regions or the semi-aquatic sedge (*C. gymnocaulos*) growing on depositing banks. The highly abundant and dominant taxa, showing preferences for all pool sections, may be associated with the nearly unbroken monospecific stand of emergent vegetation (*P. australis*) lining the littoral zone of the lower Murray, and represented as a microhabitat at all sites.

The strong longitudinal gradient imposed on the littoral zone between the weirs is caused by changes in the amplitude of water-level fluctuations (cf. Figure 4.2). This gradient is not mirrored in abiotic factors such as temperature or oxygen saturation. Salinity tends to increase in a downstream gradient, but this is a feature of the entire length of the river (cf. Macumber, 1990) and does not occur as strong sequential changes in response to weirs. Although no discontinuities were observed for any of the abiotic physico-chemical variables measured, the pattern of increased microhabitat diversity in upper and lower pools and decreased diversity in the middle regions does create biotic or habitat discontinuities for fauna.

Gradients in food resources exist between the weirs. Thin periphytic biofilms, dominated by diatoms, characterise lower pool sections, while thick films of filamentous algae occur in upper pools. This gradient may be reflected in the FFG composition of assemblages. Collector-gatherers were the most abundant group,

with respect to number of taxa and number of individuals, in all pool sections. This was also observed for floodplain habitats discussed in Chapter 3. Only a small number of predators occurred in middle and upper pool sections, similar to observations in the main channel of the Darling River (Chapter 3). In the open waters of main channel habitats vertebrates, such as small fish, are likely to be the dominant predators at this scale. Scrapers were only recorded from upper pool sections and were essentially rare. This reflects observations in previous studies (cf. Bennison *et al.,* 1989; Boulton and Lloyd, 1991; Goonan *et al.,* 1992; Chapter 3), and for the gastropod scrapers specifically, is in contrast with historical evidence of abundances in the lower Murray (cf. Section 1.2.5). FFG distribution, therefore, broadly reflects trophic shifts between weirs.

Overall, however, the pattern only partly reflects the predictions of the SDC for the recovery of systems below regulatory structures (Discontinuity Distance). On the lower Murray the distance between the weirs is small and there is perhaps insufficient scope for the normal lotic processes, suggested in the SDC, to be reset. Hauer *et al.* (1989) found the distributional pattern of trichopteran larvae, in both richness and abundance, recovered 60-80 km downstream of dams on the Gunnison River, Colorado. On the lower Murray the length of Pool 3 is 85 km, while that of Pool 2 is 69 km. Thus, the distance between sequential weirs may be insufficient for the downstream effects of one weir to be countered.

Despite the water level gradient imposed by the weirs, the invertebrate taxa appear to be responding more to local conditions at each site than any longitudinal gradient. These local conditions obviously include the microhabitat composition of the site and pool section, as well as the influence of water level changes. This, however, only provides the outcome of impacts associated with regulation on the invertebrate assemblages presently in the river. These groups are obviously able to survive and reproduce under the prevailing level of regulation. An examination of these assemblages may not provide insights into possible reasons for the recent extinction of certain groups, including the gastropods (Chapter 1).

The results of this chapter, and Chapter 3, indicate that the lower Murray supports a diverse range of microhabitats. All those habitats containing gastropods in the Cooper Creek and Diamantina River, Lake Eyre Basin, (Sheldon, unpublished data) also occur in the regulated lower Murray. Thus, physical habitat modification is unlikely to be a factor in the general gastropod decline. To elucidate how specific changes associated with flow regulation may impact fauna, Chapters 5 and 6 explore aspects of the ecology of the large prosobranch gastropods, *Thiara balonnensis* and *Notopala* spp., once abundant in the lower Murray, and demonstrate how flow regulation has contributed to their population decline.

Chapter 5

Impacts of Regulation: Erratic Water-Level Fluctuations and Gastropod Mobility

5.1 INTRODUCTION

The littoral zone of many regulated rivers is affected by artificial water-level fluctuations. These are caused by pulsed releases of water from storages, for uses in hydro-power generation or irrigation (Chapter 2). These fluctuations differ from natural water-level changes in the rate at which they rise and fall, their amplitude, timing and duration (Petts, 1984; Bayley, 1991). If the rate at which the water-level rises or falls increases, littoral fauna may be adversely affected through stranding or habitat modification. The ability of stranded fauna to survive sudden fluctuations will depend on the length of the exposure, the season and the physiology and behaviour of the relevant taxa (e.g. Corrarino and Brusven, 1983).

Littoral regions exposed to periodic dewatering support lower invertebrate richness and density than corresponding unregulated areas (Hunt and Jones, 1972; Brusven *et al.,* 1974; Kaster and Jacobi, 1978; Gerich and Brusven, 1981; Brusven, 1984). Hunt and Jones (1972) found the Mollusca, Coleoptera, Hemiptera, Odonata and Ephemeroptera to be the most affected by regulation induced fluctuations in Lake Llyn Tegid (North Wales). Likewise, Fisher and LaVoy (1972) found chironomids and oligochaetes to be the only abundant taxa below a hydropower dam on the Connecticut River (USA), often constituting 98% of the total benthic biomass.

Water-level fluctuations are also a feature of the regulated lower River Murray in South Australia (cf. Walker *et al.,* 1992). In the middle and lower sections of the river water for irrigation accounts for approximately 90% of the total regulated discharge and so largely determines the pattern of flow regulation (Maheshwari *et al.,* 1993). Under regulated conditions a near-constant pool level is maintained through channel impoundment by 10 low-level weirs and regulated releases of water from large storages in headwater regions (cf. Chapter 1: Figure 1.3; Figure 1.4). When discharge is within channel capacity weir operations maintain a stable level in the upper pool, causing daily fluctuations in the river immediately downstream (cf. Chapter 1: Figure 1.6; Figure 1.7).

Differences in the magnitude and frequency of water level changes between the upper and lower pools on the lower Murray may explain assemblage differences in these regions (cf. Chapter 4). Some species occur predominantly in lower pools while others are more abundant upper pools. Such distributions reflect microhabitat composition, but may also be related to differences in water level fluctuations between pool sections.

The erratic artificial water-level fluctuations characteristic of the lower River Murray (Walker *et al.,* 1992; Maheshwari *et al.,* 1993) may be a factor in the decline in range and abundance of aquatic snails (cf. Chapter 1). Since weir construction (1922-1937) there have been alterations in both the magnitude and the frequency of daily water-level changes in the littoral zone (Maheshwari *et al.,* 1993). This may have had adverse impacts on both aquatic plants and less mobile fauna. Aquatic snails are slow moving compared with the more highly mobile and abundant freshwater shrimps (cf. Chapters 3 and 4), and may easily be stranded or dislodged by a sudden water-level change.

This chapter examines the nature and scale of the water-level fluctuations associated with the weirs on the lower Murray and tests the hypothesis that the disappearance of aquatic snails from this region is related to their inability to rapidly accommodate to sudden water-level falls.

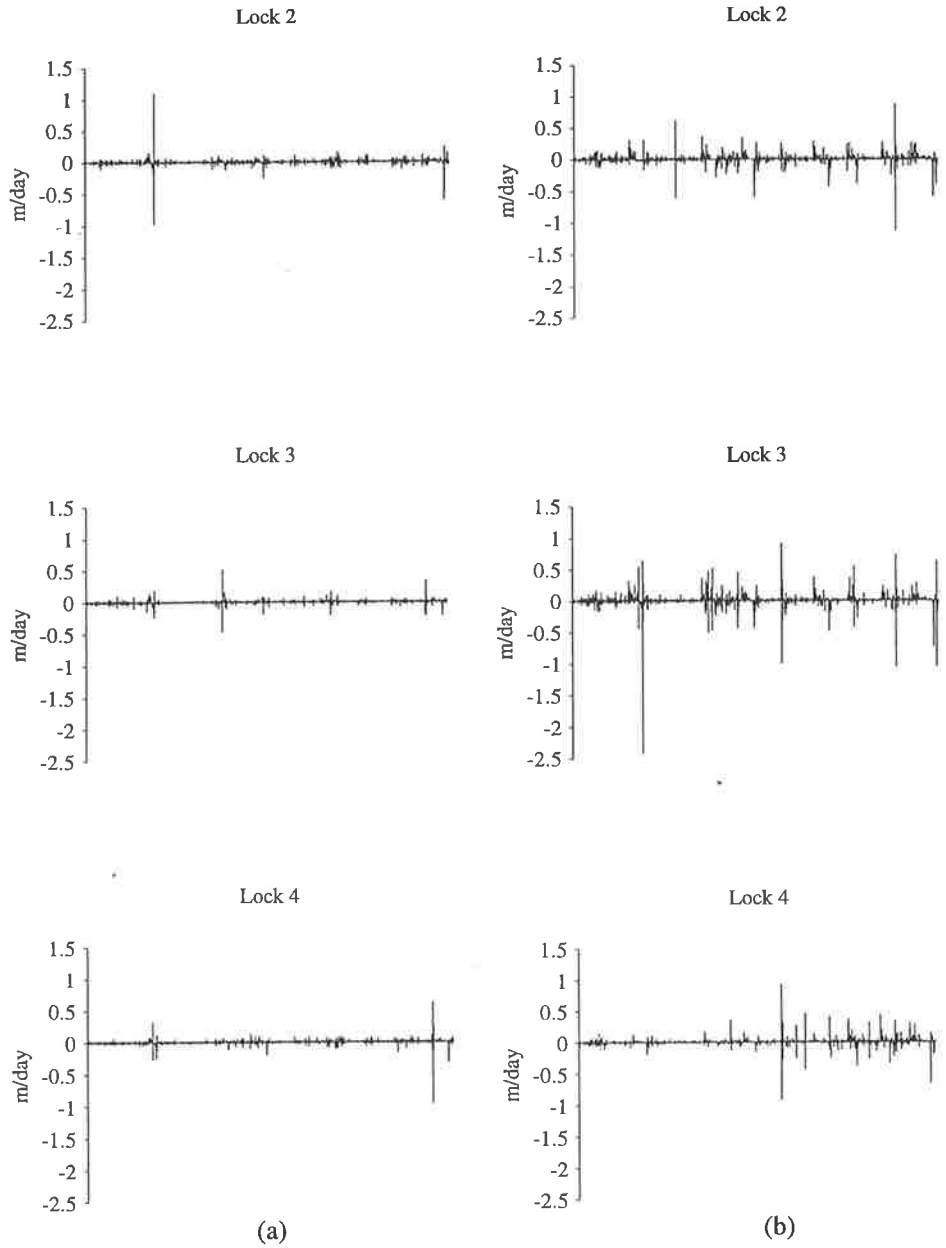


Figure 5.1 Changes in water level (m/day) in (a) upper pool sections and (b) lower pool sections of Pools 2, 3 and 4, 1980 - 1989.

5.2 THE NATURE OF ERRATIC WATER-LEVEL FLUCTUATIONS IN THE LOWER MURRAY

Each of the ten weirs on the River Murray below the Darling junction has a section of permanent concrete piers halfway across the river and a section of steel trestles that can be dismantled during floods. Flow across each weir is controlled by concrete stoplogs and Boulé panels (cf. Chapter 1: Figure 1.5).

Prior to weir construction changes in water-level exceeding 300 mm/day were rare (Maheshwari *et al.,* 1993). During the post-weir period, however, fluctuations of ±200 mm are common especially in lower pools (Figure 5.1). As can be seen in Figure 5.1 sudden water-level fluctuations are of a greater magnitude and occur more frequently in lower pools than in upper pools, with changes of ±500 mm occurring a few times a year and stage movements of greater than one metre occasionally. In association with weir operations (cf. Chapter 1), the extreme water-level changes apparent during the post-weir period may be the result of dam operations in the upper reaches of the Murray-Darling Basin, increasing the frequency of high magnitude rises and falls (Maheshwari *et al.*, 1993).

Unless otherwise stated, the data cited in the remainder of Section 5.2 are from Maheshwari, Walker and McMahon (1993). The data were originally obtained from the South Australian Engineering and Water Supply Department and were entered onto a computer database by Dr Keith Walker (University of Adelaide). An analysis is provided in Maheshwari *et al.* (1993).

Prior to weir construction average daily rates of absolute water level change (y) along the lower Murray ranged from 33-39 mm/day with an overall average of 36 mm/day. Post-weir values for the upper pools of Locks 1-6 range from 21-24 mm/day with an average of 23 mm/day compared with the lower pool sections (Locks 1-6) where changes ranged from 34-52 mm/day (Figure 5.2). Prior to weir construction average daily rates of water level rises (y_r) and falls (y_f) were generally less than 50 mm/day. The standard deviations around these values, however, are high indicating that rates often varied irregularly. After weir construction rates in the upper pools varied from 29-41 mm/day whereas in the lower pools they ranged from 40-70 mm/day.

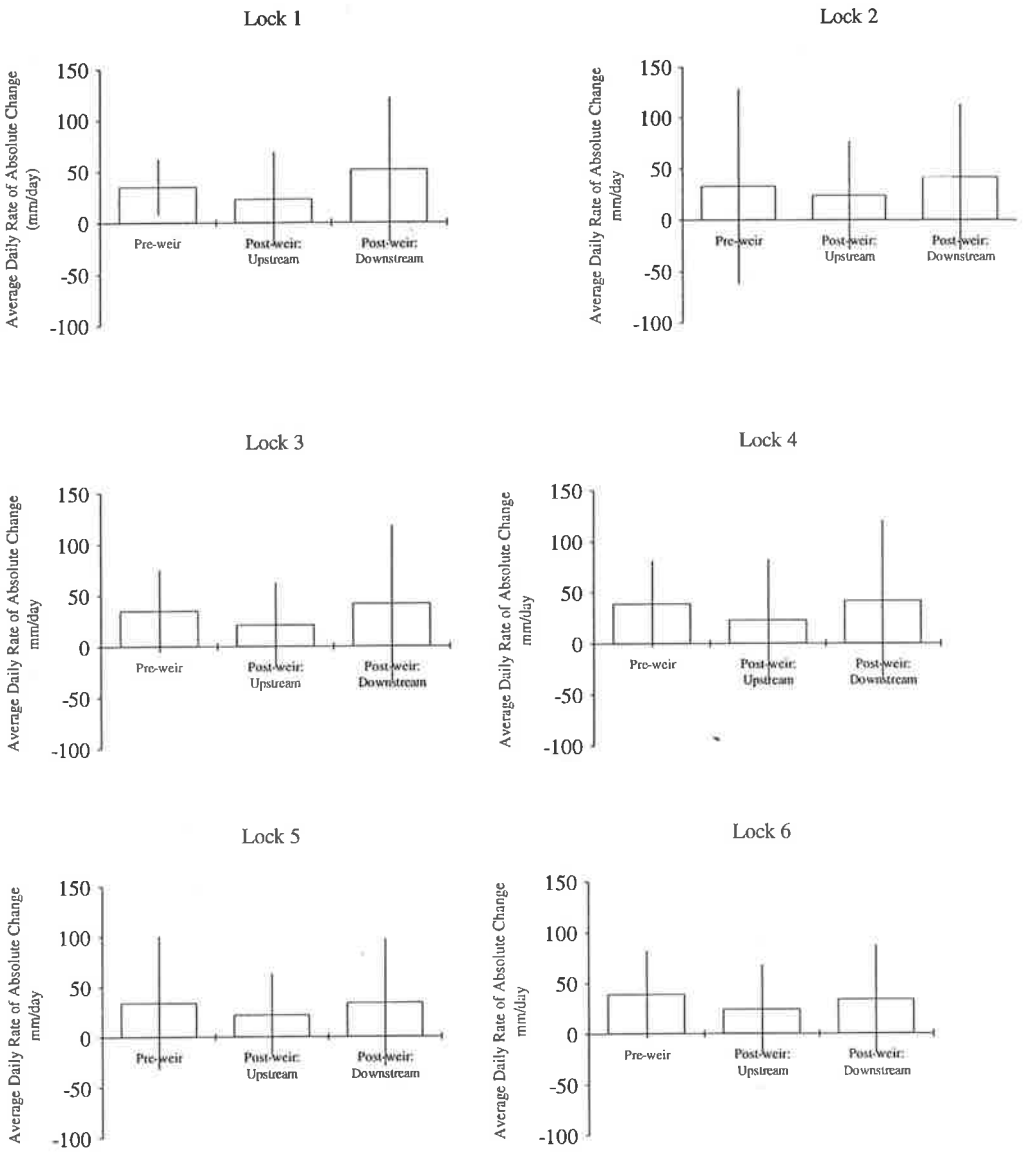
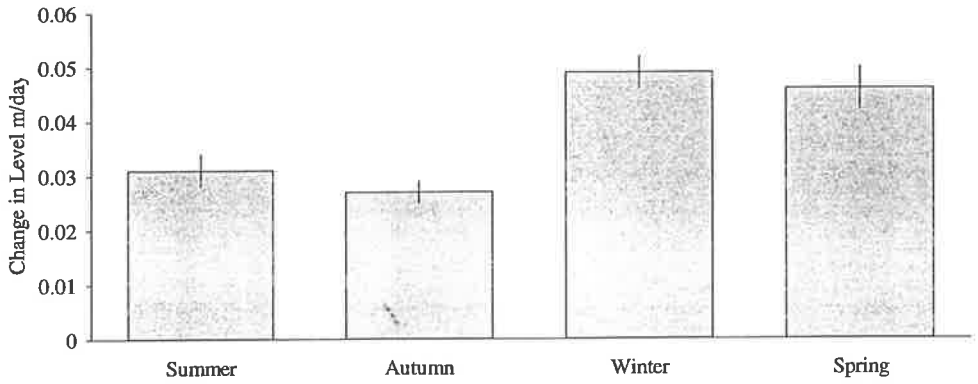


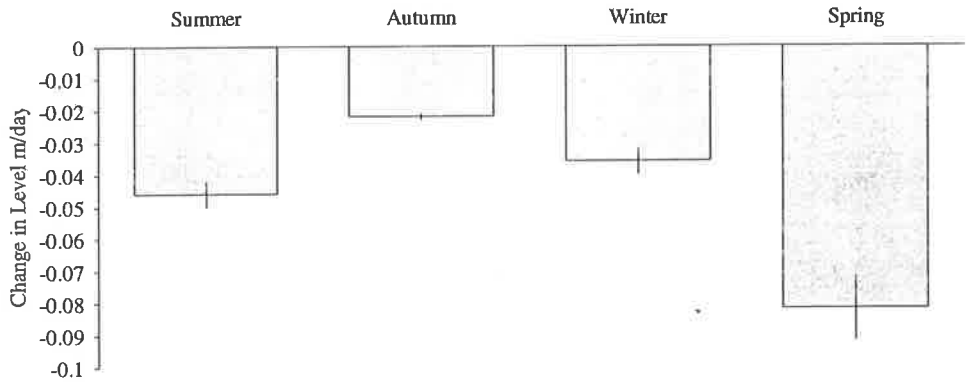
Figure 5.2 Average daily rate of water level change for Lock 1 to Lock 6, lower River Murray, South Australia. Daily stage data from the Engineering and Water Supply Department, South Australia.

Differences also exist in the seasonal distribution of water level fluctuations. Figure 5.3 depicts daily water level rises and falls as well as absolute daily changes for the lower pool of Lock 3 for each season in the period 1980 to 1989. Seasons were taken as January to March (summer), April to June (autumn), July to September (winter) and October to December (spring). The magnitude of water level rises is greater in winter and spring while the extent of water level falls is greatest during spring and summer. Yearly stage hydrographs for the same data from the lower pool of Lock 3 are given in Figure 5.4. Water level rises due to seasonal floods are predominant during late winter and early spring which may explain the greater magnitude of rises during these seasons (cf. Figure 5.3). Seasonal floods tend to recede during spring with base pool level reached and maintained by summer. The magnitude of water level changes observed in the lower pool over the summer period, particularly water level falls (Figure 5.3) may be partly due to weir operations during the irrigation season where a stable-level in the upper pool ±50 mm is maintained.

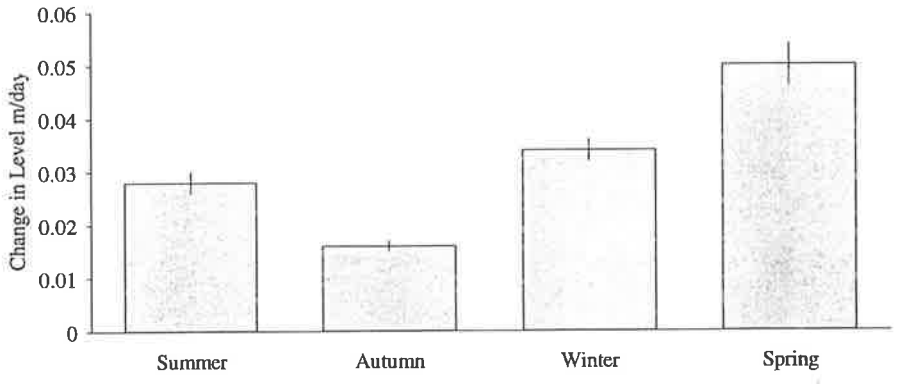
As the extent of pre-regulation water-level data is limited any apparent differences between this period and post-regulation data should be treated with caution (Maheshwari *et al.,* 1993), but it does appear that there have been marked changes in the patterns of water-level change since weir construction. Most obviously there has been an increase in the frequency of high magnitude rises and falls. The larger falls occur predominantly in spring and summer which suggests that the stranding of littoral invertebrates from sudden water level falls, due to weir operations, is most likely to occur during these times. During both seasons daily air temperatures can be approximately 25-40 °C, which will increase the mortality of stranded fauna.



(a)



(b)



(c)

Figure 5.3 Seasonal distribution of daily water level changes (m/day)in the lower River Murray below Lock 3 for the period 1980 - 1989. (a) water level rises, (b) water level falls, (c) absolute changes.

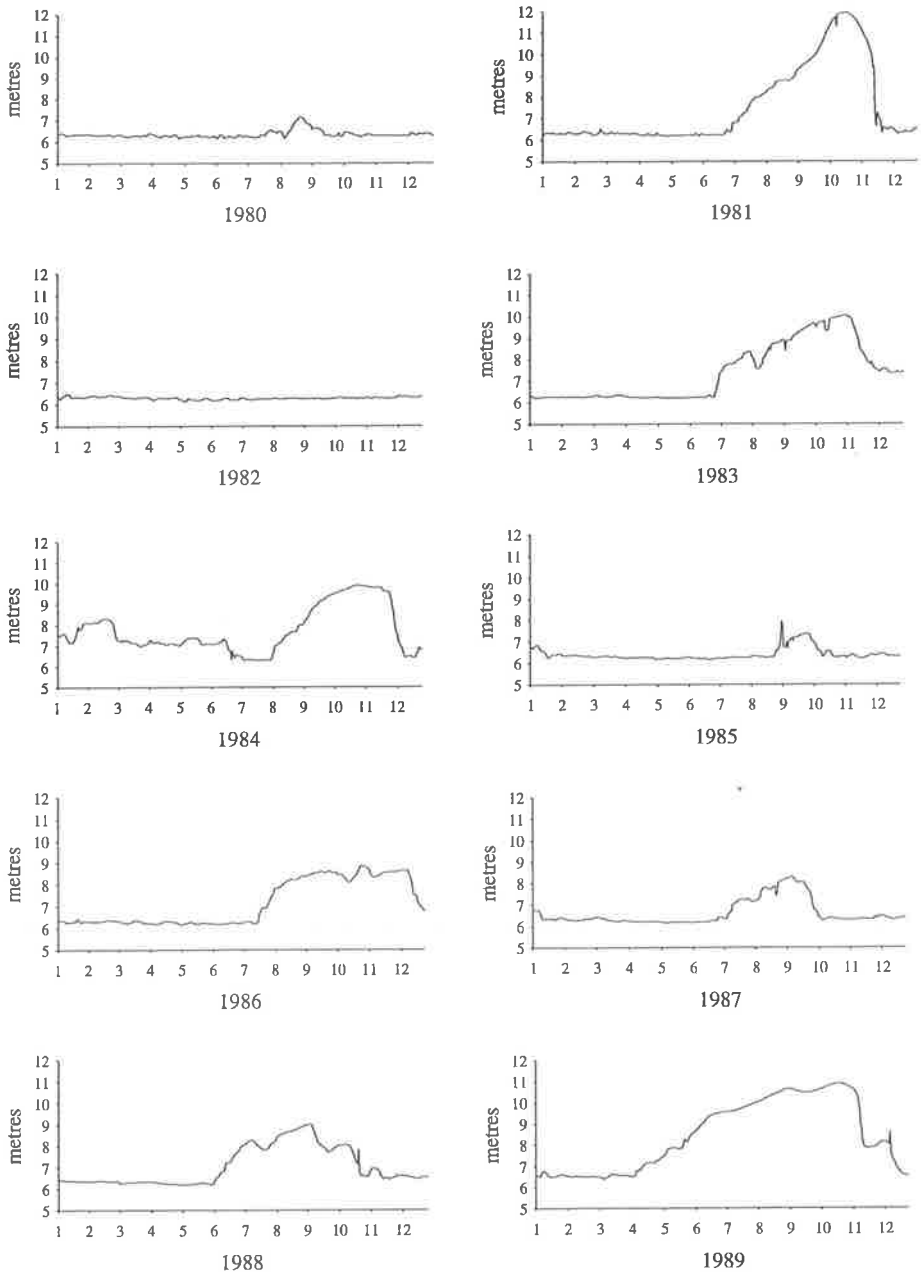


Figure 5.4 Stage hydrographs for the lower pool section of Pool 2 (below Lock 3) for 1980 to 1989.

5.3 Bank Morphology of the Littoral Zone

Changes in the magnitude and frequency of water level rises and falls will affect littoral communities. The spatial extent of the riverine littoral zone varies according to configurations in the shore terrace and the degree of water level fluctuations. A sudden water-level change of ±200 mm, common in the river immediately downstream of weirs, will expose a small area of a vertical surface but a larger area of a gently sloping surface. The littoral zone of the lower Murray comprises a mix of both gently sloping and steep vertical edges.

Bank morphology of four areas of littoral zone from the main-channel habitat of the lower Murray at Overland Corner (Figure 5.5) were mapped using a standard theodolite. Surface elevations were measured over a rectangular area of the littoral zone above and below the shoreline. Measurements were taken at 2-metre intervals along five transects eight metres apart, perpendicular to the shoreline. Figure 5.6 gives the three-dimensional plots for the four littoral areas.

The unregulated lower Murray had a compound channel with internal benches reflecting different flow events. Since flow regulation the benches have mostly eroded (Thoms and Walker, 1992) and the littoral zone of the present river is mostly composed of steep vertical surfaces. Gently sloping benches now occur most commonly in lower pool regions where the processes of erosion and deposition are still active due to regulation induced channel change (Thoms and Walker, 1993).

The physical impact of different magnitudes of water level change on the littoral zone of the regulated lower Murray can be depicted by plotting given water level changes against area exposed on a typical surface (Figure 5.7). As expected the greater the magnitude of water level change the greater the region of littoral zone exposed.

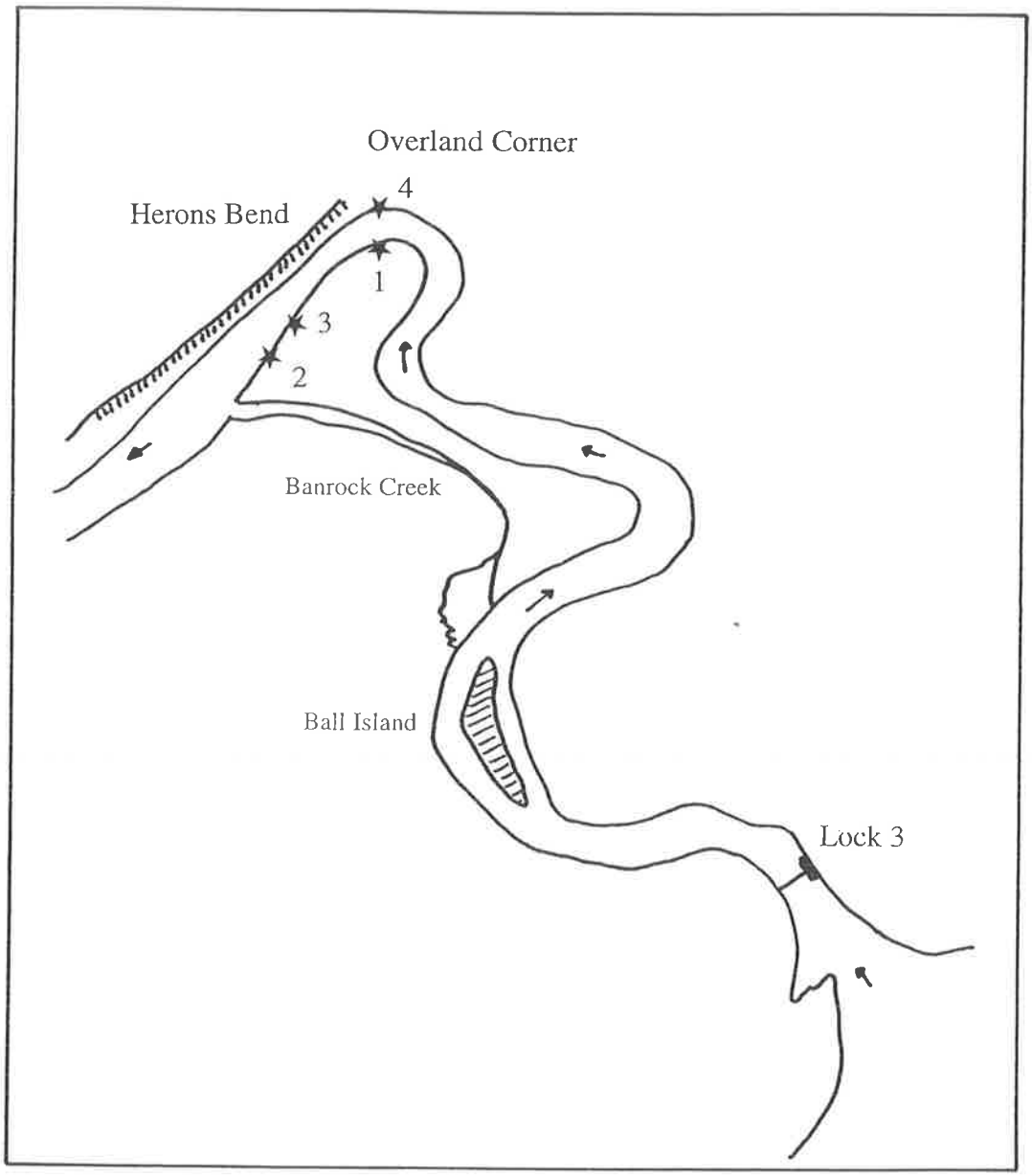


Figure 5.5 Location of sites (1-4) at Overland Corner, lower Murray, where bank morphology of the littoral zone was mapped using a standard theodolite.

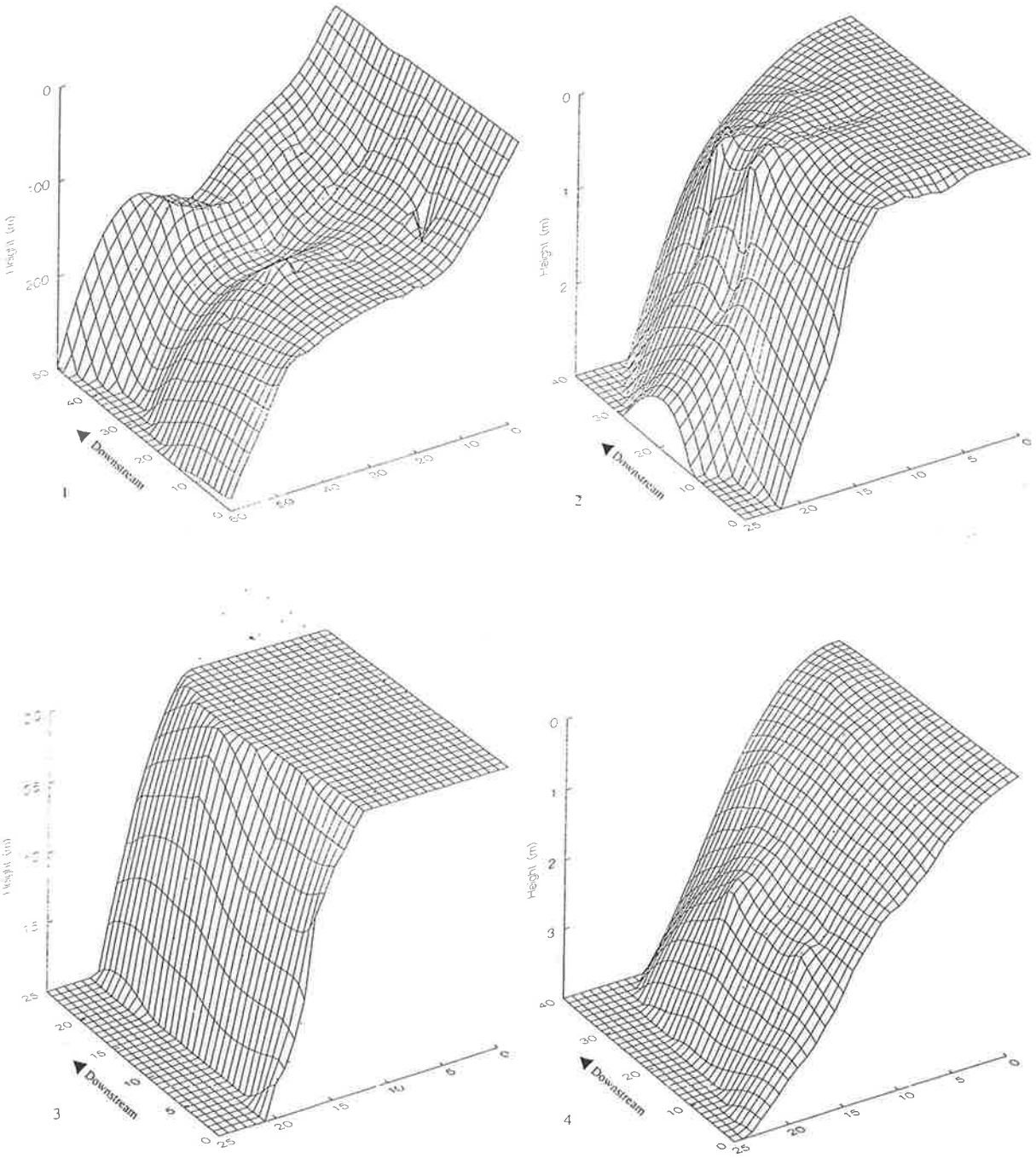


Figure 5.6 Three-dimensional plots showing bank morphology in the littoral zone of the lower Murray at Overland Corner. Bank surfaces were 'smoothed' using negative exponential interpolations (SYGRAPH v. 5.0; Wilkinson, 1990)

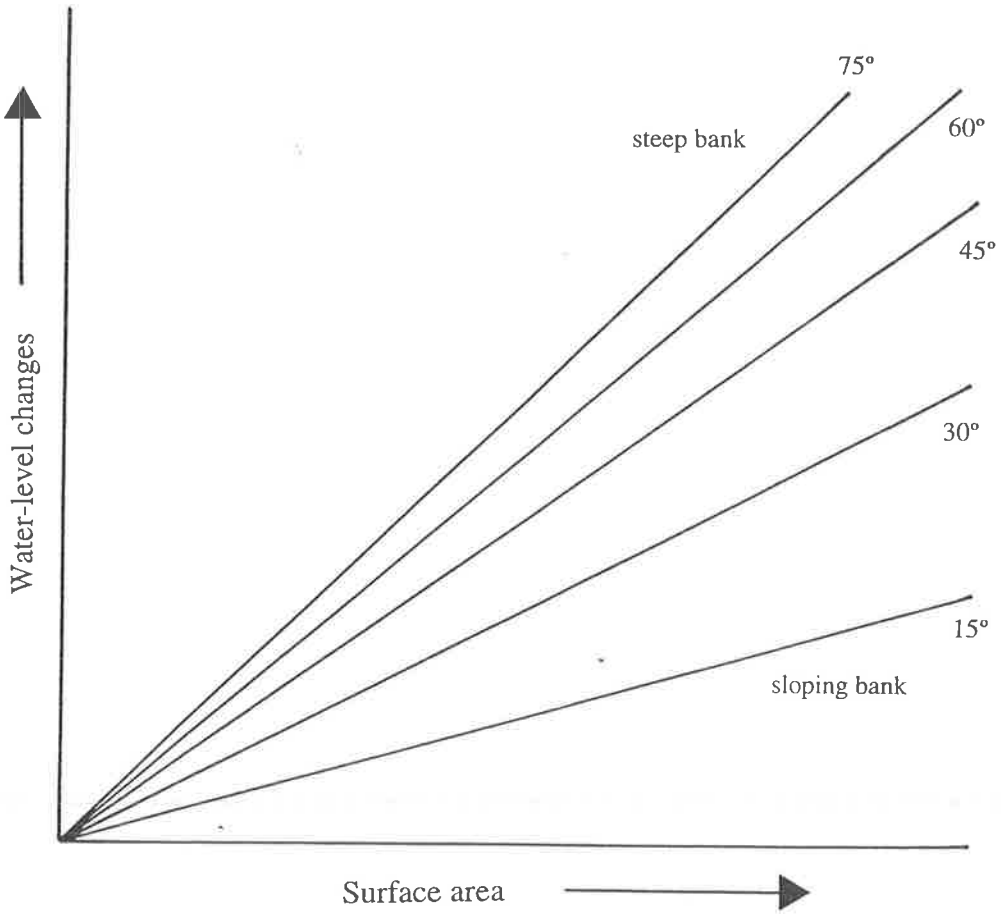


Figure 5.7 Relationship between water level changes and surface area exposed for banks with various slopes. Greater areas are exposed for small water level changes on gently sloping banks.

5.4 Erratic Water-Level Changes and Gastropod Mobility

5.4.1 Introduction

The two large prosobranch gastropods *Thiara balonnensis* and *Notopala sublineata* were used in this study as most is known of their previous abundance and distribution (Chapter 1). Early collections suggest that they inhabited the main channel of the lower Murray and are likely to have been exposed to natural water level changes. The introduced physid *Physa acuta* was used for comparison as it is one of the only gastropod taxa presently inhabiting the main channel of the lower Murray.

Field observations of the microhabitat preferences of *N. sublineata* and *T. balonnensis* (Sheldon, unpublished data) along with the cursory habitat descriptions of Cotton (1935) suggest that both species are associated with microhabitats such as emergent vegetation and snags, as well as on gently sloping depositing banks. *Physa acuta* is most commonly found amongst emergent and submerged vegetation. These microhabitats are composed of vertical and gently sloping surfaces (Section 5.3). The impact of a sudden water level change on the movement behaviour of the above three taxa was assessed over two surfaces, steep vertical and gently sloping, which reflect the surfaces common in the littoral zone of the lower River Murray.

5.4.2 Methods

Vertical Surface

Clear glass cylinders (100 cm x 15 cm) (Figure 5.8a), were employed to measure the reactions of snails exposed to a receding water-level while grazing on a vertical surface. In each tube a grazing substratum was provided by a freshly collected shoot of the emergent aquatic macrophyte *Typha sp.* The tubes were filled with pond water and aerated via a fixed airstone at the base. One snail was placed in each tube and left to acclimate for 24 hours.

Mobility was assessed at room temperature (water temperature 20-25 °C) between 0900 and 1300 hours. Individual snail positions were recorded on a 5 cm grid every five minutes for a total of 60 minutes. Each five minute period formed a *test period* and snail movement within each period was classified into one of five *reactions*:

- upwards movement
- downwards movement
- sideways (not applicable in tube experiments)
- stationary (no change in vertical position)
- float or fall

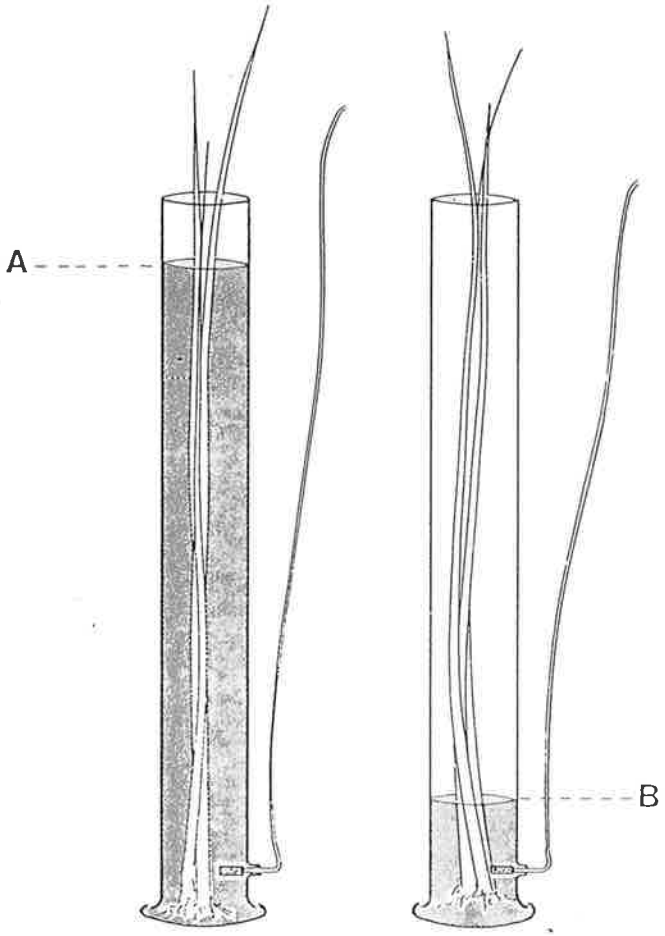
In each tube movement was initially recorded under a *stable* water-level for 60 minutes (Figure 5.8a, Position A). The water in the tube was then slowly released via the outlet at the base until the adjusted level was reached (Figure 5.8a, Position B). Movement of the water from Position A to Position B constituted the *receding* water-level. Snail movements were recorded for 60 minutes while water-levels receded, commencing as soon as the tubes began to drain.

Sloping Surface

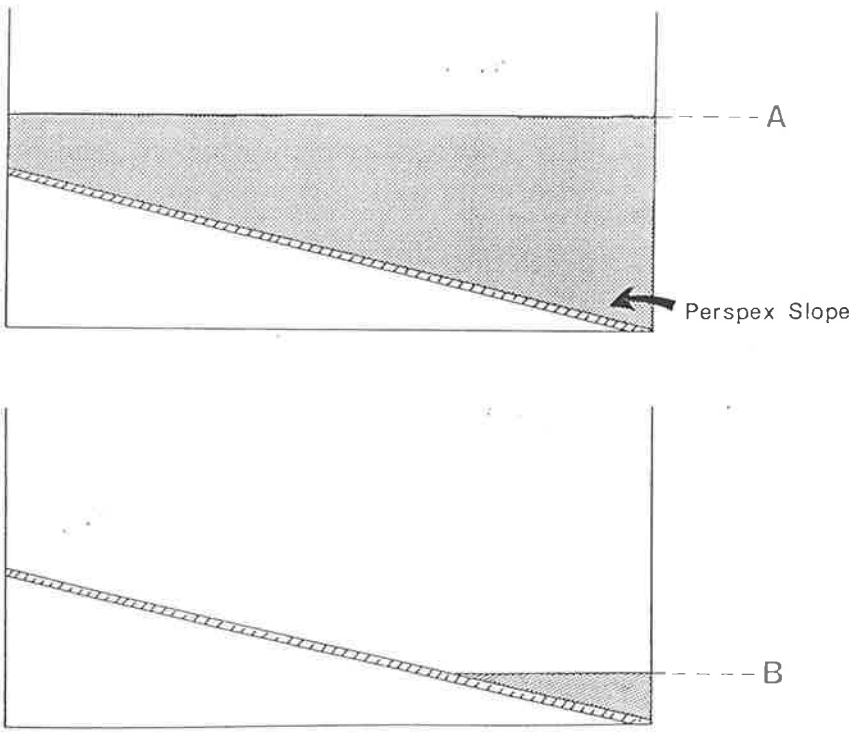
A sloping bank was created with a small glass aquarium (16 x 16 x 16 cm) in which a sheet of clear perspex was placed at 30° (Figure 5.8b). The perspex base was suspended in an outdoor pond for 48 hours, allowing a partial microbial film to develop, before being placed in the aquarium which was filled with pond water and aerated for a further 12 hours. Experiments were conducted at room temperature (water temperature 20-25 °C) between 0900 and 1400 hours. Snails were placed on the perspex slope and allowed to acclimate for an initial period of one hour, after which their position was recorded every 7.5 minutes using a 35 mm camera with a built-in motordrive and automatic timer suspended above the aquarium. In this way movements could be recorded without disturbance.

As in Method 1, each 7.5 minute period was regarded as a *test period* and snail movement within this period classified into the five *reactions* described above.

Snail movements were initially recorded at a *stable* water-level for four hours (Figure 5.8b, Position A). After this the water was siphoned from the aquarium until the adjusted level was reached (Figure 5.8b, position B), this constituted the *receding* water-level treatment. Snail movements were recorded either for a further four hours or until the snail retreated to the water remaining in the base of the aquarium and sealed its operculum.



(a)



(b)

Figure 5.8 Apparatus used to measure the responses of aquatic gastropods to sudden water level changes (a) on a vertical surface and (b) on a sloping surface.

Analysis

Data collected were the frequency of each behaviour type exhibited by individual snails under the two water-level treatments (stable and receding) over a set number of behaviour periods.

Non-parametric two-way analyses of variance (extended Kruskal-Wallis tests; Zar, 1984: page 219) were used to test for an interaction between water-level treatment and reaction. If water-level treatment modifies snail reactions then a significant interaction would be expected. Non-parametric multiple comparisons (Zar, 1984: page 199) were employed to determine which reactions occurred at different frequencies.

To determine if receding water-levels caused an increase in the frequency with which snails moved downwards observations for all individuals in a species were pooled, and the frequency of upwards and downwards movement for both treatments arranged in a 2-way contingency table. The hypothesis that there was no difference in the frequency of upwards and downwards movement between the two treatments was examined using Fisher's Exact Test (SYSTAT v5.0; Wilkinson, 1990).

5.4.3 Results

Only the mobility of *N. sublineata* was assessed using both methods (Table 5.1). *Physa acuta* was active only on the vertical surfaces of the glass tubes and the sides of the aquarium, making it impossible to examine its response to water-level changes on a bank slope (Sloping Surface). Likewise, *T. balonnensis* did not move freely on the sloping surface. *Notopala sublineata* moved freely both within the glass tubes and on the bank slope.

Table 5.1. Species tested using each method.

Vertical Surface	Sloping Surface
Physa acuta	*Notopala sublineata*
Thiara balonnensis	
Notopala sublineata	

As river levels are recorded only once a day it is impossible to determine rates of water-level movement from stage data for periods of less than one day. The rate of water-level change used in both methods was approximately one metre over one hour, a rate which is likely to be much faster than that experienced by littoral fauna in the lower Murray. However, if the gastropods are able to respond to changes in water-level of this magnitude then they are likely to cope with lesser changes.

Physa acuta

The pond snail *P. acuta* moved actively within the tubes for the duration of observations. Movements, in response to stable and receding water-levels, were recorded for ten individuals (Table 5.2).

Table 5.2. Frequency of behaviour types mean *(SE)*, over 60 minutes (12 test periods) for *Physa acuta* under stable (n=10) and receding (n=10) water-level treatments.

		Up	**Down**	**Stationary**
Water-level	Stable	3.66 *(0.74)*	3.33 *(0.72)*	5.0 *(1.06)*
	Receding	0 *(0)*	6.0 *(0.75)*	5.2 *(1.01)*

Significant differences existed between the frequencies of each reaction displayed by the snails ($H=11.01$, $p<0.01$). There was also a significant interaction between water-level treatment and reaction type ($H=15.22$, $p<0.001$), suggesting that the frequency of a reaction was determined by changes in water-level.

Physa acuta showed no difference in the frequency of upwards, downwards or stationary movement while water-levels were stable. The frequency of downwards movement, however, was greater when water-levels were receding. The difference in the frequency of upwards and downwards movement displayed by *P. acuta* under different water-level treatments was supported by Fisher's Exact Test on pooled data ($p<0.001$)

Thiara balonnensis

Thiara balonennsis moved slowly within the tubes during the period of observations spending a large proportion of its time stationary. Movements in response to both water-levels were recorded for eight individuals (Table 5.3).

Table 5.3. Frequency of each observed reaction type, mean *(SE)*, over 60 minutes, 12 test periods, for *Thiara balonnensis* for stable (n=8) and receding (n=8) water-level treatments.

		Up	Down	Stationary	Fall
Water Level	Stable	3.33 *(0.84)*	1.33 *(0.55)*	7.33 *(0.83)*	0 *(0)*
	Receding	3.12 *(0.61)*	0.37 *(0.18)*	6.37 *(1.47)*	1.12 *(0.42)*

Although there were differences in the observed frequencies of each reaction type ($H=35.65$, $p<0.001$), there was a non significant interaction between water-level treatment and reaction ($H=3.08$, $p>0.05$). This suggested that water-level treatment did not change the reactions of *T. balonnensis*. Fisher's Exact Test confirmed that there was no difference in the frequency of upwards and downwards movement ($p>0.05$) between the two treatments. *Thiara balonnensis* fell from the vertical surface of the glass tubes and substratum only when water-levels receded.

Notopala sublineata

Movements in response to stable and receding water-level treatments using the Vertical Surface method for seven individuals are given in Table 5.4.

Table 5.4. Frequency of each observed behaviour type, mean *(SE)*, over 60 minutes, 12 test periods, for *Notopala* for stable (n=7) and receding (n=7) water-level treatments.

		Up	Down	Stationary	Fall
Water Level	Stable	3 *(0.92)*	2.14 *(0.66)*	6.85 *(1.27)*	0 *(0)*
	Receding	0 *(0)*	1.28 *(0.99)*	10 *(0.84)*	0.71 *(0.18)*

These results show a difference between the observed frequency of each reaction type ($H=28.02$, $p<0.001$) and a significant interaction between water-level treatment and behaviour ($H=8.72$, $p>0.05$). *Notopala sublineata* showed no difference in the frequency with which it moved upwards, downwards or remained stationary under stable water-level conditions. Fisher's Exact Test on pooled data indicated a significant difference ($p<0.01$) in the frequency of upwards and downwards movement between treatments.

Movements in response to stable and receding water levels using the Sloping Surface method for seven individuals are given in Table 5.5.

Table 5.5. Frequency of each observed behaviour type, mean *(SE)*, over 240 minutes, 48 test periods, for *N. sublineata* under stable (n=7) and receding (n=7) water-level treatments.

		Up	Down	Sideways	Stationary
Water Level	Stable	5.86 *(1.14)*	5.57 *(0.92)*	4.0 *(1.0)*	6.14 *(3.47)*
	Receding	0 *(0)*	1 *(0)*	0 *(0)*	0 *(0)*

A Kruskal-Wallis Test suggested no difference in the frequency of reactions exhibited under stable water-level conditions ($H=2.774$, $p>0.05$). It is obvious from Table 5.5 that when water-levels recede individuals show only downwards movement. In all cases snails reached the water at the base of the aquarium within one seven minute test period. Individuals then retreated into their shells, sealed their opercula and remained immobile until water-levels were restored.

5.4.4 Discussion

Basic differences in responses to receding water-levels were observed between the three species. The two "river" snails, *N. sublineata* and *T. balonnensis,* did not move downwards from a vertical surface when water levels fell. However, their heavy shells rendered them unable to support themselves on the vertical surface once the water had receded, and they fell to the base of the tubes. *Physa acuta*, with a comparatively thin and light shell was able to maintain its position on the vertical surface after the water had receded; individuals then moved downwards in order to

reach the new water-level. On the sloping surface *N. sublineata* also moved actively downwards in response to sudden receding water-levels.

This suggests that adults of all three species are able to accommodate to sudden changes in water-levels of magnitudes and rates greater than commonly occur in the river below the weirs. It is therefore unlikely that water-level fluctuations, *per se,* have directly affected snail populations through stranding of individuals.

This result is not entirely unexpected. Although weir operations have increased the magnitude and changed the rate of daily water level variations, the changes are not as extreme as is the case below many hydro-electric systems. The hydrograph of the unregulated River Murray was essentially a series of sequential flood pulses, ranging from within channel floods to large overbank flows. The littoral zone was never stable for extended periods, and as such littoral fauna were likely to be pre-adapted to a moving littoral zone. Many of the gastropods may also be able to avoid dehydration if stranded by sudden water level changes through sealing their opercula; *N. sublineata* can survive at least 3 weeks out of water in summer conditions (Sheldon, unpublished data).

5.5 CONCLUSION

Although short-term water level variations may not be directly linked to the decline in snail populations through stranding they have undoubtedly impacted fauna through habitat modification. Erratic water level fluctuations can alter the nature of the substrate and cause loss of aquatic vegetation (Hunt and Jones, 1972; Walker *et al.,* 1992). Weir construction is associated with a 30% decrease in substrate median grain size with coarser sediments being trapped in upstream weirs and impoundments (Thoms and Walker, 1992). The nature of the substrate also varies between weirs being slightly coarser in the region below each weir (Thoms and Walker, 1992).

The position of weirs along the channel causes discontinuities in the distribution of both emergent and submergent aquatic plants, possibly related to changing erosive powers of the water within a weir pool (cf. Roberts and Ludwig, 1992; Thoms and Walker, 1992; Walker *et al.,* 1994). The emergent aquatic *Typha sp.* is restricted to the stable environment of the upper pool while others, such as *Myriophyllum verrucosum* and *Cyperus sp.*, are found in the more unstable lower pool regions (Walker *et al.,* 1994). This creates patchiness in the availability of microhabitats so

that species with specific microhabitat requirements may be indirectly impacted by the weirs. This is unlikely to be the situation for either of the prosobranchs studied as field evidence from rivers in the Lake Eyre Basin suggests that they are found in a diverse range of habitats from vegetation and snags to unvegetated regions with silt substrata (Sheldon, unpublished data).

In the lower Murray impacts of short-term water variations on aquatic plants are also likely to be enhanced by turbidity as the euphotic zone averages only 300 mm. A narrow photic depth combined with weir induced water level fluctuations means that the river in the region below a weir may fluctuate through a depth range roughly equivalent to the zone where plant growth occurs (Maheshwari *et al.,* 1993). The area available for primary production is therefore limited and unstable. The stability of the photic zone is minimised immediately downstream of a weir, increasing with distance towards the next weir and a decrease in the magnitude and frequency of erratic water-level changes. For the majority of the main channel habitat of the lower Murray, water levels in the littoral zone, and therefore photic zone, are stable, particularly when compared with the seasonal changes in preregulation levels (Chapter 2). The increase in littoral stability is related to the overall maintenance of near-bankfull flows in the entire lower river (Maheshwari *et al.,* 1993). An increase in stability of the photic zone favours benthic algal production on littoral substrata (cf. Petts, 1984).

Organic detritus was found to be the dominant food item in the guts and faecal pellets of a diverse group of invertebrate taxa from the Buffalo River in South Africa (cf Palmer *et al.,* 1993a; Palmer *et al.,* 1993b). Detritus also forms the dominant food item for a number of viviparid taxa (cf. Browne, 1978; Dudgeon and Yipp, 1983; Pace and Sczuch, 1985; Brown *et al.,* 1989). If the dominant food items available in the littoral zone of the lower Murray changed as a result of flow regulation then invertebrate assemblages may be affected. The diets of natural populations of both *Notopala sublineata* and *Thiara balonnensis* along with the type and quality of food available in the regulated lower River Murray are considered in Chapter 6.

Chapter 6

Impacts of Regulation: Gastropod Diet and Food Availability

6.1 INTRODUCTION

Food in rivers is derived from two main sources: *allochthonous* sources (e.g. leaves, twigs and wood), from outside the river or *autochthonous* sources (e.g. algae and aquatic macrophytes), from within the river. In both river channels (cf. Anderson and Sedell, 1979; Winterbourn *et al.,* 1986; Bunn *et al.,* 1989) and floodplain wetlands (cf. Hamilton *et al.,* 1992) detritus (non-living particulate organic matter with associated microbes: Baker and Bradnam, 1976) of both allochthonous and autochthonous origin is the dominant energy source for aquatic animals. The detritus finds its way into the river from terrestrial and riparian vegetation, from bank erosion, and decomposing products of upstream and instream algal and macrophyte growth (Bowen, 1987).

The relative importance of each energy source to the detritus base varies along the course of the river as a function of gradient, depth, stream order, flow, season and the development of terrestrial riparian vegetation (Drake, 1984). The River Continuum Concept (RCC: Vannote *et al.,* 1980) predicts that, as stream size increases and the influence of the riparian forest diminishes, instream photosynthesis will increase and the primary energy source will shift from an allochthonous towards an autochthonous source. Studies of temperate Northern Hemisphere streams support the notion that allochthonous detritus becomes less important as a food source with increasing stream order (Conners and Naiman, 1984). This trend may not hold for large, turbid rivers, as although the influence of the riparian forest is limited, the combined action of high turbidity (low photic depth) and a continually moving water level will reduce autochthonous production. In such systems the primary food base may be allochthonous detritus, inundated during floods (cf. Junk *et al.,* 1989).

The quantity and quality of available food affects the life history characteristics of aquatic insects (Sweeney and Vannote, 1986). Food quantity determines patterns of invertebrate distribution, density and production (Drake, 1984; Richardson, 1991; Corkum, 1992), whereas food quality can affect growth and reproduction (cf.

Anderson and Sedell, 1979; Sweeney and Vannote, 1986). It is not enough for an animal to merely find an adequate quantity of food; this food must be of sufficient quality (in both trace nutrients and energy content) to sustain growth and adequate reproduction (Lane, 1991).

Stream grazers, especially gastropods, may be particularly susceptible to food limitation, affecting fecundity and therefore production (Eisenberg, 1966; Calow, 1970; El-Eman and Madsen, 1992; Hill 1992). Some grazers are able to compensate for low food quality by increasing ingestion, such that food quality rarely limits their growth (Hill, 1992). In other grazers ingestion is already maximal, and food quality is therefore important.

In rivers where the photic depth is limited by dissolved matter (blackwater rivers of North and South America) and/or changing water levels, benthic algal productivity is restricted and heterotrophic microbes tend to dominate the periphyton (Findlay *et al.,* 1986; Edwards and Meyer, 1987; Couch and Meyer, 1992). This situation probably characterised the lower River Murray prior to flow regulation, where high turbidities and moving water levels (cf. Chapter 1) would have favoured microbial-detrital, rather than algal, food sources for the aquatic invertebrates.

If a stable photic depth is maintained, benthic algae are likely to dominate the littoral periphyton (cf. Lowe, 1979). Naturally constant current velocities in the Ogoochee River, a blackwater river in Georgia (USA), result in a stable photic depth, producing conditions favourable for a thick biofilm dominated by algae on littoral snags (Couch and Meyer, 1992). In many New Zealand rivers low flows create conditions favourable for the development of nuisance levels of benthic algae (Biggs and Price, 1987; Biggs, 1990). Constant discharge to the rivers downstream of reservoirs and dams also tend to stabilise water levels and therefore favour increased algal (autochthonous) production, so that submerged surfaces in many regulated rivers tend to become coated with dense mats of filamentous green algae (cf. Lowe, 1979; Williams and Winget, 1979; Petts, 1984; Dufford *et al.,* 1987).

In the lower River Murray flow regulation has changed the natural pattern of flows, with both extreme low flows and small floods virtually eliminated (cf. Chapter 1). Regulation has stabilised seasonal water levels and created conditions favourable for the increased production of benthic algae. This may be one factor in the decline in range and abundance of the prosobranch gastropods *Notopala* spp. and *Thiara balonnensis* in the lower Murray (cf. Chapter 1).

In general, members of the Viviparidae and Thiaridae have low fecundities (Browne, 1978; Taki, 1981; Jokinen *et al.,* 1982; Brown *et al.,* 1989). Observations of embryo numbers in *N. sublineata* and *T. balonnensis* from the North West Branch of Cooper Creek in north-east South Australia and *N. hanleyi* from the Loveday irrigation pipeline (cf. Appendix E) suggest that each species is typical of its family. The number and size of offspring in the North American *Viviparus ater* are correlated with female size; larger females giving birth to more numerous large offspring than smaller females (Ribi and Gebhardt, 1986). The same relationship was found for the Japanese viviparid *Cipangopaludina japonica* (Taki, 1981). Small size affects reproductive output through energy limitation and the physical constraints of the number of embryos maintained in the uterus (Browne, 1978).

Stanczykowska *et al.* (1971) and Stanczykowska *et al.* (1972) suggest that in *Viviparus malleatus* (Reeve) female size at maturity is a reflection of the quality of their food supply. The measurement of food quality, however, was based on the relative abundance of algal material in the guts of dissected specimens. This may not be an adequate indication of food quality for breeding females, as the presence of algal material in gut contents does not mean that snails are assimilating algal carbon. Ribi and Gebhardt (1986) suggest that in at least one population of *V. ater* low food availability and low temperatures account for the lower fecundity of the females.

Food also plays an essential role in regulating populations of other gastropods (cf. Eisenberg, 1970), affecting egg laying (El-Eman and Madsen, 1982) and female size (Hill *et al.,* 1992). In the pulmonate *Lymnaea elodes* food regulates population dynamics at two distinct levels. At one level food required for "maintenance nutrition" was easily obtained by the snails. Although individuals operating at this level did not die, their growth was inhibited and reproduction was limited. The second level, of "positive nutrition", was not easily attained but enabled individuals to realise some of their potential for growth and reproduction (Eisenberg, 1970).

An hypothesis regarding the disappearance of snails from the lower River Murray concerns changes in the nature of available food resources. Before regulation most of the periphytic biomass in the lower River Murray probably was microbial, as fluctuating water levels would have maintained littoral periphyton in a state of early succession. By stabilising seasonal water levels flow regulation has promoted the production of filamentous algae (e.g. *Spirogyra* spp.). Such a change may pose two problems for the gastropods *Notopala* sp. and *T. balonnensis*. Both taxa are likely to

be detritivores, and perhaps unable to remove filamentous algae from the substratum. Large quantities of algal material in their diets may be an inadequate food supply in terms of energy requirements which, in turn, would decrease female fecundity. This may either cause or contribute to extinction.

This chapter initially considers the diets of *Notopala sublineata* and *Thiara balonnensis*. *N. sublineata* is used to enable the examination of diet in a natural population. Three methods are employed:

- radula morphology,
- the contents of guts and faecal pellets, and
- ratios of carbon stable-isotopes.

A feeding experiment is conducted using *N. hanleyi,* a species closely-related to *N. sublineata* (cf. Sheldon and Walker 1993b) and locally obtained from irrigation pipelines. Scanning electron micrographs are examined to determine if *N. hanleyi* is physically able to remove filamentous algae from the substratum by grazing. By comparing items in periphyton grazed by the snails with the content of the guts and faecal pellets after grazing it is possible to determine if *N. hanleyi* is selecting for particular elements of the periphyton.

To test the hypothesis that regulation-induced changes in food quality have contributed to the extinction of *Notopala* sp. and *T. balonnensis* in the lower River Murray, information on diet and grazing selectivity is related to data on the food available in two environments. The North West Branch of Cooper Creek in north-east South Australia, and irrigation pipelines in the South Australian Riverland, where the species are present, and the entire lower River Murray in South Australia, where they are presumed extinct.

6.2 RADULA MORPHOLOGY

6.2.1 Significance of the Radula in Diet Determination

Molluscan grazers possess a complex feeding apparatus that includes the radula, associated buccal muscles, jaws and cartilage (Steneck and Watling, 1982). The radula plays a direct role in the procurement of food items. It is a membranous belt stretched over an elongated cartilaginous base, with chitinous teeth arranged in longitudinal rows, each tooth comprising a basal plate attached to the radula membrane and an erect cusp directed backwards (Barnes, 1982). The radula can function as a scraper, removing attached periphyton from the substratum, as well as a collector. Over time there is a gradual loss of both membrane and radular teeth at the anterior end of the ribbon, and new teeth are continually secreted at the posterior end.

Adaptations in radula morphology and feeding behaviour have enabled the Gastropoda to occupy a wide range of marine and freshwater habitats (Hawkins *et al.,* 1989). Gastropod diet is known to differ with overall radula shape and the morphology of the radular teeth (Kesler *et al.,* 1986; Blinn *et al.,* 1989). However, radula function, in terms of specific food items selected, cannot be inferred from tooth form alone (Hickman, 1980; Raffaelli, 1985; Barnese *et al.,* 1990; Dillon and Davis, 1991). Taxa with similar radulae can modify the way in which the radula is used if feeding on different substrata (Hickman and Morris, 1985) while taxa with morphologically different radulae can ingest similar food items by using different feeding movements. This was demonstrated in five co-occurring intertidal gastropods with morphologically different radulae (Rhipidoglossid, Taenioglossid and Doccoglossid). These taxa utilised different feeding movements to exploit the same microfloral film covering intertidal rocks, with only minimal resource partitioning resulting from differences in radula morphology (Hawkins *et al.,* 1989). This argues for caution when correlating a specific diet and a gastropod group using only tooth and radula morphology.

Despite these limitations, Steneck and Watling (1982) divided the herbivorous molluscs (excluding opisthobranch and pulmonate herbivores) into functional groups based on radula morphology: Rhipidoglossa, Taenioglossa, Docoglossa and Polyplacophora. These groups reflect the estimated "toughness" of the algae or food source in the gastropod diet and the "excavating abilities" of the radula (Hickman and

Morris, 1985). Gastropods with rhipidoglossid and taenioglossid radulae tend to graze small algae such as diatoms, blue-greens and smaller filamentous greens, and consume large quantities of amorphous organic matter. Many of these snails are described as 'detritivores'. This contrasts the other radula types, typical of the Docoglossa and Polyplacophora, where larger algae and macrophytes form the predominant foods. These snails are essentially herbivores.

Many species of freshwater prosobranchs, including members of the Viviparidae, have a supplementary capacity to filter feed using the gill (Aldridge, 1983). The importance of filter feeding usually depends on life-cycle stage and availability of food (cf. Tashiro and Coleman, 1982). The Oneida Lake (New York, U.S.A.) population of *Bithynia tentaculata* used filter feeding as cost-effective mechanism of accruing additional protein and carbon, particularly in the breeding season. The benefits of filter feeding, however, would be expected to vary with the concentration of suspended solids in the environment.

In this section the radulae of *Notopala sublineata* and *Thiara balonennsis* are examined using the Scanning Electron Microscope (SEM). Radula morphology and the 'functional group' approach are then used to indicate the diets of the two taxa.

6.2.2 SEM Preparation

Radulae were extracted from snails by macerating the body for 40-50 minutes in a solution of 10% potassium hydroxide in a 20 mL test tube placed in a boiling water bath. The extracted radulae were dried through an ethanol series (70, 80, 90, 100%) then stored in 100% ethanol until use. Individual radulae were prepared for SEM examination by mounting on an aluminium stub. Stubs were initially covered with double-sided sticky tabs onto which a thin glass capillary (0.2-0.5 mm diameter) was placed. Under a dissecting microscope the radula was positioned over the capillary, simulating the feeding position (Ploeger, 1977). Radulae were coated with gold/palladium and examined with a Phillips Model 505 SEM. Photographs were taken on Kodak T Max 100 size 120 black and white roll film.

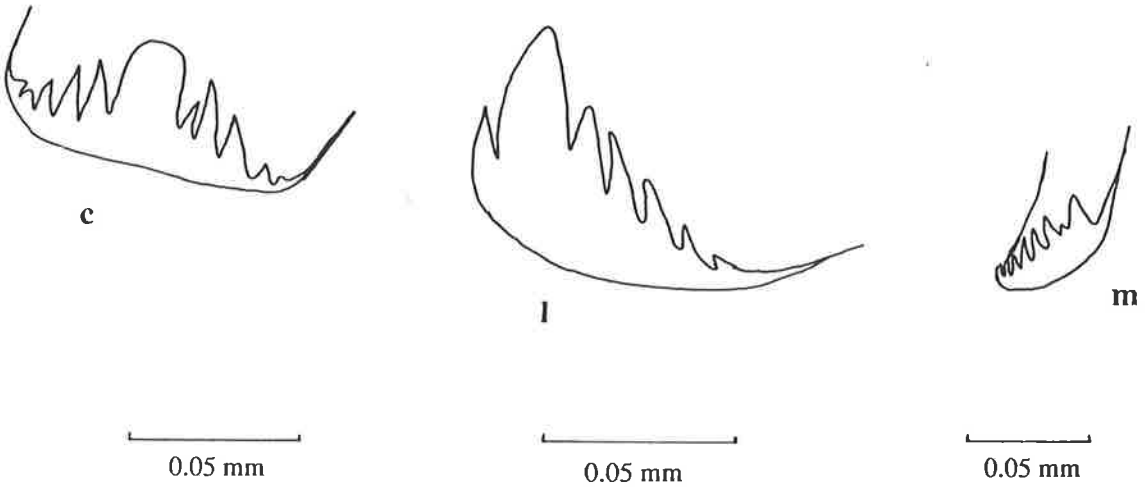


Figure 6.1 Radula teeth of *Notopala sublineata* from the centre (c) to the right of the ribbon with lateral teeth (l) and marginal teeth (m).

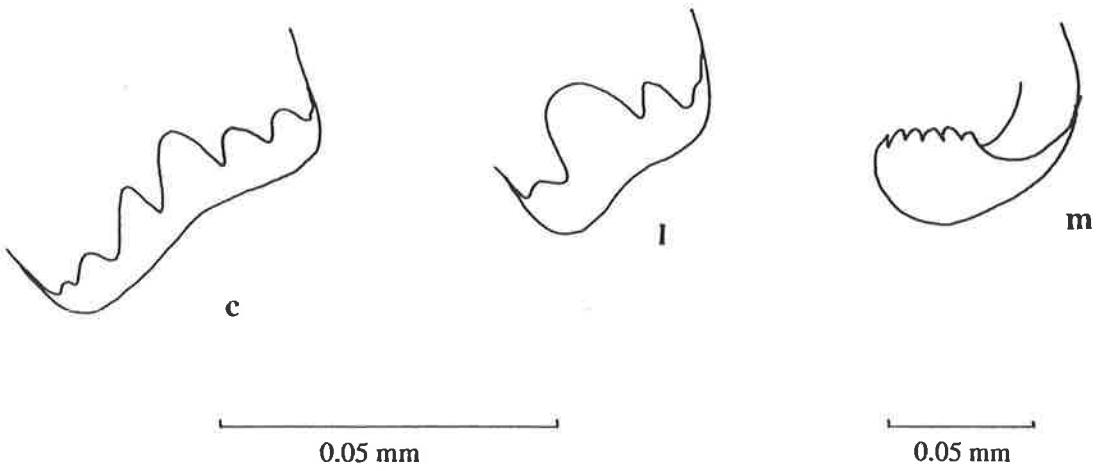


Figure 6.2 Radula teeth of *Thiara balonnensis* from the centre (c) to the right of the ribbon with lateral teeth (l) and marginal teeth (m).

6.2.3 Radula Description

The radula teeth of pulmonates are classified as *central* (one central tooth per row), *lateral* (teeth to each side of the central tooth) and *marginal* (teeth on the edge of the ribbon) (Kesler *et al.,* 1986). The radulae of both *N. sublineata* and *T. balonnensis* are of the taenioglossid type (cf. Steneck and Watling, 1982), and approximate one centimetre in length in adult specimens of both species.

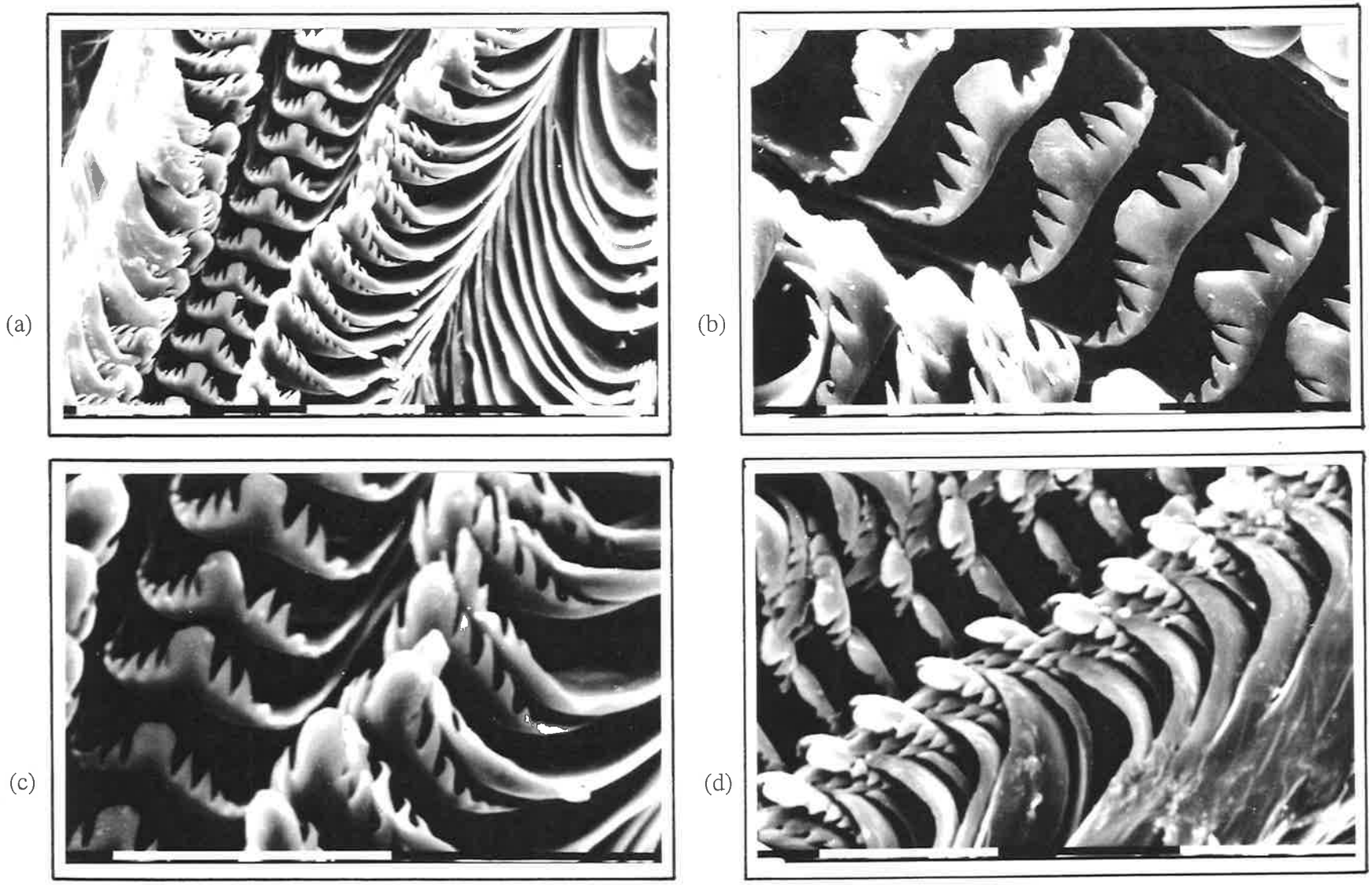
The radula of *N. sublineata* has seven teeth in each row: a single central tooth with two lateral teeth on either side and an outer marginal tooth (Photograph 6.1a). The central tooth has a large, rounded central cusp with five pointed cusps on either side (Figure 6.1a; Photograph 6.1b). The lateral teeth also have a single large central cusp with five pointed cusps on either side (Figure 6.1b; Photograph 6.1c). The marginal teeth are distinctive, being cup shaped and edged with a number of similar sized small cusps (Figure 6.1c; Photograph 6.1d)

The radula of *T. balonnensis* also is typical taenioglossid, with seven teeth in each row: a central tooth, a single lateral tooth on either side and two outer marginal teeth (Photograph 6.2a). The central tooth has a pointed central cusp with four smaller pointed cusps on either side (Figure 6.2a; Photograph 6.2b). The lateral is similar to the middle tooth, with a pointed central cusp and two smaller pointed cusps on each side (Figure 6.2b; Photograph 6.2c). The marginal teeth are elongated, folding towards the centre of the radula completely covering each lateral tooth. The marginal teeth are cup- or hook-shaped and edged with numerous small rounded cusps (Figure 6.2c; Photograph 6.2d).

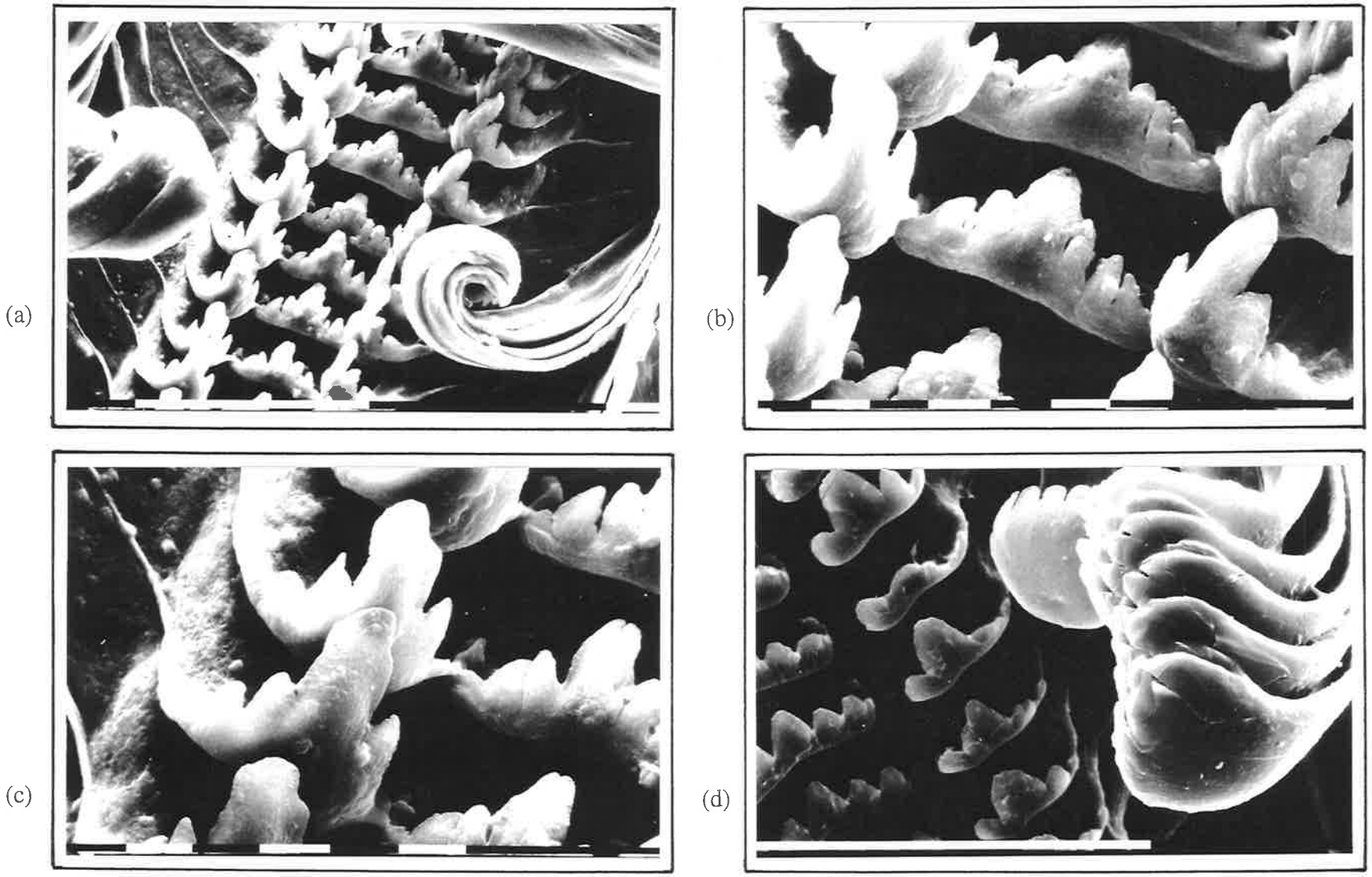
6.2.4 Radula and Diet

Based on radula morphology, both *T. balonnensis* and *N. sublineata* are taenioglossid gastropods, with the most probable food items being microalgae, including diatoms, and detritus.

Taenioglossid radulae are of equivalent hardness to a human fingernail (Hawkins *et al.,* 1989). They are used like 'rakes' (Steneck and Watling, 1982), when the radula is retracted the marginal hook-shaped teeth collect torn or detached particles from the substratum and funnel them towards the centre (Barnes, 1982). The grazing style of the taenioglossid radula results from both the adaptive form of the teeth and the complex way in which they interact with each other (cf. Barnes, 1982; Hickman and



Photograph 6.1 (a) Radula of *Notopala sublineata* showing all teeth (scale = 0.1 mm)
(b) Central teeth, *N. sublineata* radula (scale = 0.1 mm)
(c) Lateral teeth, *N. sublineata* radula (scale=0.1 mm)
(d) Marginal teeth, *N. sublineata* radula (scale = 0.1mm)



Photograph 6.2 (a) Radula of *Thiara balonnensis* showing all teeth (scale=0.1 mm)
(b) Central teeth, *T. balonnensis* radula (scale = 10 mm)
(c) Lateral teeth, *T. balonnensis* radula (scale = 10 mm)
(d) Marginal teeth, *T. balonnensis* radula (scale = 0.1 mm)

Morris, 1985). A detailed description of the feeding movements of a taenioglossid radula, that of *Littorina littores,* is given by Hawkins *et al.* (1989).

In comparing the grazing efficiency of prosobranch snails with pulmonates, Barnese *et al.* (1990) found that the taenioglossid radula of the prosobranch *Elimia livescens* was less effective at removing attached particles from hard substrata than the radula ribbon of the pulmonates *Physella gyrina* and *Lymnaea stagnalis*. The larger central and lateral teeth of the rake-like taenioglossid radula appeared to be better adapted for removing large food particles, particularly detritus, from substrata such as sand, with the marginal teeth trapping the particles for ingestion.

Functional groups based on radula morphology (cf. Steneck and Watling, 1982) may broadly indicate diet. The type of food ingested by a snail, however, depends on what is available in the environment, as well as the way in which the radula is moved, regardless of morphology (cf. Dudgeon and Yipp, 1983; Hickman and Morris, 1985; Raffaelli, 1985). This may be especially true for freshwater gastropods, as the functional approach of Steneck and Watling (1982) was based on studies of diet and radula morphology in marine taxa where autochthonous algal production is possibly greater than in systems such as rivers. In lotic habitats the most abundant food source may be detritus (Cummins *et al.,* 1973). Radula morphology can therefore only be used to suggest a broad diet area for a particular taxon; other techniques, such as the examination of gut contents need to be used to isolate more specific aspects of the diet.

6.3 Gut Content and Faecal Pellet Analysis

6.3.1 Introduction

Identifying items in the guts of herbivorous molluscs is difficult (Hawkins *et al.,* 1989), and there have been few quantitative attempts. Dudgeon and Yipp (1983) used gut contents to investigate the diets of nine gastropod taxa from Hong Kong streams. Although up to 90% was detritus, they used the proportion of food items present to separate the species into three dietary groups: those with a wide range of food items in the gut, those whose gut contents were dominated by organic detritus, and those whose gut contents were dominated by inorganic detritus.

Although the analysis of gut contents gives a more precise indication of gastropod diet than does radula morphology alone, it is still a poor indication of what is being consumed. To determine more accurately the component of the periphyton food source being utilised by the snail from that merely passing through the gut, the ingestion of periphyton by *N. sublineata* and *T. balonnensis* is investigated through the microscopic examination of gut contents and faecal pellets. The presence of food items in guts and faeces is then compared to their relative abundance in the periphyton from habitats where both species are present.

6.3.2 Methods

Study Site

Snails were collected from the littoral zone of the North West Branch of Cooper Creek near Coongie Lakes, north-east South Australia in December 1991 (hereafter referred to as Cooper Creek). The North West Branch diverges from the Main Branch approximately 25 km west of Innamincka, and feeds a series of temporary shallow lakes known as the Coongie Lakes (Figure 6.3). Descriptions of the hydrology and ecology of both Cooper Creek and Coongie Lakes are given by Reid and Gillen (1988) and Reid and Puckridge (1990). Environmental data for Cooper Creek at the time of collection may be found in Section 6.7.

Sample Collection and Analysis

At the time collection was undertaken both species were rare, a factor that may be related to seasonal patterns in life history.

Owing to the limited number of specimens available gut samples could not be obtained from freshly collected individuals so both gust contents and faeces were collected from each snail. Individual snails were kept in 2-L ice-cream containers for 12 hours, the faecal pellets produced in this time were collected and preserved in Lugol's solution. Snails were then killed, removed from their shells, and their gut dissected and also preserved in Lugol's solution. Samples of periphyton were collected from two littoral microhabitats: redgum snags and leaf litter. Periphyton was removed from the surface of each substratum by gently scrubbing with a soft toothbrush in distilled water.

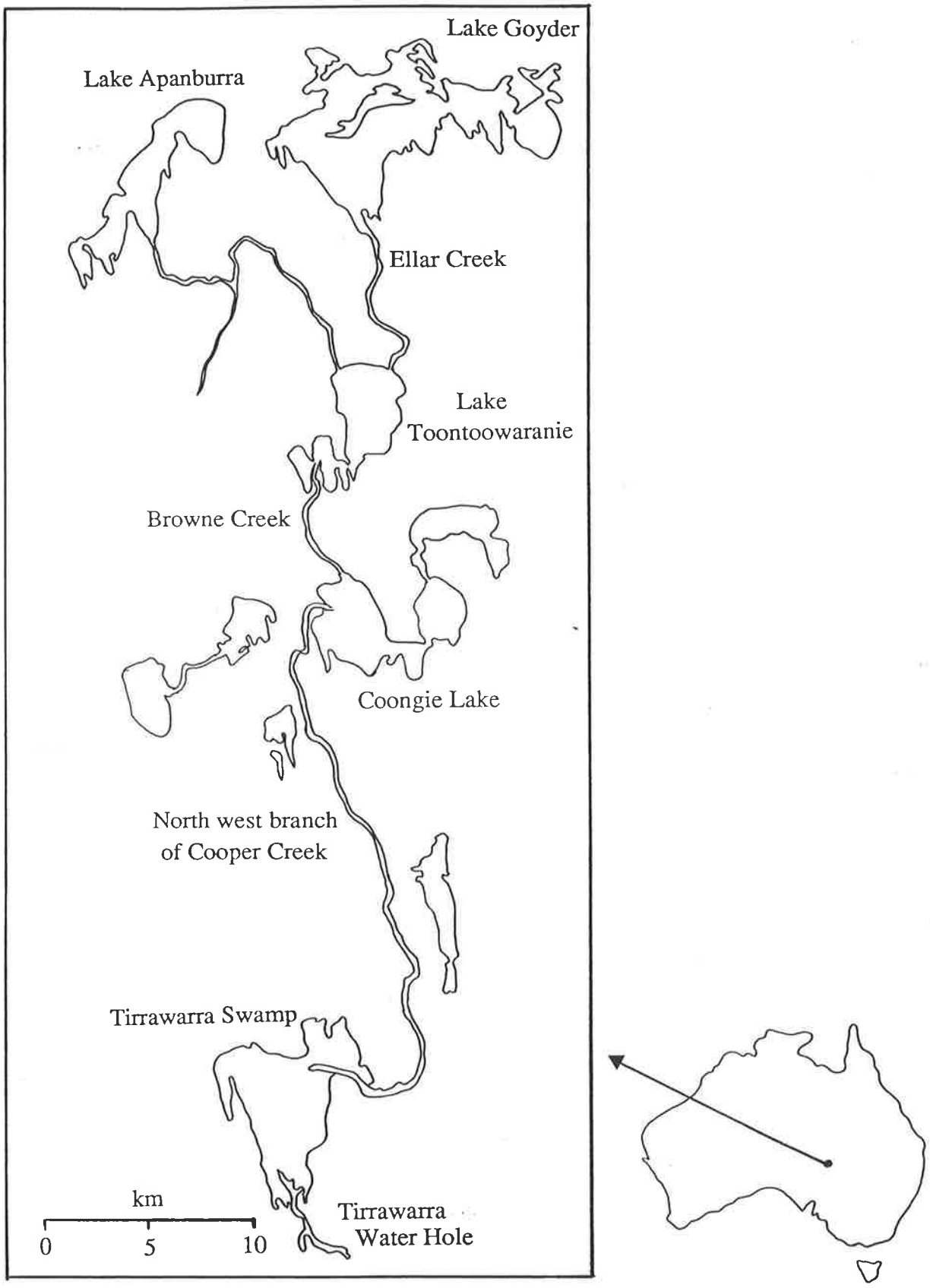


Figure 6.3 Coongie Lakes region of the Lake Eyre Basin, South Australia.

The composition of the periphyton, snail guts and faecal pellets was determined as described by Lodge (1986). Two drops of suspension were placed on a microscope slide, covered with a 22x22 mm coverslip and examined at 400x magnification using a 10x10 ocular grid. Items in the guts and faecal pellets of herbivorous molluscs are difficult to identify to species level, so algae were grouped by gross morphology (cf. Steneck and Watling, 1982). Particles (including detritus) were thus classified into one of seven groups: inorganic detritus, organic detritus, diatoms, filamentous green algae, other green algae, blue-green algae (Cyanobacteria) and animal material. The percentage abundance of particles from each of the seven food groups was estimated by their percentage cover in each field of view (400x magnification). Five random fields of view were examined for each periphyton, gut content and faecal pellet sample.

6.3.3 Results

Periphyton

Items from all seven groups were present in periphyton from both snags and leaf litter (Table 6.1), with detritus comprising the major portion from both microhabitats. Organic detritus constituted a greater percentage of the periphyton scrubbed from the leaf litter, compared with scrubs from snags. Diatoms, present in scrubs from both microhabitats, appeared to be more abundant on snags as were filamentous green algae and blue-green algae. Animal material, mostly Cladocera, was recorded in small amounts in samples from both snags and leaf litter.

Table 6.1 Estimated abundance of food items in periphyton samples from leaf litter (n=6) and snag (n=6) microhabitats of Cooper Creek, December 1991.

	Leaf Litter	Snag
Inorganic Detritus	50%	20-30%
Organic Detritus	20-30%	20-30%
Diatoms	20%	30%
Filamentous Algae	<5%	10-20%
Other Algae	<5%	<5%
Blue-green Algae	<5%	<15%
Animal Material	<5%	<5%

Gut Contents and Faecal Pellets

Specimens of *T. balonnensis* were found abundantly in leaf litter as well as on snags, whereas *N. sublineata* was rare with only a few specimens found in leaf litter and most on snags in deeper water.

Items from six of the seven food groups were present in the guts of both species (Table 6.2). Organic and inorganic detritus made up the major component of gut contents. Diatoms and filamentous green algae were present in small abundances whereas blue-green algae and animal material were present but rare.

Items from six of the seven food groups were also present in the faecal pellets of both species (Table 6.3). Organic detritus constituted the major component of faecal material, with inorganic detritus in the form of sand grains also abundant. Diatoms, filamentous green algae and blue-green algae were present but less abundant than detritus. In both species the faecal pellets contained the identifiable remains of small invertebrates (Cladocera and Copepoda), but these were rare. There appeared to be no difference in the abundance of any food item between the material present in the guts and faecal pellets.

Table 6.2 Presence of food items in the guts of *N. sublineata* (n=5) and *T. balonnensis* (n=5), collected from the littoral zone of Cooper Creek, December 1991.

	N. sublineata	*T. balonnensis*
Inorganic Detritus	30-50%	30-50%
Organic Detritus	>50%	>50%
Diatoms	10-30%	10-30%
Filamentous Algae	10-30%	10-30%
Other Algae	0	0
Blue-green Algae	<10%	<10%
Animal Material	<10%	<10%

Table 6.3. Presence of food items in the faecal pellets of *N. sublineata* (n=6) and *T. balonnensis* (n=10), collected from the littoral zone of Cooper Creek, December 1991.

	N. sublineata	*T. balonnensis*
Inorganic Detritus	30-50%	30-50%
Organic Detritus	>50%	>50%
Diatoms	10-30%	10-30%
Filamentous Algae	10-30%	10-30%
Other Algae	0	0
Blue-green Algae	10%	10%
Animal Material	<10%	<10%

6.3.4 Discussion

The items present in the guts and faecal pellets of both *N. sublineata* and *T. balonnensis* were representative of that available from the periphyton on both snags and leaf litter. Organic detritus was more abundant in gut contents and faecal pellets than in periphyton, suggesting selective ingestion of organic material over inorganic detritus. This notion is supported by Barnese *et al.* (1990) who suggest that the rake-like action of the taenioglossid radula actively selects against inorganic material allowing the gastropods to remove organic matter from inorganic substrata such as sand grains.

Conclusions here are limited by the small number of individuals examined, and by not knowing the items present within guts on immediate collection, prior to further digestion or defecation. This may contribute to an overestimation within the guts of those food items having a slow passage time, and an increase in abundance in the faeces of those items with faster passage times. Despite these limitations this analysis suggests that both species have a diet dominated by amorphous organic detritus and could therefore be classified as detritivores. A similar result was found for the prosobranchs *Sinotaia quadrata* (Viviparidae) and *Melanoides tuberculata* (Thiaridae) by Dudgeon and Yipp (1983). Detritus constituted more than 90% of the gut content volume with green algae (unicellular and filamentous) and diatoms forming only a minor, but regular, part of the diet. Other viviparids have also been described as detritivores (cf. Browne, 1978; Jokinen *et al.,* 1982).

The presence of animal material in the guts and faeces of *N. sublineata* and *T. balonnensis* is interesting. The material may be ingested inadvertently with algal and detrital food offering an additional nitrogen resource (cf. Kesler *et al.,* 1986). The material may also be merely exoskeletal remains of small invertebrates deposited within the periphyton and accidentally consumed. Animal material may also take longer to pass through the digestive system and its presence in the food consumed may therefore be overestimated.

Many aquatic animals assimilate only the most labile fraction of what they consume (cf. Bowen, 1987; Hamilton *et al.,* 1992). Further, some periphytic algae are resistant to digestion by aquatic gastropods and may release dissolved organic carbon to the snail during gut passage (Thomas, 1990). The presence of similar abundances of algal material in guts and faecal pellets therefore does not preclude a role for algae in nutrition. Supplementary information from other techniques, such as digestive tract cellulase activity or the ratio of carbon stable-isotopes in animal tissue may provide a more accurate description of the diet.

6.4 DIET DETERMINATION: STABLE CARBON ISOTOPE ANALYSIS

6.4.1 The Use of Stable Isotopes to Determine Diets

Gut content analysis provides an instantaneous picture of the food ingested, but says nothing of its utilisation and assimilation (Rounick *et al.,* 1982). The measurement of carbon stable-isotopes in animal tissue, however, allows the source of biomass carbon, and thus diet, to be determined more accurately from a range of habitats and potential food sources (Rounick and Winterbourn, 1986). The comparison of the carbon isotopic composition of animals and their presumed foods has been used to indicate diets in groups such as salt-marsh invertebrates (Haines and Montague, 1979) and terrestrial grasshoppers (Fry *et al.,* 1978; Petelle *et al.,* 1979). In freshwater systems stable isotopes have also been used to trace food webs in tundra rivers (Bunn *et al.,* 1989) and billabongs (Boon and Bunn, in press). The variation in ^{13}C:^{12}C is measured by ratio mass spectrometry, and the ^{13}C:^{12}C ratio is expressed as $\delta^{13}C$ in parts per thousand (‰), either enriched (more positive) or depleted (more negative) relative to a CO_2 standard (Rounick and Winterbourn, 1986).

Terrestrial plants differ in their ^{13}C:^{12}C ratios depending on the pathway (C_3 or C_4) used during the photosynthetic fixation of CO_2 (Bender, 1971; Smith and Epstein, 1971). The ratio in aquatic plants is further determined by the $\delta^{13}C$ value of the dissolved inorganic carbon in their habitat (Rounick and Winterbourn, 1986). At the broadest level, owing to the difference in $\delta^{13}C$ between terrestrial and aquatic vegetation, the technique allows discrimination between the assimilation of autochthonous and allochthonous material.

The ratio of ^{13}C to ^{12}C in a consumer organism summarises recent feeding history - it reflects materials actually assimilated and incorporated into animal tissues as opposed to the total materials ingested (Rounick and Winterbourn, 1986; Hamilton *et al.,* 1992). The distinctive ^{13}C:^{12}C ratio of a plant tissue passes along the food chain with little further fractionation (Petelle *et al.,* 1979) so that most consumers are slightly ^{13}C enriched (1‰) compared to their diet (Rau *et al.,* 1983; Petersen and Fry, 1987). This is due to the preferential loss of ^{12}C during animal respiration (DeNiro and Epstein, 1978).

The aim here is to use carbon stable-isotopes to determine the principal source of biomass carbon, and therefore diets, for the prosobranch gastropods *N. sublineata* and *T. balonnensis* from the relatively unmodified habitat of the littoral zone of

Cooper Creek. Given the above dietary information for *N. sublineata* and *T. balonnensis* as well as data from related species (cf. Browne, 1978; Jokinen *et al.*, 1982) we may expect both taxa to assimilate the majority of their carbon from a detrital food source.

6.4.2 Methods

Collection

The methods used to compare the carbon stable-isotope compositions of the snails and their presumed food sources are modified from Fry (1984). Samples were collected from the littoral zone of Cooper Creek (Figure 6.3) in December 1991.

Coarse organic carbon was obtained from the top 10 cm of sediment using a sediment corer with a 15 cm diameter. Five separate core samples were taken from the littoral zone, where snails were abundant. After collection the sediment was air dried, sieved through a 2 mm mesh screen to remove large pieces of debris such as twigs, and collected on a 250 µm mesh screen. The coarse organic carbon was acidified with 2M HCl (to remove calcareous material) until bubbling ceased, then evaporated to dryness.

Particulate organic carbon samples were collected by filtering 1 L of water from the littoral zone through pre-combusted (4 hours at 450 °C) glass fibre filters. The filters were acidified briefly in watch glasses, then air dried. The dried particulate organic carbon was later removed from the filter.

Periphyton was gently removed from the substratum by scraping with a soft toothbrush, then precipitated onto precombusted glass fibre filters, acidified and evaporated to dryness. The dried periphyton layer was later removed from the filter.

Leaves from the emergent macrophyte *Ludwigia peploides* were cleaned of periphyton with a soft toothbrush, rinsed in a mild acid bath and air dried. Each macrophyte sample used in the analysis was a composite of five leaves.

Samples of red gum (*Eucalyptus camaldulensis*) *bark* and *leaves* (allochthonous debris) were collected from the littoral zone. The debris was cleaned with a soft toothbrush, rinsed in a mild acid bath and air dried.

Gastropods were held alive for 12 hours to allow evacuation of the gut contents and then frozen in liquid nitrogen for transport to the laboratory. Later, bodies were removed from the shells, guts dissected and the remaining tissue air dried.

After drying all samples were ground with a mortar and pestle and stored in a desiccator until used.

Analysis

Samples were analysed for their carbon stable-isotope composition with an isotope ratio mass spectrometer (Europa Tracermass). The analysis was conducted by Dr Stuart Bunn at the Division of Environmental Sciences, Griffith University, Queensland. Delta values were calculated against a conventional standard (PDB carbonate) according to

$$\delta^{13}C = [(\frac{R(sample)}{R(standard)}) - 1] \times 1000 (‰)$$

where $R = {}^{13}C/{}^{12}C$

6.4.3 Results

The littoral zone of Cooper Creek, where snails were collected, provides limited potential food sources. Bark and twigs, coarse organic detritus are found at all depths in the littoral zone. Owing perhaps to high turbidities and therefore low photic depths (cf. Section 6.7), only the emergent macrophyte *Ludwigia peploides* is present. A similar situation was apparent for benthic algae: thin mats only are found on snags present in shallow water.

The $\delta^{13}C$ values of the organic matter, both fine particulate (FPOM: -26.51 to -25.93) and coarse (CPOM: -27.59 to -26.69) are similar to the potential detritus sources: leaves of *Ludwigia peploides* (-27.38 to-26.51), redgum bark and twigs (-27.46 to -27.23) and redgum leaves (-27.57 to -26.7). The periphytic algae scrubbed from shallow snags are $\delta^{13}C$-enriched (-24.56 to -22.94) compared with the detrital sources, whereas algae from deeper snags are considerably $\delta^{13}C$-depleted, -34.73 to -31.73 (Figure 6.4).

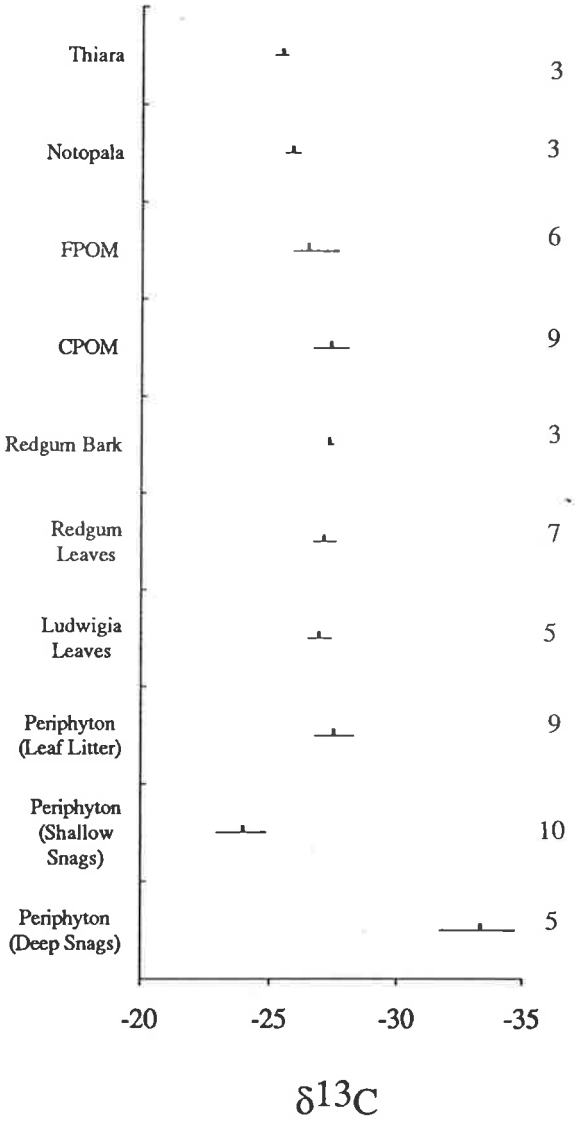


Figure 6.4 Means (range) of $\delta^{13}C$ values for the gastropods *Notopala sublineata* and *Thiara balonnensis* and their possible food sources from Cooper Creek, December, 1991. Numbers are the values of n.

The $\delta^{13}C$ values of the gastropods *N. sublineata* (-25.87 to -25.6) and *T. balonnensis* (-25.46 to -25.15) are slightly enriched, within 3‰, compared with the $\delta^{13}C$ values of the detritus (CPOM and FPOM), suggesting that detritus is a potential food source. Periphytic algae from deep snags are far too $\delta^{13}C$-depleted (approximately 8‰) to be a major food source for the gastropods, while periphytic algae from shallow snags are too $\delta^{13}C$-enriched (2‰).

The $\delta^{13}C$ values obtained in this study are similar to those of Rounick *et al.,* (1982), where the allochthonously derived detritus had a $\delta^{13}C$ value of approximately -26‰, and diatoms a $\delta^{13}C$ value of -33‰ (Rounick *et al.,* 1982). The periphytic algae from deeper snags in Cooper Creek had a $\delta^{13}C$ value of -34‰, suggesting a composition predominantly of diatoms.

Based on the $\delta^{13}C$ values of the gastropods and their potential food sources, both *N. sublineata* and *T. balonnensis* appear to derive most of their biomass carbon from the abundant amorphous organic detritus present in the littoral zone.

6.4.4 Discussion

As most consumers are only slightly ^{13}C enriched (1‰) compared to their diet (DeNiro and Epstein, 1978; Petersen and Fry, 1987), it is unlikely that periphytic algae, from either shallow or deep snags, are a major source of biomass carbon for *N. sublineata* or *T. balonnensis.* It seems likely, therefore, that both species are detritivores. A possible explanation for the higher than expected $\delta^{13}C$-enrichment of the gastropods compared with the detritus may be that heterotrophic micro-organisms are using the detritus as their primary carbon source becoming $\delta^{13}C$-enriched by approximately 1‰. The gastropods then may be consuming the micro-organisms from the detritus and becoming further enriched by 1-2‰. This would explain why both species are about 3‰ $\delta^{13}C$-enriched when compared to the detritus alone. Alternatively they may be consuming a small amount of their carbon from the $\delta^{13}C$-depleted algae on deep snags, with a diet dominated by detritus, in this way bacteria would not be involved in the diet. In a feeding study of *Planorbis contortus,* Calow (1974) found individuals to selectively ingest detritus containing live bacteria over heat sterilised detritus.

A similar situation was described by Winterbourn and Rounick (1985) where the $\delta^{13}C$ value of stream insects suggested a diet dominated by algae, but an examination of gut contents found algae to be only a minor component (by volume) of the diet.

They suggested that heterotrophic micro-organisms were consuming algal exudates as their primary source of dissolved organic carbon, the stream invertebrates were then consuming the bacteria and adventitiously assimilating algal carbon. One way in which these complex food webs may be investigated is through radioactive tracers.

A dependence on allochthonous detritus as the primary food source has also been recorded for invertebrates in small forested streams, where autochthonous production is limited (Rounick *et al.,* 1982). The same has been observed for invertebrate communities in Northern Hemisphere tundra rivers (Bunn *et al.,* 1989), where nutrient limitation results in low levels of primary productivity (Petersen *et al.,* 1985). In habitats where autochthonous primary productivity is naturally high, invertebrate diets tend to be dependent on both epilithic algae and detritus (Bunn *et al.,* 1989).

6.5 Periphytic Bacteria as a Food Source

The morphology of the radula in *N. sublineata* and *T. balonnensis* suggests that both species are likely to consume periphytic microalgae and detritus. Items present in the contents of the guts and faecal pellets supports this prediction, with amorphous organic detritus being present in the greatest abundance. This is a situation also observed in other prosobranch gastropods (cf. Browne, 1978; Jokinen *et al.,* 1982; Dudgeon and Yipp, 1983). Evidence from carbon stable-isotopes takes the isolation of the diet one step further, suggesting that although both taxa are consuming detritus they are perhaps assimilating carbon from the heterotrophic periphytic bacteria present on this detritus.

Bacteria are essential for the decomposition of plant material in aquatic systems, and dominate in the later stages of decomposition (Suberkropp and Klug, 1976) Their role is two-fold: they are the primary metabolisers and their presence enriches the palatability and nutrient quality of the material for macroinvertebrates (Hill *et al.,* 1992), so it is the living microbiota rather than the detritus itself that represents the principal protein source for consumer organisms (Newell and Field, 1983). This has lead to ideas relating the microbiota living on the substratum to a nutritious paste covering a non-nutritious base (cf. Cummins *et al.,* 1973).

There has been considerable debate, however, regarding the importance of bacteria living in detritus versus the detritus itself as a food source for aquatic gastropods

(Newell and Field, 1983; Findlay and Meyer, 1984). Studies of some marine and freshwater taxa suggest positive correlations between the abundance of detritivores and micro-organisms. For example, the deposit feeding marine prosobranch *Hydrobia ulvae* digests the micro-organisms present in its fine detritus food source, with the population dynamics of the species closely following the population curves of the sediment micro-organisms, as estimated by nitrogen analysis (Newell, 1965). The planorbid *Planorbis contortus* selectively ingests detritus containing living bacteria when given a diet choice (Calow, 1974). Using radiotracers Kofoed (1975) showed that *Hydrobia ventrosa* assimilated bacteria with a 75% efficiency. Likewise, less than 10% of the daily bacterial production in sediments consumed by the amphipod *Hyalella azteca is* sufficient to meet its energy requirements (Hargrave, 1971). Food quality, in terms of microbial biomass, is also positively correlated with growth rates in chironomid detritivores (Ward and Cummins, 1979).

Other studies question whether the standing stocks of bacteria in detritus are sufficient to represent a significant carbon resource for consumers (Baker and Bradnam, 1976). Bacterial biomass usually constitutes only a small proportion of the total sediment organic carbon and therefore a small fraction of total organic carbon. Low bacterial standing stocks, and therefore productivity, suggest that bacteria may not be the sole source of nutrition for detritivores in all systems, especially in terms of carbon flow (Findlay and Meyer, 1984). However, their biomass in detritus may represent an essential nitrogen resource for consumers (Findlay and Tenore 1982; Newell and Field, 1983).

An alternate view of the role of bacteria in gastropod nutrition was proposed by Thomas (1990). He suggested that snails may not actually digest the bacteria present in the detritus, but that evolution has lead to a mutualistic interaction involving the exchange of nutrients between the snail and its food supply. When detritivorous snails consume decaying plant material they also ingest large amounts of short chain carboxylic acids (products from bacterial fermentation of the decaying matter) which can be absorbed through the alimentary canal, providing an additional source of carbon. Bacterial fermentation of the plant material continues as it passes through the gut, further increasing the food available to the snail.

Studies of detritivorous protozoans suggest that the microbially produced extra-cellular polysaccharides present in detritus are assimilated as a food resource (Sherr, 1988; Decho and Moriarty, 1990). In these protozoans bacteria are contributing more

to their nutrition than bacterial biomass alone suggests. A similar situation may exist for detritivorous gastropod nutrition.

The importance of any food item to a detritivorous freshwater snail will be a complex function of snail, environment and the abundance of food available in the habitat (Dudgeon and Yipp, 1983; Dillon and Davis, 1991). It is realistic, therefore, to expect that the role of bacteria in the nutrition of freshwater gastropods varies between different systems and with different taxa.

6.6 Aspects of Grazing Selection: A Feeding Study

6.6.1 Introduction

In Cooper Creek both *N. sublineata* and *T. balonnensis* are detritivores, consuming and assimilating carbon from the abundant organic detritus. When comparing the composition of gut contents and faecal pellets with the composition of the periphyton available in the habitat, both species appear to be selectively ingesting organic detritus in preference to inorganic material and other food items. The preferential selection of particular food items is documented for various gastropod taxa (Lodge, 1986; Barnese *et al.,* 1990) and other invertebrate grazers (Peterson, 1987). Lodge (1986) found that although detritus comprised less than 60% of the gut contents of the snail *Planorbis vortex* from natural habitats, individuals in laboratory studies selected against detritus and for diatoms.

As in other regulated rivers (cf. Williams and Winget, 1979; Petts, 1984; Dufford *et al.,* 1987), the dominant food source for snails in the littoral zone of the regulated lower River Murray appears to be algal rather than detrital. If, in the unregulated Cooper Creek, both *N. sublineata* and *T. balonnensis* gastropod taxa consume detritus (even when filamentous algae are available), it is possible that when grazing they are unable to remove filamentous algae from the substratum. If this is the case, then much of the food currently present in the littoral zone of the regulated lower Murray would be unavailable to the snails.

Gastropod feeding tracks provide a reliable description of food items removed from substrata by grazing (Hickman and Morris, 1985). This study determines whether

N. hanleyi removes strands of filamentous algae and attached diatoms from the substratum and selects organic detritus over inorganic material.

Samples of grazed and ungrazed periphyton are examined using the scanning electron microscope (SEM), providing a visual confirmation of food items removed by grazing. Further, the contents of guts and faecal pellets are compared with the composition of the ungrazed periphyton to determine if *N. hanleyi* selects particular food items when grazing. By selectively removing particular elements of the periphyton when grazing, snails may change the composition of the community. Five indicators of periphyton composition and quality are measured for samples from both grazed and ungrazed treatments.

6.6.2 Methods

Collection and Experimental Design

Small red gum snags with attached periphyton were collected from the littoral zone of the River Murray at Overland Corner (Site M10; Figure 4.6) in October 1992, placed on ice, in water and transported to the laboratory. Fourteen individual snags were sawn into two equal portions and each half placed in a separate small aquarium. Each aquarium was filled with pond water and aerated. The two halves of each snag formed a sample pair to which a treatment of either "grazed" or "ungrazed" was randomly assigned.

Specimens of *N. hanleyi* were collected from an irrigation pipeline at Kingston, South Australia (Chapter 1; Figure 1.4), in October 1992 and not fed for 24 hours. One adult snail was then placed in each aquarium assigned to the "grazed" treatment, and left to feed for 72 hours. At the end of this period snails were removed and immediately frozen. On thawing, bodies were separated from the shells and the guts removed and preserved in Lugol's solution. Faecal pellets were collected from the aquaria and also preserved in Lugol's solution.

Scanning Electron Microscope

A portion of intact periphyton from a "grazed" and an "ungrazed" treatment was removed from the snag with a razor blade and prepared for examination under the SEM. The periphyton was fixed in a solution of 2.5% gluteraldehyde for 48 hours, dried through an alcohol series (70, 80, 90 and 100%), spending a minimum of one

hour at each concentration, critical point dried, mounted on an aluminium stub with a double sided sticky tab and coated with gold/palladium. Specimens were examined with the Phillips SEM. Photographs were taken on Kodak T Max 100 size 120 black and white roll film.

Periphyton Quality

The amount of periphyton remaining in each treatment was removed from the snags by gently scrubbing with a soft toothbrush. Weight of plastic surfactant film ("Glad Wrap") was used to estimate surface area for each substratum. Weights of known surface areas were measured and the relationship between surface area and weight determined. The surface area of each snag substratum was then determined using this relationship (Appendix F).

A portion (2mL) of periphyton suspension was preserved in Lugol's solution for estimation of community composition (cf. Section 6.3). The remaining periphyton suspension was divided into four equal sub-samples using a modified Motoda sampler (Motoda, 1956). From these sub-samples five descriptors of the periphyton were determined: dry weight (DW), ash-free dry weight (AFDW), chlorophyll *a* (mg/m^2): pheophytin *a* (mg/m^2) and phospholipid as µmol/gram organic content.

The composition of the periphyton, gut contents and faecal pellets was determined by the methods described in Section 6.3. For each field of view at 400x magnification the percent cover of organic and inorganic detritus was estimated and the abundance of the two dominant algal types (filamentous green algae and diatoms) recorded. Owing to the different biovolumes of the two algal types, abundances of filamentous algae were corrected for larger size by dividing their abundance, in each field of view, by 3.5. The value 3.5 represents the average difference in biovolume between filamentous green algae (3.5 times larger) compared with diatoms. For each field of view the corrected abundance values for both algal types were summed and the percentage of each calculated. Five fields of view were counted for each sample of periphyton, gut contents and faecal pellets.

Organic content of samples was determined as recommended by Aloi (1990). The sample was filtered onto a pre-weighed Whatman No. 44 (ashless) filter paper and dried to a constant weight at 60°C. This weight minus that of the filter paper was recorded as the dry weight of the sample (DW). The dried sample was then ashed at 550°C for 4 hours in a muffle furnace, re-wetted with double distilled water then

dried to constant weight at 105°C. Aloi (1990) recommends the rewetting after combustion for samples with a high sediment content to restore the water of hydration to the clay fraction. The *ash-free dry weight* (AFDW) of the sample was calculated as the difference between the dry weight and the weight of the ash after combustion. AFDW, or organic content, represents the combined autotrophic (algal) plus heterotrophic (fungi, protozoa, bacteria) components of the periphyton (Biggs and Close, 1989).

Chlorophyll a (mg/m^2) for each sample was measured spectrophotometrically following Tett *et al.* (1975). Methanol was used as the solvent as it allows better discrimination between chlorophyll *a* and pheophytin *a*, an essential characteristic when examining river periphyton because more than half the total pigments may be breakdown products (Tett *et al.,* 1975).

At all times during pigment extraction samples were kept on ice at 4°C. Each sample was filtered onto a Whatman No. 3 filter paper and placed in a test tube to which 150 mg of $MgCO_3$ for each 10 mL of reagent quality methanol was added. The $MgCO_3$ renders the methanol alkaline and prevents premature acidification of the solution by cell products (Tett *et al.,* 1975).

Pigments were extracted in methanol by placing the sample at 4°C in the dark for 12-18 hours then transferring to a 70°C water bath and allowing the methanol to boil for 2 minutes. Short periods of boiling aid pigment extraction without converting significant amounts of chlorophyll *a* into pheophytin (Tett *et al.,* 1975). The solvent and washings were then poured into a centrifuge tube and the particulate matter spun at 2000 RPM.

After the first extraction a further quantity of methanol was added to the particulate matter which was then re-extracted at 4°C for 24 hours (second extract). After extraction pigment solutions were examined immediately to avoid the effects of decomposition. Optical densities were measured against a methanol blank at 750, 666 and again at 750 nm with a Varian UV/Visible Spectrophotometer. After initial readings extracts were acidified with two drops of 8% (2N) HCl, and optical densities remeasured at the same wavelengths. The readings at 750 nm were used to correct for background absorptions which may be significant in extracts from muddy sediments or dense periphyton. As post-acidification readings may increase with time two background readings were used (cf. Tett *et al.,* 1975). The concentration of

chlorophyll *a* for each sample was calculated from the optical density of the extracts before and after acidification using the following equation (cf. Tett *et al.,* 1975):

$$\text{Chlorophyll } a \text{ (mg/m}^2\text{)} = \frac{[G(O-A)\times V]}{\text{Area}}$$

where:

$O = O_{666} - 0.5(O_{750(1)} + O_{750(2)})$ optical density before acidification

$A = A_{666} - 0.5(A_{750(1)} + A_{750(2)})$ optical density after acidification

$G = 18.8$ cm mg M^{-1} the extract chlorophyll *a* concentration that results in a 666nm optical density difference pre- and post-acidification of 1 cm^{-1}.

V = Volume of sample extract (Litres)

Area = Area of substrate scrubbed (m^2)

The measure of chlorophyll *a* represents the autotrophic (algal) component of the periphyton (Biggs and Close, 1989).

Total *phospholipid content* expressed as mg/m^2 and µmol/ gram organic content was determined using methods modified from White *et al.* (1979), with recipes for solutions used given in Appendix G. Periphyton samples were initially freeze dried (DYNAVAC Model FD-5) then ground using a mortar and pestle. Approximately 300 mg of ground periphyton was added to an acid washed 250 mL conical flask and suspended in 25 mL of 50 mM phosphate buffer. Anhydrous methanol (75 mL) and chloroform (37.5 mL) were added to the suspension, mixed vigorously and allowed to extract for 2.5 to 3.5 hours. After this initial period an additional 37.5 mL chloroform and 37.5 mL distilled water were added to the suspension which was again mixed vigorously and allowed to separate for a further 24 hours.

A portion (20 mL) of the chloroform layer (lower phase) was removed with a bulb pipette. From this 20 mL a 1 mL aliquot of chloroform was added to the bottom of three acid washed (50 mL) test tubes. The solvent was removed by heating the test tube base in a 40°C waterbath for 12 hours. The dried lipid was digested with 1.5 mL

of 35% perchloric acid by heating to 180-200°C for 2 hours in a sand tray on a laboratory hotplate. After cooling 2.4 mL of molybdate reagent and 2.4 mL of diluted ANSA were added. The mixture was heated in a boiling water bath for 7-10 minutes, cooled and the absorbance determined at 830 nm on a Varian UV/Visible Spectrophotometer. The phosphate content of each sample was determined colorimetrically.

Phospholipids are derived from both the autotrophic and heterotrophic components of the periphyton. As they are rapidly degraded in aquatic ecosystems, the phospholipid content provides a measure of the total viable biomass of the sample (White *et al.,* 1979; Vestral and White, 1989).

The *acidification ratio* (ratio of pre- and post-acidification optical densities at 666nm) can provide an indication of the concentration of living pigment (chlorophyll *a*) compared with pigment breakdown products (pheophytin *a*) in a pigment solution. As one molecule of chlorophyll *a* converts to one molecule of pheophytin *a*, the ratio of a pure solution of chlorophyll *a* in methanol can be defined as "H". H is dimensionless and solutions containing a mixture of chlorophyll *a* and pheophytin *a* show values between 1 and 3.8, the closer the ratio is to 3.8 the nearer the pigment to a solution of pure chlorophyll *a* (cf. Tett *et al.,* 1975). The ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2) is a measure of the heterotrophy/autotrophy of the sample, smaller values are representative of communities dominated by autotrophs or algae with high chlorophyll *a* concentrations, whereas larger values are representative of samples dominated by heterotrophs such as fungi and some bacteria.

Analysis

To determine if snails were actively selecting either algal taxa from the periphyton, a Kruskal-Wallis one way ANOVA was used for each snail in the "grazed" treatments to compare the percentage of diatoms and filamentous green algae in its periphyton food source with percentages in the gut contents and faecal pellets. A Wilcoxon Signed Rank test for paired samples (Zar, 1984) was used to explore differences in each food quality parameter between grazed and ungrazed treatments.

6.6.3 Results

Scanning Electron Micrographs

Attached periphyton from ungrazed treatments contains thick mats of filamentous green algae (Photograph 6.3a). Trapped within the filaments are clumps of amorphous organic material, inorganic material and abundant diatoms (Photograph 6.3b). Despite the presence of abundant organic matter, filamentous green algae appear to constitute the majority of the periphyton biomass (by volume).

Grazing removes the bulk of the attached algae, leaving occasional loose strands of filamentous forms, closely attached diatoms and occasional clumps of organic material (Photograph 6.3c). This can be visualised by comparing Photograph 6.3d, showing organic matter trapped within the mats of filamentous algae on an ungrazed surface, with a photograph of a grazed surface taken at the same magnification (Photograph 6.3e). In the later picture nearly all filamentous algae has been removed leaving only loose strands.

Food Item Selection

Inorganic detritus was more abundant in the periphyton (40%) than in either the gut contents or faecal pellets (20%). In comparison, organic detritus was more abundant in the gut contents and faecal pellets (>50%) than it was in the periphyton (30-40%). Algae, predominantly diatoms and filamentous greens, were found in similar abundances in periphyton, gut contents and faecal pellets for all snails. No zooplankton remains were found.

By comparing the biovolume percentages of diatoms from filamentous algae between the periphyton, gut contents and faecal pellets, it is possible to determine if the snails are preferentially consuming either major algal taxa. The biovolume percentage of diatoms, compared with filamentous green algae for each snail and grazing treatment, along with values for Kruskal-Wallis H, are given in Table 6.4. Although each comparison (and therefore test) is independent, the number of tests conducted (11 separate tests) suggests that a significance level lower than $p=0.05$ should be used to control the chance of making a Type I error. A Bonferroni adjusted (cf. Neter *et al.*, 1985) significance level of $p=0.01$ was chosen.

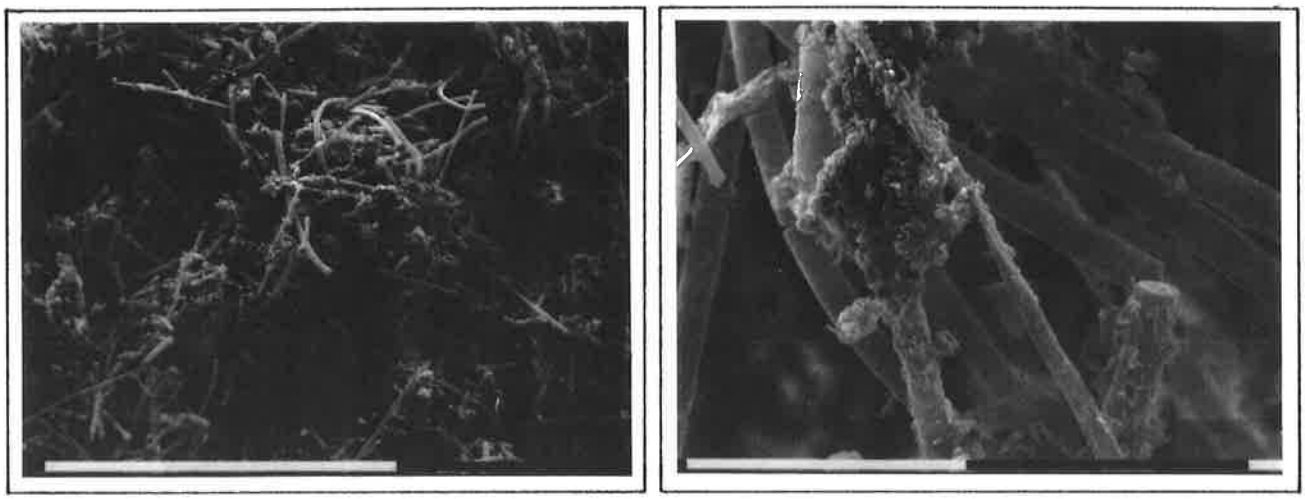
Non-significant differences were found in the percent abundance of diatoms/filamentous algae between the periphyton food source and the contents of guts and faecal pellets for all comparisons except Snails G and H. In these cases the percentage of filamentous algae in the periphyton was higher than in either the gut contents or faecal pellets. It is likely that this reflects random variation in the periphyton sampled rather than avoidance of algae by either snail.

Table 6.4 Percent abundances (SE) of diatoms compared with filamentous green algae (corrected for biovolume) for the gut contents and faecal pellets of *N. hanleyi* grazing on the periphyton food source. Values for Kruskal-Wallis H are given.

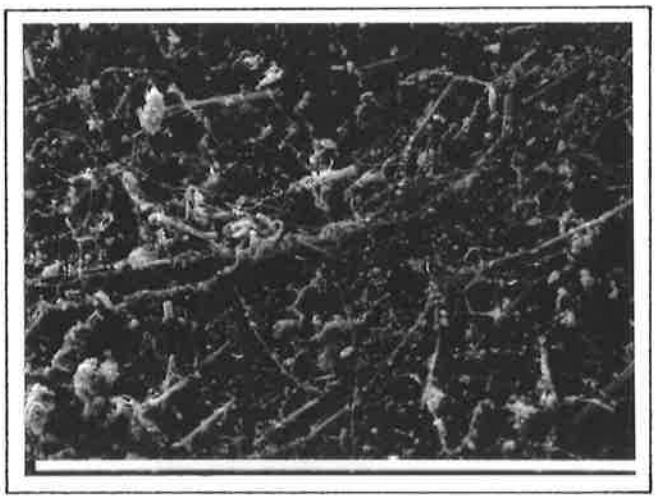
Snail	Periphyton	Gut Contents	Faecal Pellets	Kruskal-Wallis H
A	89.26 *(1.92)*	91.47 *(0.89)*	88.63 *(1.39)*	1.82, p>0.01
B	91.94 *(0.78)*	92.95 *(1.03)*	90.50 *(1.95)*	1.38, p>0.01
C	88.49 *(0.64)*	80.58 *(2.01)*	85.45 *(2.54)*	7.84, p>0.01
D	91.94 *(0.96)*	92.16 *(1.21)*	90.32 *(1.77)*	0.42, p>0.01
E	85.41 *(2.07)*	89.53 *(0.94)*	84.89 *(1.30)*	5.29, p>0.01
F	79.82 *(2.36)*	81.73 *(1.94)*	84.45 *(1.55)*	2.22, p>0.01
G	65.76 *(4.75)*	86.85 *(1.22)*	84.24 *(1.59)*	9.80, p<0.01
H	66.48 *(2.06)*	87.85 *(1.18)*	77.90 *(2.48)*	11.59, p<0.01
I	66.75 *(4.48)*	66.22 *(2.27)*	78.33 *(2.27)*	6.02, p>0.01
J	80.18 *(3.04)*	82.72 *(2.56)*	84.09 *(1.32)*	1.00, p>0.01
K	85.20 *(1.67)*	84.94 *(0.39)*	83.69 *(2.16)*	0.56, p>0.01

Periphyton Food Quality Parameters

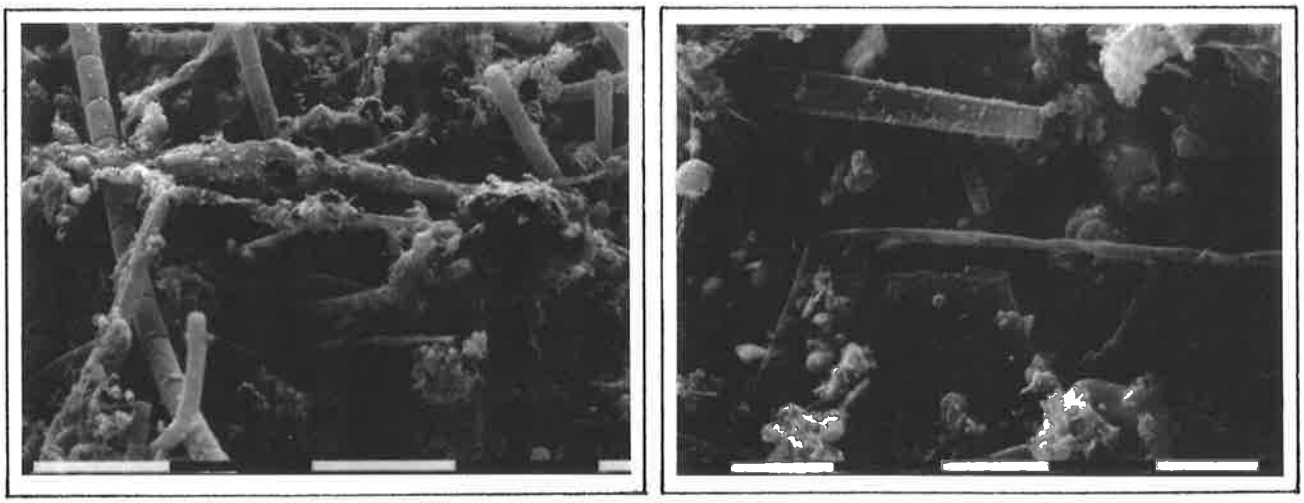
The high acidification ratio and the low ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2) from both grazed and ungrazed treatments suggest a periphyton dominated by algae (Table 6.5). Using the Wilcoxon Signed Ranks test non-significant differences were found in all food quality parameters between grazed and non-grazed treatments. This suggests that the snails did not remove any one element of the periphyton (e.g. algae) in sufficient quantities to significantly modify its composition after 72 hours of grazing.



(a) (b)



(c)



(d) (e)

Photograph 6.3 Scanning Electron Micrographs from grazing experiment.
(a) ungrazed periphyton (scale = 1 mm)
(b) closeup of ungrazed periphyton showing trapped detritus (scale = 0.1 mm)
(c) grazed periphyton (scale = 1 mm)
closeup of (d) ungrazed, and (e) grazed periphyton for comparison (scale = 0.1 mm).

Table 6.5 Food quality parameters, means (SE) for periphyton from grazed and ungrazed treatments, Wilcoxon Z Scores for the Wilcoxon Sign Ranks Test and probability values are also given.

	Grazed	Ungrazed	Wilcoxon Z
Chlorophyll *a* (mg/m^2)	36.99 *(9.08)*	34.67 *(6.33)*	0.384, p>0.05
Phospholipid (µmol/g organic weight)	149.49 *(26.93)*	138.97 *(18.98)*	-0.14, p>0.05
% Organic Content	22.2 *(1.64)*	19.42 *(1.01)*	-1.224, p>0.05
Acidification Ratio	2.93 *(0.04)*	2.89 *(0.04)*	-1.852, p>0.05
Phospholipid (mg/m^2): Chlorophyll *a* (mg/m^2)	4.22 *(0.89)*	3.22 *(0.61)*	-1.352, p>0.05

6.6.4 Discussion

The grazing style of *N. hanleyi* resembles the action of a vacuum cleaner. The taenioglossid radula appears to be capable of removing nearly all loosely attached particles from the surface of the substratum including strands of filamentous green algae, leaving only closely attached forms. This corresponds with the observations of Barnese *et al.* (1990), where the taenioglossid radula of *Elimia livescens* removed all loosely attached particles but was unable to remove closely attached forms.

Observations of the composition of gut contents and faecal pellets compared with the periphyton food source suggest that during grazing *N. hanleyi* may be selecting organic detritus in preference to inorganic material and other items. This may be a result of the morphological adaptations of the taenioglossid radula as Barnese *et al.* (1990) observed that *Elimia livescens* was also able to select organic material in preference to sand grains.

With similar abundances of diatoms and filamentous algae in the periphyton food source, guts and the faecal pellets it appears that *N. hanleyi* is not selectively ingesting either algal form. Dillon and Davis (1991) found no difference in the abundance of diatoms between the food source and gut contents of three gastropod taxa with morphologically different radulae and suggested that the abundance of diatoms in gut contents is primarily a function of their relative abundance in the habitat. Despite such similar abundances, algae may still be involved in snail nutrition. Thomas (1990) proposes that a mutualistic interaction exits between freshwater gastropods and epiphytic algae with at least some algal taxa being resistant to digestion but releasing dissolved organic carbon as they pass through the gut, thereby contributing to nutrition as well as being viable when eliminated.

The present study does not distinguish between living and dead algae in the guts or faeces. It is difficult to determine therefore if cells have passed through the digestive tract unharmed, and are thus resistant to digestion, or if the cells have been killed and partly digested. Peterson (1987) found only 50% of the diatoms consumed by grazing caddis larvae were viable when eliminated. The apparent lack of algal carbon assimilated by the gastropods in Cooper Creek (Section 6.4), however, argues against a role for algae in the nutrition of these taxa.

This investigation suggests that *N. hanleyi* has a diet dominated by organic detritus and does not appear to avoid consuming algae. Therefore, if algae were to become the dominant item in the available food source would these snails become food limited? Many studies assume that if algae is present then food quality will be high (cf. Couch and Meyer, 1992). Surely this is only the case if the algae can be utilised as a food resource by the taxa in question. If the natural food source has been displaced at the expense of an increase in the abundance of algae taxa may become food limited. Such a situation is envisaged for the lower River Murray where the natural food sources for the gastropod taxa, organic detritus, has been replaced with benthic algae.

6.7 Food Availability and Quality

6.7.1 Food in the Environment

Food *quality* is the growth-producing nutritive content per unit mass of food (Naiman, 1983) whereas food *quantity* is the density per unit of environment of the food source (Ward and Cummins, 1979). Food quality is known to affect growth, fecundity and secondary production in a number of freshwater invertebrates (Eisenberg, 1966; Calow, 1970; El-Eman and Madsen, 1992; Hill 1992), and is important in regulating some populations of gastropods through a reduction in reproductive potential (Eisenberg, 1970). One way of assessing food quality is through the ratio of carbon to nitrogen (C:N) in the food source. Nitrogen is vital for growth and production, so that food sources with a low C:N tend to be better quality foods (cf. McMahon *et al.*, 1974).

In unregulated lowland rivers most of the periphytic biomass is likely to be bacterial, especially where light penetration is limited (cf. Couch and Meyer, 1992) and where

changeable levels maintain a highly productive, early stage of succession in littoral communities (Junk *et al.,* 1989). In the River Murray regulation has stabilised seasonal water levels (Chapter 1), providing a favourable environment for increased algal production so that most surfaces are coated by mats of filamentous green algae (*Spirogyra* spp.). Similar changes have been observed in other rivers where water levels have been stabilized (Williams and Winget, 1979; Petts, 1984). As *N. hanleyi*, *N. sublineata* and *T. balonnensis* are deposit feeding detritivores an increase in the algal biomass of the periphyton may represent a decline in the quality of available food which has the potential to impact growth and fecundity leading to a decrease in abundance.

In this section the nature of the food available in habitats with, and without, snails was examined. Periphyton food sources were collected from the littoral zone of Cooper Creek where populations of both *Notopala sublineata* and *Thiara balonnensis* are abundant. As both taxa are presumed extinct in the lower River Murray (cf. Sheldon and Walker, 1993a and 1993b), the nature of the food available in the littoral zone of this habitat was also examined. The existence of a population of *N. hanleyi* in an irrigation pipeline in the South Australian Riverland (Sheldon and Walker, 1993a) provided an opportunity to compare the quality of food available to the snails in the pipelines with that present in the lower Murray.

6.7.2 Methods

Collection

Periphyton was collected from three areas, the littoral zone of Cooper Creek in north-east South Australia (Figure 6.3), where *N. sublineata* and *T. balonnensis* co-occur, and the littoral zone of the main channel of the lower River Murray (Chapter 4, Figure 4.6), where both species of *Notopala* are presumed extinct (cf. Sheldon and Walker 1993a, 1993b) and *T. balonnensis* is extremely rare. Specimens of periphyton were also collected from the Loveday irrigation pipeline near Barmera in the South Australian Riverland (Chapter 1, Figure 1.4) where *N. hanleyi* is abundant (cf. Sheldon and Walker, 1993a).

In the littoral zone of Cooper Creek periphyton was collected from the two most abundant microhabitats, red gum (*E. camaldulensis*) snags and red gum leaf litter.

At sites in the littoral zone of the main channel of the lower River Murray between Locks 2 and 4 (Sites M1, M4, M8, M10, M12, and a site immediately above Lock 2; Figure 4.4 and 4.6) periphyton was collected from red gum snags only. These sites were chosen to represent lower pool, middle pool and upper pool regions of the river (Chapter 4).

In each case periphyton was removed by gently scrubbing each substratum in distilled water with a soft toothbrush. Weight of surfactant film was used to estimate surface area of snag substrata, surface area of leaf litter was calculated using the detergent displacement method. For the irrigation pipelines a standard surface area from the inside of a freshly drained pipe was scrubbed.

Periphyton Quality

Dry weight, ash free dry weight, chlorophyll *a* and total phospholipid content (for Murray and pipeline samples only) were calculated for each periphyton sample by the methods described in Section 6.6.

The total carbon content and the total nitrogen content for each sample were determined by Mr Colin Rivers of the Waite Agricultural Research Institute, University of Adelaide. The ratio of carbon to nitrogen was calculated as a measure of the nutritional quality of the periphyton (cf. McMahon *et al.*, 1974). Higher values of this ratio are representative of samples with a high carbon content relative to nitrogen and therefore a low nutritional quality. A sub-sample of the periphyton (2 mL) was preserved in Lugol's solution for estimates of community composition (cf. Section 6.6).

A portion of intact periphyton from the red gum snags and leaf litter from Cooper Creek was removed from the substratum with a razor blade and prepared for examination under the SEM using methods outlined in Section 6.6.

Analysis

Mann-Whitney U tests were used to explore differences between food quality parameters of the different microhabitats on Cooper Creek and also between samples from the littoral zone of the lower Murray and from the Loveday irrigation pipeline. Kruskal-Wallis one-way ANOVAs were used to explore differences in food quality parameters between the different pool types of the lower Murray. Differences were

isolated using Tukey's Honestly Significant Difference procedure. The statistical package SYSTAT v 5.0 was used (Wilkinson, 1990).

As the percentage abundance of each food item was only estimated for each sample (cf. Section 6.6), differences between samples were not explored statistically.

6.7.3 Results

Cooper Creek

Periphyton samples were collected from Cooper Creek in December 1991 in the ebb of a flood. Flows in the system were extremely low at this time (J.T. Puckridge, University of Adelaide, personal communication) the water temperature was 24°C, oxygen saturation 71%, salinity 200 mg/L and Secchi depth 10 cm.

Periphyton from leaf litter contains approximately 50% inorganic detritus, 20-30% organic detritus, less than 20% diatoms, and less than 10% filamentous green algae, other green algae and animal material (cf. Table 6.1). Samples from snags contain less inorganic material (20-30%) than scrubs from leaf litter but approximately the same amount of organic detritus (50%). The snag scrubs have a higher proportion of diatoms (30%), filamentous green algae (10-20%) and blue green algae (15%) than leaf litter scrubs. The higher algal biomass in the snag periphyton is due to the position of the snags higher in the littoral (photic) zone than the leaf litter.

Means (SE) for each food quality parameter for scrubs from both microhabitats are given in Table 6.6. Periphyton collected from snag substrata within the photic zone contains a higher abundance of algae than periphyton from leaf litter resting on the bottom (cf. Table 6.1). This is reflected in a higher organic content ($U=5$, $p<0.05$; Figure 6.5a) and a greater chlorophyll *a* concentration ($U=0$, $p<0.01$; Figure 6.5b). The acidification ratio is also higher in the snag periphyton ($U=0$, $p<0.01$; Figure 6.5c), suggesting that more of the periphyton biomass is living plant material, probably algae, rather than decomposing plant material.

Food quality, measured as the ratio of carbon: nitrogen, does not differ between periphyton from the two microhabitats ($U=29>0.05$; Figure 6.5d). Snag periphyton, however, has a higher percent carbon content ($U=3$, $p<0.05$; Figure 6.5e) due to the higher algal biomass of this periphyton.

Table 6.6 Mean (*SE*) for five characteristics of the periphyton collected from snag and leaf litter microhabitats from the littoral zone of Cooper Creek in December 1991.

	n	Leaf	n	Snag
Chlorophyll *a* (mg/m^2)	7	0.42 *(0.084)*	7	8.48 *(1.655)*
% Organic Content	7	16.12 *(0.882)*	7	25.72 *(3.593)*
Acidification Ratio	7	2.212 *(0.084)*	7	3.03 *(0.091)*
Carbon: Nitrogen	6	10.33 *(1.254)*	7	8.22 *(0.698)*
%Carbon Content	7	7.56 *(0.967)*	7	13.11 *(1.879)*

Within River Differences

Environmental data for each site are given in Table 6.7.

Table 6.7 Environmental data for sites in the littoral zone of the lower River Murray where periphyton samples were collected, July 1992.

Site	Temperature °C	Oxygen (% saturation)	Salinity (mg/L)	Secchi Depth (cm)
M1	14	100	401	30
M4	13.5	100	425	26
M9	13	100	500	26
M12	14	100	542	28
M14	14	100	515	29
M16	15	100	529	28

Periphyton from snag substrata from all three pool regions comprised less than 30% inorganic detritus and more than 50% organic detritus (Table 6.8). Diatoms were most abundant (20-30%) in samples from upper pool sites (M8 and above Lock 2) and least abundant (<10%) in samples from lower pool sites (M1 and M10). Filamentous green algae comprised between 10 and 20% of samples from all pools with blue-greens comprising <10%. Animal material was present in some samples but overall it was rare.

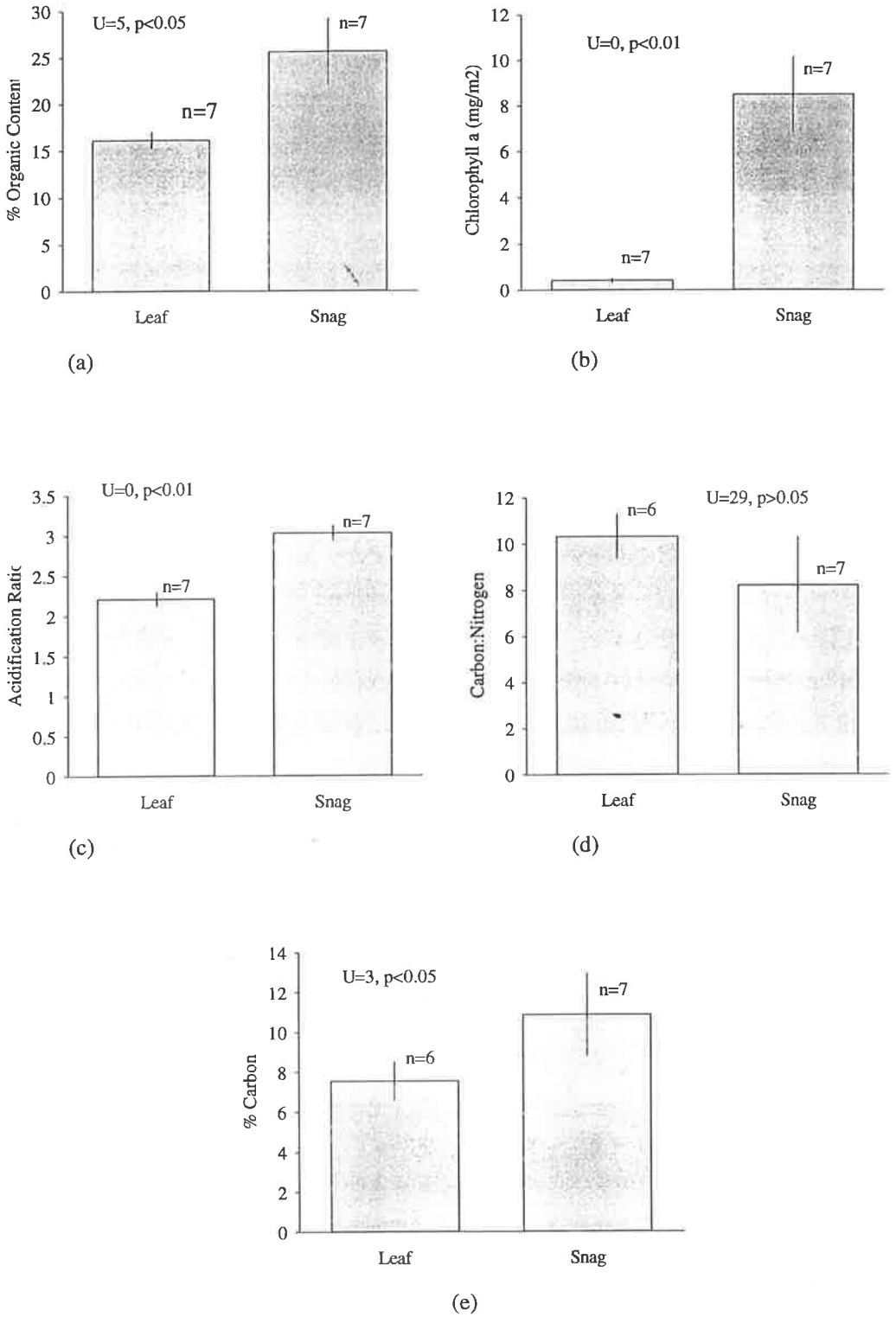


Figure 6.5
Food quality indicators for periphyton from leaf litter and snags in Cooper Creek; (a) % organic content, (b) Chlorophyll *a* concentration (mg/m^2), (c) acidification ratio (d) carbon: nitrogen ratio, (e) % carbon content.

Table 6.8 Estimated abundance of food items in periphyton samples scrubbed from snags collected from sites in lower pool (n=15), middle pool (n=15) and upper pool (n=15) regions of the lower River Murray, July 1992.

	Lower Pool	Middle Pool	Upper Pool
Inorganic Detritus	<30%	<30%	<30%
Organic Detritus	>50%	>50%	>50%
Diatoms	<10%	10-20%	20-30%
Filamentous Algae	10%	10-20%	10-20%
Other Algae	<5%	<5%	<5%
Blue-green Algae	<10%	<10%	<10%
Animal Material	<5%	<5%	<5%

Means (SE) for each food quality parameter are given in Table 6.9. The organic content of periphyton from the different pool regions does not differ ($H=5.74$, $p>0.05$; Figure 6.6a), however, there are differences in the chlorophyll *a* concentration ($H=36.44$, $p<0.001$; Figure 6.6b). Samples from lower pools have less chlorophyll *a* than those from middle pool and upper pool regions. Diatoms were far more abundant in samples from middle and upper pools than they were in lower pool samples. Periphyton from lower pool sites has the same organic content as from the other pools but a lower chlorophyll *a* concentration, this suggests that periphyton in this region contains organic matter from a source other than algae.

Table 6.9 Mean *(SE)* for five characteristics of the periphyton from snag habitats in the lower, middle and upper pool regions of the littoral zone of the lower River Murray, July 1992.

	n	Lower	n	Middle	n	Upper
Chlorophyll *a* (mg/m^2)	30	44.3 *(5.93)*	30	108.8 *(13.38)*	30	133 *(9.44)*
Phospholipid (µmol/g organic weight)	21	192.3 *(29.65)*	19	208.3 *(36.6)*	21	115.7 *(11.06)*
% Organic Content	30	16.3 *(2.18)*	30	15.2 *(1.39)*	30	20.1 *(1.68)*
Acidification Ratio	30	3.1 *(0.52)*	30	3.1 *(0.03)*	30	2.8 *(0.02)*
Phospholipid (mg/m^2): Chlorophyll *a* (mg/m^2)	21	5.9 *(2.05)*	19	1.5 *(0.31)*	21	0.8 *(0.07)*
Carbon: Nitrogen	10	11.8 *(0.95)*	9	10.3 *(1.9)*	10	7.9 *(0.75)*
% Carbon Content	10	6.9 *(0.63)*	9	6.9 *(1.01)*	10	4.9 *(0.66)*

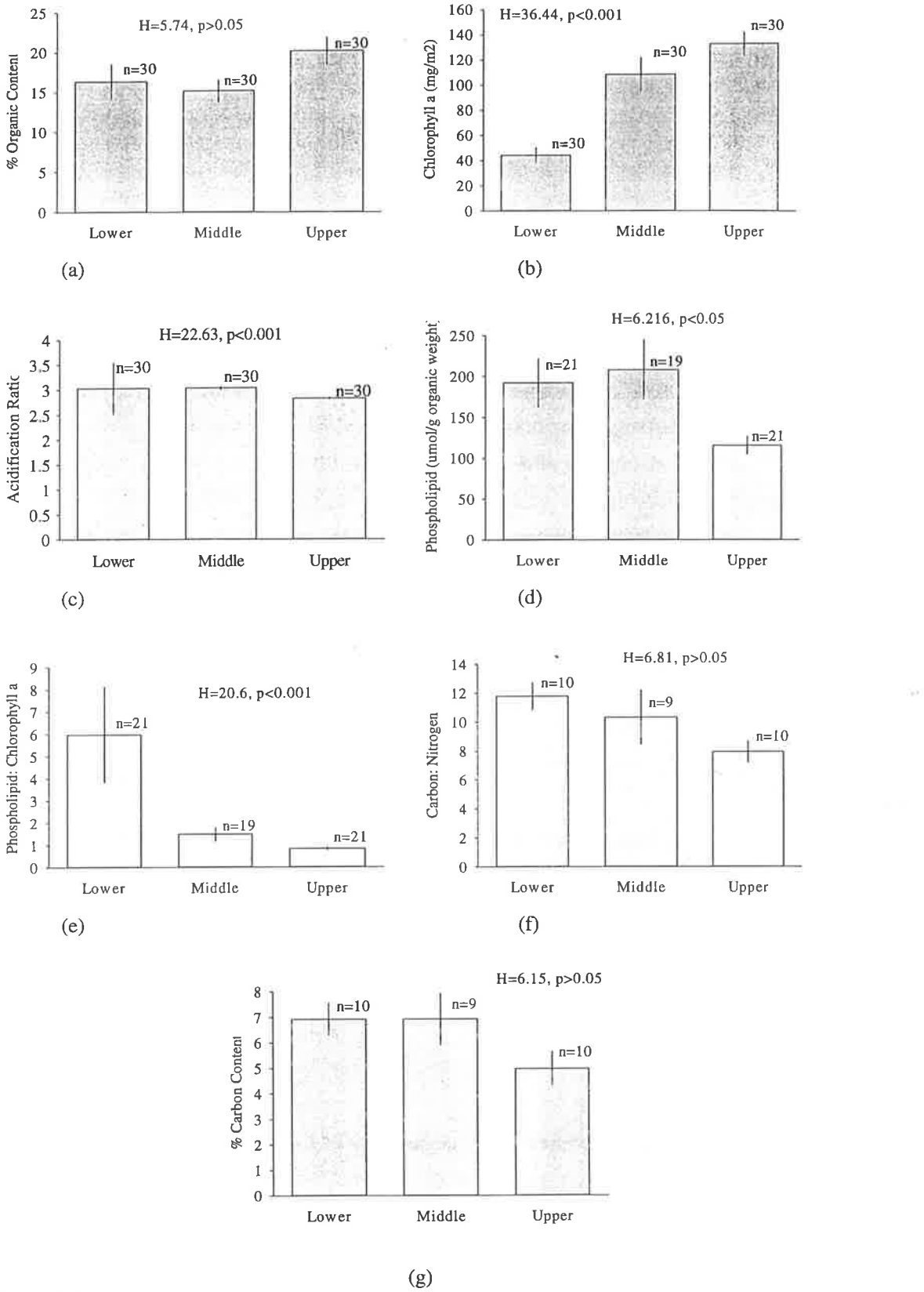


Figure 6.6

Food quality indicators for periphyton from Lower, Middle and Upper Pool regions of the littoral zone of the main channel of the lower River Murray; (a) % organic content, (b) chlorophyll *a* concentration (mg/m^2), (c) acidification ratio, (d) phospholipid concentration (µmol/g organic weight), (e) ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2), (f) carbon: nitrogen ratio, (g) % carbon content.

The acidification ratio also differs between pools ($H=22.63$, $p<0.001$; Figure 6.6c) with samples from upper pools having lower ratios than those from middle or lower pools. The lower ratio of periphyton from the upper pool suggests a greater abundance of decomposing material and therefore pigment breakdown products.

The phospholipid content (µmol/ gram organic weight) provides a measure of the total heterotrophic and autotrophic biomass of the periphyton community. Differences exist between pools ($H=6.216$, $p<0.05$; Figure 6.6d) with upper pool samples having less phospholipid (µmol/gram organic weight) than middle or lower pool samples. The ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2) gives a measure of the heterotrophy/autotrophy of the periphyton community and differences exist in this ratio between the pools ($H=20.6$, $p<0.001$; Figure 6.6e). The ratio is lower in middle and upper pools compared with lower pools which suggests the periphyton community in the middle and upper regions is dominated by algae or autotrophs whereas in the lower pool regions the periphyton contains a higher abundance of heterotrophs. This is in agreement with the lower chlorophyll *a* concentration of lower pool periphyton.

The periphyton of the different pool regions did not differ in the food quality ratio of carbon: nitrogen ($H=6.81$, $p>0.05$; Figure 6.6f) or in the percent carbon content of the periphyton ($H=6.155$, $p>0.05$; Figure 6.6g)

River Murray and Irrigation Pipelines

To obtain an overall representation of the food value of periphyton in the riverine environment of the lower River Murray samples from all three pool regions were used. Food quality parameters from total river periphyton were than compared with samples taken from the Loveday irrigation pipeline in July 1992.

Periphyton from snags in the lower Murray had a higher abundance of all algal types than did periphyton scrubbed from the inside walls of the pipelines which is expected as the pipelines are enclosed and at least two metres below ground (Table 6.10). Pipeline periphyton did contain occasional diatoms which were most likely trapped as the river water moved through the pipe. Means (SE) for each parameter are given in Table 6.11. The higher algal biomass in the river is reflected in the periphyton having a higher chlorophyll *a* concentration ($U=88$, $p<0.001$; Figure 6.7a). River periphyton also had a higher organic content than that collected from within the

irrigation pipeline (U=170, p<0.001; Figure 6.7b) which can be attributed to the larger biomass of filamentous green algae in riverine periphyton (cf. Table 6.10).

Table 6.10 Estimated abundance of food items in periphyton scrubbed from snags in the littoral zone of the lower River Murray (n=45) and from the inner walls of the Loveday irrigation pipeline (n=11), July 1992

	River	Pipeline
Inorganic Detritus	30%	20-30%
Organic Detritus	>50%	>50%
Diatoms	10-30%	<5%
Filamentous Greens	10-20%	<5%
Other Greens	<5%	0
Blue-greens	<10%	<1%
Animal Material	<5%	0

Table 6.11 Mean (*SE*) for seven characteristics of the periphyton from snag habitats in the littoral zone of the lower River Murray and periphyton from the inner walls of the Loveday Irrigation Pipeline, July 1992.

	n	River	n	Pipeline
Chlorophyll *a* (mg/m^2)	90	95.4 *(6.98)*	11	14.67 *(1.62)*
Phospholipid (µmol/ g organic weight)	61	170.9 *(16.35)*	8	342.57 *(69.64)*
% Organic Content	90	17.2 *(1.04)*	10	8.48 *(1.06)*
Acidification Ratio	90	2.9 *(0.02)*	11	2.49 *(0.08)*
Phospholipid (mg/m^2): Chlorophyll *a* (mg/m^2)	61	2.82 *(0.76)*	8	63.42 *(7.43)*
Carbon: Nitrogen	29	10 *(0.76)*	8	4.24 *(0.36)*
% Carbon	29	6.26 *(0.46)*	8	3.33 *(0.26)*

Riverine periphyton has a higher acidification ratio (U=108, p<0.001; Figure 6.7c) suggesting this periphyton source is dominated by living algal pigment rather than breakdown products. The higher concentration of breakdown products in pipeline periphyton may be attributed to the accumulation of decomposing amorphous organic matter on the pipeline walls.

Pipeline periphyton has a higher phospholipid content, expressed as µmol per gram of organic weight than river periphyton ($U=402$, $p<0.01$; Figure 6.7d) which indicates a higher living biomass per gram of organic content. This is confirmed by the ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2), which is lower in river periphyton suggesting a dominance by algae ($U=488$, $p<0.001$; Figure 6.7e).

The ratio of carbon to nitrogen was higher in periphyton from the river than from the pipelines ($U=8$, $p<0.001$; Figure 6.7f) which suggests lower food quality for river periphyton. This could be caused by a higher percentage of carbon in river periphyton. There is a difference in the percent carbon of the two periphyton sources ($U=27$, $p<0.001$; Figure 6.7g) however, when this is corrected for differences in organic content, carbon constitutes approximately 35% of the total organic content of both river and pipeline periphyton. Differences in the ratio of carbon to nitrogen between the two sources must therefore be attributed to pipeline periphyton having a higher concentration of nitrogen.

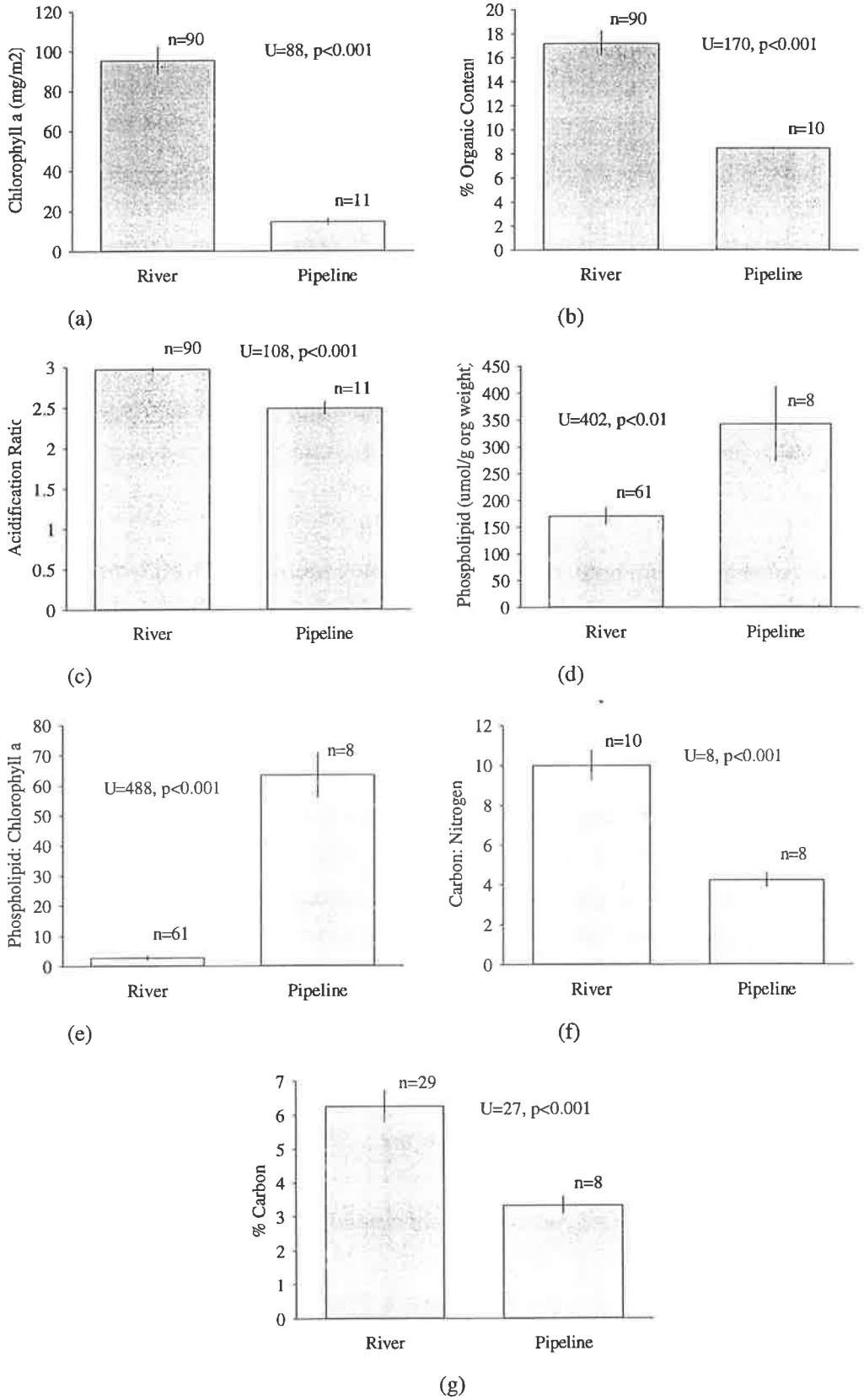


Figure 6.7
Food quality indicators for periphyton from littoral zone of the lower River Murray and the Loveday Irrigation Pipeline; (a) Chlorophyll *a* (mg/m^2), (b) % organic content, (c) acidification ratio (d) phospholipid concentration (µmol/g organic weight), (e) ratio of phospholipid (mg/m^2): chlorophyll *a* (mg/m^2), (f) carbon: nitrogen ratio, (g) % carbon content.

6.7.4 Discussion

It is not possible to draw confident comparisons between the periphyton collected from Cooper Creek with that from the lower River Murray, as the samples from the two systems were obtained at different times of the year, under different flow conditions and water temperatures, factors which affect the nature and production of periphyton (cf. Golladay and Sinsabaugh, 1991). Samples from Cooper Creek, however, were collected at a time (December 1991) when flow was minimal and it could be argued that under such conditions the system would have been at its most autotrophic with relatively stable water levels and a constant photic depth. Similar conditions are known to cause increases in algal biomass in other rivers (cf. Biggs and Price, 1987; Biggs and Close, 1989), even where light penetration is limited (cf. Findlay *et al.,* 1986).

Periphyton collected from both the lower Murray (Section 6.7) and the middle Murray (cf. Scholtz and Boon, 1993a, 1993b) in winter, when water temperatures are lowest and algal production therefore minimal, still had a higher algal biomass than periphyton collected from Cooper Creek during summer. This suggests that the periphyton currently dominating the substrata of the lower River Murray is more autotrophic (algal based) than that from Cooper Creek. Owing to high concentrations of suspended solids Cooper Creek has a restricted photic zone, with a Secchi depth of less than 10 cm during most of the year (Puckridge, unpublished data). The blackwater rivers of the USA also have narrow photic depths, caused by high levels of dissolved organic matter, and for most of the year tend to be heterotrophic. However, during summer when flow is minimal and the photic depth increases, autochthonous algal production increases (cf. Findlay *et al.,* 1986). Like Cooper Creek, prior to regulation the lower River Murray had a narrow photic depth which, when combined with continually moving water levels (Chapter 1), suggests the system would have tended towards heterotrophy. Flow regulation has stabilised seasonal water levels and allowed a constant and stable photic depth to develop, this is likely to have increased periphytic algal, autochthonous, production.

The comparison of the food quality of periphyton from the irrigation pipelines with that from the lower Murray is directly related to the respective presence and absence of prosobranch gastropods from the two habitats. A simple estimate of food quality is reflected in the ratio of carbon to nitrogen, essentially providing a measure of the percentage of protein in the food (Russell-Hunter, 1970; McMahon *et al.,* 1974). A low ratio can result from either a high percentage of nitrogen, good food quality, or a

low carbon content combined with a residual amount of refractory nitrogen, indicating poor food quality (Naiman, 1983). Although the percentage carbon content was low in all periphyton samples from river and pipeline habitats, the total organic content was also low, carbon content actually ranged from 30 to 50% of the total organic content of the samples. This suggests that the carbon to nitrogen ratios observed in this study are providing a reasonable indication of food quality. The ratio in pipeline periphyton was much lower than in the river, which suggests food from this habitat is of higher quality in terms of nitrogen supply than river periphyton.

The higher nitrogen content of the pipeline periphyton may be partly due to the presence of bryozoans on pipeline walls (cf. Woolford, 1984 Unpubl. Hons. thesis) as well as from microbial activity in the accumulated organic matter. The presence of bryozoans on the walls of the pipelines increases the surface area of the substratum for microbial production and organic matter accumulation (Suren and Winterbourn, 1992) adding to the nutritional value of pipeline periphyton.

Thus, pipeline periphyton is entirely heterotrophic with a high percent nitrogen and therefore a relatively high food quality. Periphyton from Cooper Creek was more autotrophic with a lower food quality value, which may be partly attributed to the time of year collected. Samples from the lower River Murray had the highest algal biomass combined with a relatively low food quality in terms of nitrogen content. If this is then related to the presence and absence of the gastropods, the highest diversity and abundance of gastropods is currently found in the irrigation pipelines where food quality is high.

6.8 CONCLUSIONS

This study suggests that *N. hanleyi*, *N. sublineata* and *T. balonnensis* are deposit feeding detritivores assimilating carbon either directly from amorphous organic material or from heterotrophic microbes inhabiting the organic matter. Detritus diets have been reported for other thiarid and viviparid gastropods (cf. Browne, 1978; Dudgeon and Yipp, 1983; Pace and Szuch, 1985; Brown *et al.,* 1989). The benefits of such a diet may be in the relatively constant supply of food that it provides (Browne, 1978), compared with often seasonal algal production as well as the higher nitrogen compared with carbon content of detritus over algae (cf. Russell-Hunter, 1970). Benthic invertebrates in many streams and rivers are known to utilise organic matter as their primary food source (Winterbourn *et al.,* 1986). In general, as the

biomass of organic detritus decreases during decomposition the relative protein content increases, owing to enhanced microbial production (Browne, 1978). Organic detritus can therefore provide a rich source of nitrogen for grazing invertebrates (Russell-Hunter, 1970).

The importance of food in animal population dynamics may not be related to the quantity required to maintain basic energetic requirements but of the quality needed to realise the potential for growth and reproduction (Eisenberg, 1970; Russell-Hunter, 1970). The component of the environment exerting the major influence on animals is therefore not just a shortage of food, but an overall shortage of the right type of food particularly for very young animals and breeding females (White, 1978). For the majority of time, White (1978) suggests that there is an inadequate supply of too-thinly or too-patchily dispersed nitrogenous food in the environment, with most young animals unable to obtain enough nitrogen to meet rapid growth rates and females unable to maintain adequate reproduction. This may be particularly true for viviparous gastropods as viviparity is an expensive mode of reproduction and the protein drain on reproductive females is high (Browne, 1978).

Thus, both *N. hanleyi* and *N. sublineata* as well as *T. balonnensis* may be especially sensitive to changes in food quality. In natural populations viviparid female fecundity is uncommonly low, compared with other freshwater gastropod families. *Viviparus georgianus* from four lakes in New York State (USA) had fecundities ranging from less than 10 young per year in one year old females to a maximum of about 25 young per year in the most fecund populations of two and three year old females (Browne, 1978). While *Viviparus subpurpureus* and *Campeloma decisum,* from an alluvial plain river in Louisiana (USA), produced 13.4 ± 0.2 and 24.3 ± 1.7 young per year respectively (Brown *et al.,* 1989).

Of the taxa in this study the numbers of embryos found in female *N. hanleyi* collected from the Loveday irrigation pipeline (South Australia) in October 1992 ranged from less than 5 to a maximum of 14. In *N. sublineata* collected at various times from 1989 until 1992 from Cooper Creek embryo numbers ranged from 4 to a maximum of 12 (Appendix E). Dissection of *T. balonnensis* reveals that this taxa also has a low fecundity with approximately 30 embryos per individual. This suggests that all three species have low fecundities, consistent with reports for some similar taxa in the literature.

Such reproductive levels are a direct reflection of the energy costs of viviparity (Browne, 1978). Russell-Hunter (1970) suggests that those gastropod eggs giving rise to "miniature adults", as in viviparous taxa, have low ratios of carbon to nitrogen. For viviparous females to produce an adequate number of low C:N eggs they would need to consume a high protein, low C:N, food source. Total organic carbon content, and the ratio of carbon to nitrogen, are related to the nutritional value of the food as evidenced by growth and fecundity (McMahon *et al.,* 1974). The maximum ratio of carbon to nitrogen for maintaining animal growth has been estimated as 17:1, however, during periods of reproduction and rapid growth food requirements in terms of C:N may lie well below this maximum (Russell-Hunter, 1970). This was observed for *Lymnaea palustris* and *Laevapex fuscus* where the highest levels of growth and fecundity occurred in populations consuming food with C:N ratios closer to 3:1 (McMahon *et al.,* 1974).

The high algal biomass and high C:N (approximately 10:1) of periphyton from the lower Murray in this study suggests that in this habitat the viviparous gastropods may be unable to obtain enough nitrogen to maintain their energy expensive mode of growth and reproduction. When exposed to a food supply in which the biomass of algae relative to organic detritus is high, *N. hanleyi* does not preferentially select detritus (Section 6.6) thus the bulk of food items ingested are algal. Under natural conditions, these snails are not assimilating algal carbon (Section 6.4), so that when exposed to a food supply dominated by algae they may become food limited. The biomass of filamentous algae, and therefore cellulose, present in lower Murray periphyton means that the bulk of the food ingested will be carbon. If such periphyton were to remain dominant in the lower Murray for an extended period it may be impossible for snails to extract sufficient nitrogen from the bulk of fibre they are forced to consume (cf. White, 1978), at least in terms of "positive nutrition" (Eisenberg, 1970).

The presence of large populations of snails in the irrigation pipelines, where the available food has a relatively low C:N (approximately 4:1) and is dominated by amorphous organic matter supports the notion that in the river food may be limiting snail populations. As both *Notopala* taxa and *T. balonnensis* were abundant in the lower Murray, at least until the 1950's (Chapter 1), the factor(s) responsible for degrading food resources, shifting them from a comparatively nutritious "microbial-detrital" form to one that is less nutritious and dominated by algae, must have either been initiated or have accelerated since this time.

One of the most important hydrological determinants of algal biomass is flooding, as periphytic algae can only respond fully to available nutrients under low or stable flow conditions (Biggs and Close, 1989). Flow regulation in the Murray-Darling Basin has virtually eliminated seasonal floods and droughts such that at least the lower reaches of the river remain at stable levels for extended periods. Although major regulation in the Murray-Darling Basin commenced in 1922, with construction of the first weirs, it has accelerated at a near exponential rate since the 1950's, with increases in the volume of water diverted for irrigation and a marked increase in storage capacity (Chapter 1; Close, 1990).

The relationship between flow regulation, and the impact of stable water levels on the nature of the periphyton growing on substrata in the lower River Murray will be explored in Chapter 7.

Chapter 7

Impacts of Regulation: Flow Stabilisation and Changes in Food Quality

7.1 INTRODUCTION

Periphyton is the biofilm of diatoms, blue-green algae (Cyanobacteria), unicellular and filamentous green algae, bacteria, fungi, protozoans and organic matter that forms on substrata such as snags and macrophytes in aquatic systems (McMahon *et al.,* 1974; Lock *et al.,* 1984). In rivers periphyton forms the base of food webs and is a source of dissolved and particulate organic matter (Luttenton *et al.,* 1986). Energy flow through biofilms may be autotrophic, via algal production, or heterotrophic, relying on microbial decomposition, the uptake of external carbon and the accumulation of organic material (cf. Rounick and Winterbourn, 1983; Lock *et al.,* 1984). Biofilms developing on well-lit substrata tend to be dominated by autotrophs, whereas those developing under shaded conditions tend towards heterotrophy (Golladay and Sinsabaugh, 1991). The nature of the periphyton may directly affect the distribution and abundance of those animals relying on it for food (cf. Dudgeon and Chan, 1992).

The dynamics of riverine periphyton assemblages are controlled by a combination of hydrological, chemical and biological processes (e.g. Fisher *et al.,* 1982; Kaufman, 1982; Reiter and Carlson, 1986; Graham, 1988; Biggs and Close, 1989 Golladay and Sinsabaugh, 1991). These include the physical stability of the substrata and events such as floods or strong currents (Fisher *et al.,* 1978; Golladay and Sinsabaugh, 1991; Biggs and Gerbeaux, 1993). Stream diatom communities developing in direct currents do so more slowly and reach lower densities than those in sheltered regions (Peterson, 1987). In many streams the period between floods is the single most important factor determining periphyton biomass (Grimm and Fisher, 1986; Grimm and Fisher, 1989; Lohman *et al.,* 1992).

Invertebrate colonisation may also affect biofilm development, either by enhancing biomass and complexity through retreat building, or by removing biomass through feeding activity (Golladay and Sinsabaugh, 1991). The chemical composition of the substrata will determine nutrient availability to the periphyton with consequences for

development, total biomass and community composition (Melillo *et al.,* 1983; Scholtz and Boon, 1993).

Although a single disturbance can affect a river for years (see Lamberti *et al.,* 1991) smaller, repeated events, can keep systems in a perpetual 'disturbed' state. Repeated events create conditions whereby biofilms remain successionally immature and have low overall biomass (cf. Resh *et al.,* 1988; Biggs and Close, 1989). In streams, high discharge events are a frequent form of disturbance (Webster *et al.,* 1983). They are the major resetting mechanism for periphyton assemblages, through the initiation of new cycles of accrual and metabolic and structural succession (Fisher *et al.,* 1978; Biggs and Gerbeaux, 1993). The flash floods common in Sonoran desert streams (Arizona, USA) completely scour the substrata and reset the process of biofilm development (Fisher *et al.,* 1978). This prevents competitively superior taxa from dominating and tends to maintain the biofilm in a perpetual state of early succession.

In large lowland rivers, water velocity during small and moderate floods may not be sufficient to reduce periphyton biomass and discourage late successional taxa. A combination of physical factors other than discharge may act to maintain biofilms that are highly productive. In the large blackwater rivers of the USA, light penetration is limited by high levels of dissolved organic matter (cf. Edwards and Meyer, 1987). In these rivers a heterotrophic biofilm is maintained by the action of the restricted photic zone and seasonal water level changes (cf. Findlay *et al.,* 1986).

Thus, in many large rivers mature (climax) biofilms may rarely occur: a restricted and constantly moving photic zone may be a sufficient disturbance to prevent dominance by late successional autotrophs. This conforms with ideas of "the moving littoral" (cf. Junk *et al.,* 1989), where new substrata are inundated and pass through the photic zone as river levels rise, and again as levels fall. The heterotrophic blackwater rivers of the USA rely on organic matter input from the floodplain to maintain bacterial colonisation and heterotrophic production (cf. Findlay *et al.,* 1986; Grubaugh and Anderson, 1989). The moving water levels associated with small to moderate floods augment inputs to the channel of coarse and fine organic matter (cf. Mulholland, 1981; Cuffney, 1988; MacArthur, 1988).

Prior to regulation, biofilms developing in the littoral zone of the lower River Murray may have been similar to those documented for blackwater rivers (cf. Findlay *et al.,* 1986; Edwards and Meyer, 1987). The naturally high levels of suspended solids of the lower Murray (Mackay *et al.,* 1988) would have restricted the photic depth with

little light penetrating below 50 cm (cf. Walker *et al.*, 1992). A restricted photic depth, combined with the magnitude of seasonal water-level changes in the unregulated river (Chapter 1), would push developing biofilms towards heterotrophy. Seasonal water level movements would also enhance organic matter transport from the surrounding riparian and floodplain areas into the channel, providing substrata for heterotrophic production (cf. MacArthur, 1988).

Flow regulation has restricted the movement of the littoral zone of the lower River Murray (Chapter 1). The weirs, combined with controlled releases from upstream storages during naturally dry periods (Chapter 1), create a stable water level (and therefore stable photic zone) for extended periods along the lower river. Stabilisation occurs at the 'microtime' scale, resulting from decreased annual or seasonal water level changes (cf. Chapter 2). This allows substrata to remain within the photic zone for a longer time than prior to regulation, and encourages development of a mature biofilm and enhances autochthonous production.

In this chapter the colonisation of wood substrata in the regulated lower Murray is described in terms of total biomass, algal biomass and food quality (expressed as the ratio of carbon to nitrogen). We may predict that periphyton grown under stable conditions would initially have a high nitrogen and a low carbon content, and therefore a high food quality value. Quality would then decrease with time since the substrata were inundated, corresponding to an increase in the biomass of late successional, high carbon-containing, taxa. Information on the time frame for changes in periphyton is then used to determine the approximate time required, under conditions of a stable photic zone, for a substantial decline in the food quality of the biofilm.

7.2 PERIPHYTON DEVELOPMENT ON WOOD SUBSTRATA UNDER STABLE WATER LEVEL CONDITIONS

7.2.1 Introduction

Biofilm development may be followed by examining growth on submerged surfaces, with many studies employing glass microscope slides as the substratum (cf. Luttenton *et al.,* 1986). Glass, however, is an artificial surface and carries less total microbial biomass and fungal biomass than wood (e.g. Sinsabaugh *et al.,* 1991; Hax and Golladay, 1993; Sholtz and Boon, 1993). These differences have been attributed to the use of wood as a minor supplemental source of nutrients.

The type of biofilm developing on a particular substrata will, in part, determine the faunal assemblage relying upon it. As the biofilm develops there are changes in community structure (Lock *et al.,* 1984; Scholtz and Boon, 1993) so there will be corresponding changes in food quality, particularly in terms of nitrogen content. During colonisation, the initial period after submergence, assemblages are likely to be active in cell division with minimal amounts of non-proteinaceous supporting structures like cellulose (McMahon *et al.,* 1974). Such biofilms will have a low ratio of carbon to nitrogen (in the range of 6:1), indicating a large percentage of protein, and are likely to be dominated by diatoms, bacteria and fungi (cf. Russell-Hunter, 1970). Mature biofilms will have a larger proportion of cellulose and comparatively low proportions of protein (McMahon *et al.,* 1974). These communities will tend to have high ratios of carbon to nitrogen and be dominated by larger algae, such as filamentous greens.

In this section changes in food quality of the biofilm growing on newly submerged wooden substrata are described and compared with changes occurring on background natural substrata. The study was conducted in a backwater of the lower Murray where water levels are stable. This information is used to estimate the length of time substrata can remain within the photic zone before there is a decline in the food quality of the biofilm.

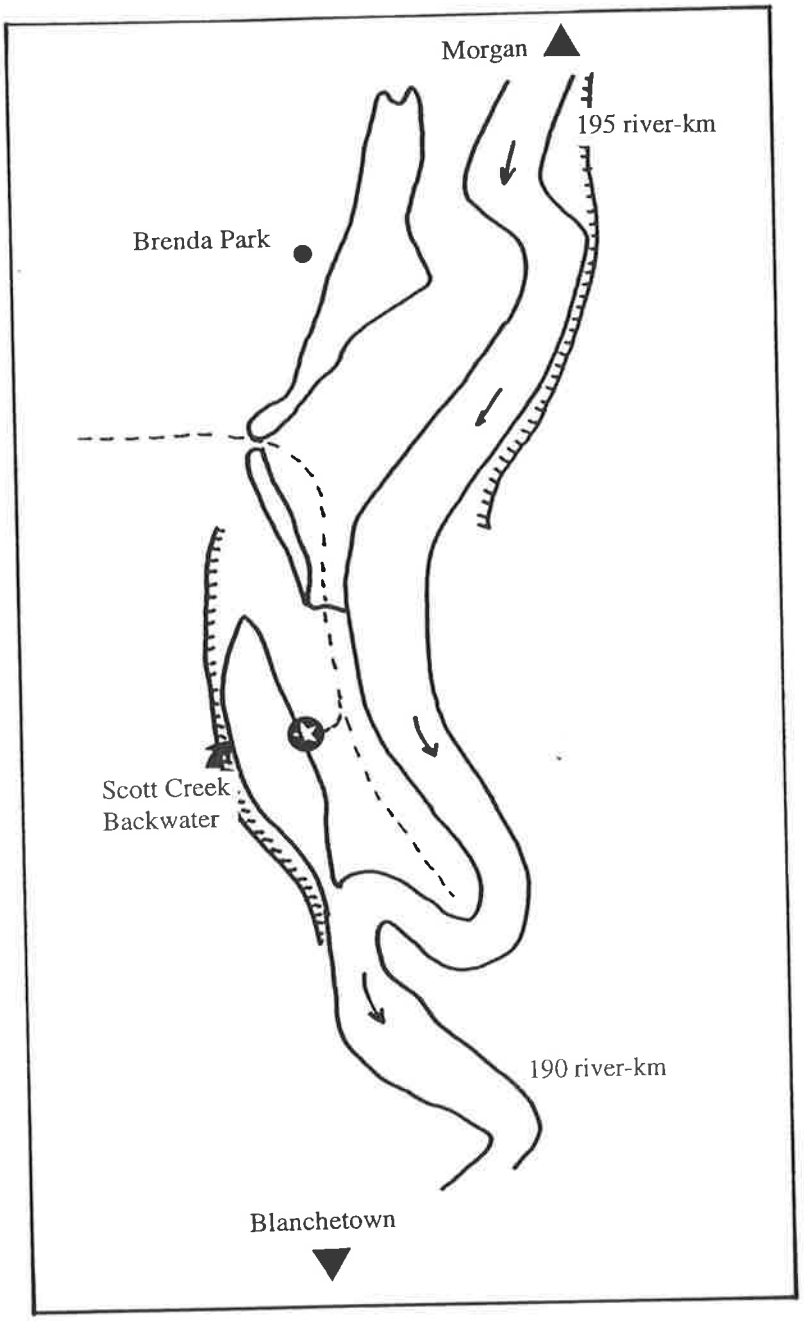


Figure 7.1 ✪ Backwater at Scott Creek, 10 km downstream of Morgan, where artificial substrata were used to monitor biofilm development.

7.2.2 Methods

Study Site

Periphyton was grown on wooden substrata in a permanent backwater of the River Murray at Scotts Creek, 10 km downstream of Morgan (cf. Figure 7.1) during summer 1992. The water level in the backwater is stabilised by Lock 1 at Blanchetown, 30 river-km downstream (Chapter 1).

Sampling

Artificial substrata were constructed from three 30 cm pieces of 1.5 cm diameter wooden dowel wired in a 45° angle at the centre to form a crossed pyramid (Figure 7.2); these are subsequently referred to as 'dowel' substrata. They were arranged in three rows on a rectangular plastic grid (60 cm x 100 cm), and suspended at a depth of 35 cm by plastic floats. A constant depth was maintained by securing the grids between 4 wooden stakes by 1 m lengths of rope (Figure 7.3), allowing the whole frame to rise or fall with changes in water level.

Three replicate frames, each containing 21 substrata arranged in three rows of 7, were placed in the backwater on 21 February 1992. All substrata within a row were randomly assigned a number (1 to 7) representing a sampling date. Substrata from each row of the three frames were sampled at 2-week intervals for 15 weeks from February to May 1992. Samples were collected on 28 February, 14 March, 28 March, 11 April, 28 April, 9 May and 27 May 1992 representing 9, 24, 38, 52, 69, 80 and 90 days respectively of submergence at a stable water level.

At each sampling date the nine substrata corresponding to the sampling date (one from each row of each frame) were removed and the periphyton scrubbed into distilled water with a soft toothbrush. Each substratum was then returned to the frame so as not to change the total density of substrata within a frame. To monitor background changes in the nature of the biofilm on natural substrata, five samples were collected from snags in the backwater at each sampling date using the same scrubbing methods applied to the dowel substrata. These background samples are subsequently referred to as 'natural' substrata.

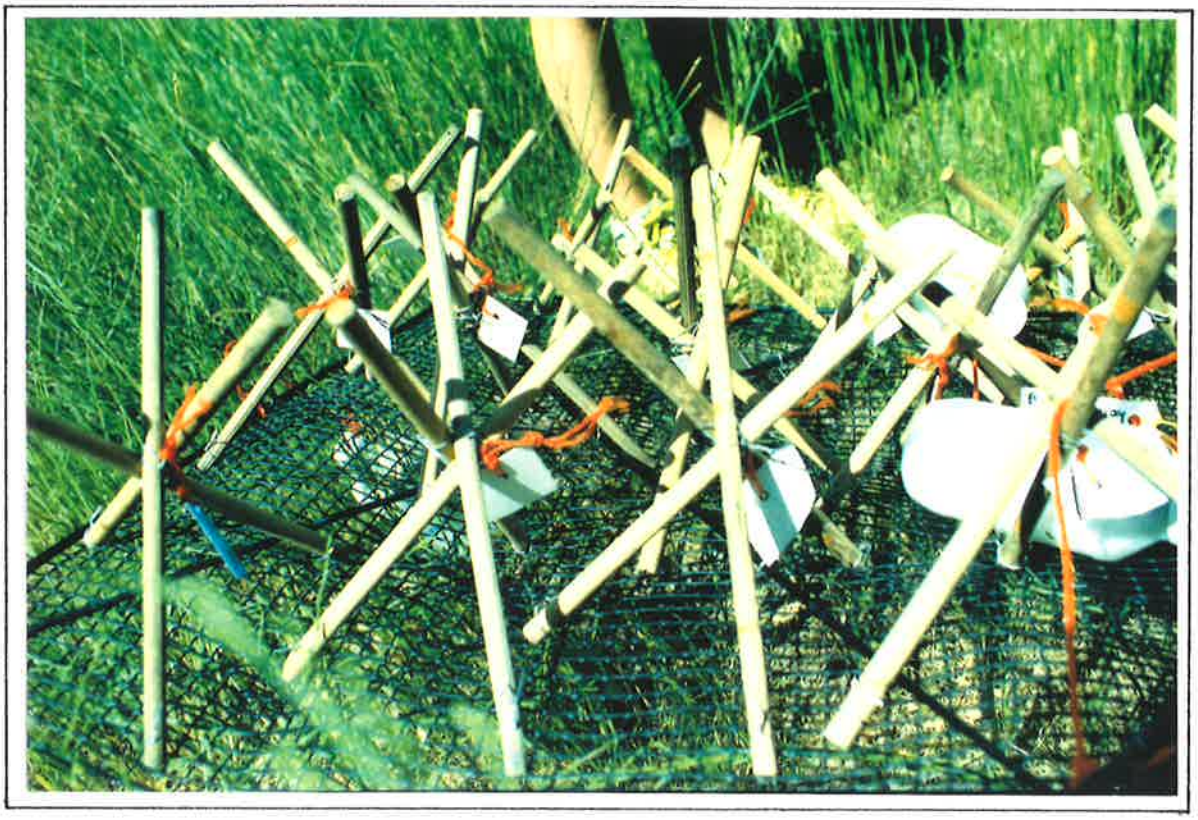


Figure 7.2
Artificial 'dowel' substrata used to monitor biofilm development.

Figure 7.3 Arrangement of frames in the backwater at Scotts Creek.

The scrubbed periphyton from both dowel and natural substrata was placed on ice. In the laboratory it was subsampled using a modified Motoda sampler (Motoda, 1956). From the subsamples a number of periphyton 'variables' were measured using methods described in Section 6.6; these included: community composition, dry weight, ashfree dry weight, chlorophyll *a* concentration, acidification ratio, percent carbon content and carbon to nitrogen ratio.

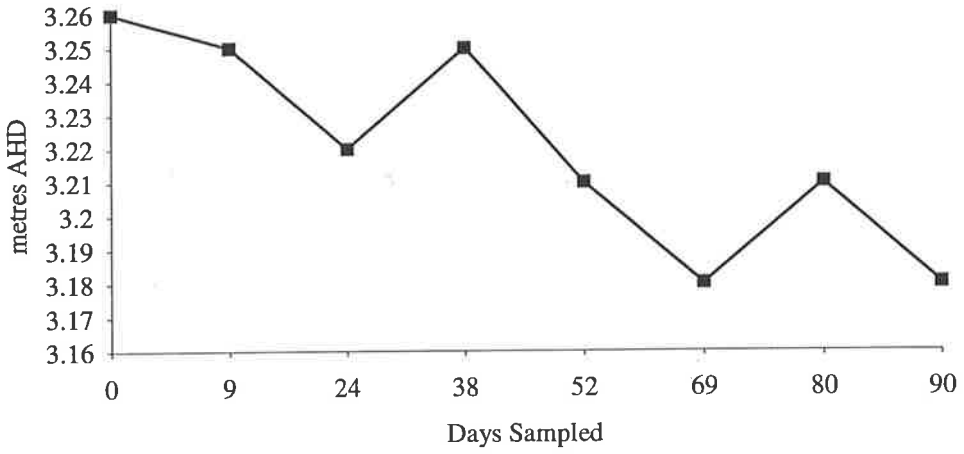
Environmental variables were also measured routinely: dissolved oxygen (YSI Dissolved Oxygen Meter), conductivity (Hannah Conductivity Meter HI8733), temperature (°C), total water depth (cm) and Secchi depth (cm).

Analysis

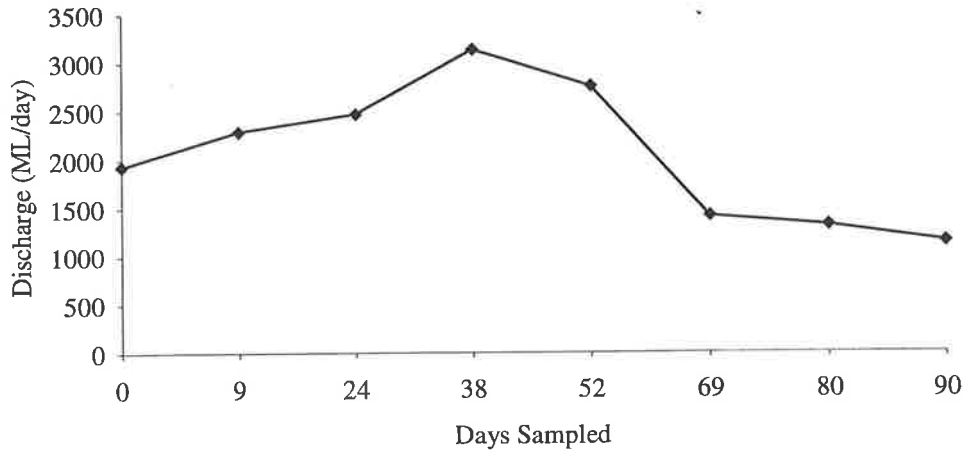
Differences in each periphyton variable over the seven sample days, for periphyton growing on natural substrata, were explored using a one-way ANOVA and isolated using Tukey's Honestly Significant Difference Procedure (SYSTAT v. 5.0: Wilkinson 1990).

To test for differences in each periphyton variable at each sample date between the three frames, a one-way ANOVA was applied. As no differences were apparent between frames for any parameter (Table 7.1), data at each sample date for substrata from all three frames were pooled. The samples collected at each sample date are essentially independent from those collected on any other sample date, and differences in periphyton from the dowel and natural substrata, on each sample date, were explored using Students *t*-test. At each sampling however, the parameters measured for the samples are not independent, thus the error rate was adjusted by the Bonferroni procedure (Neter *et al.,* 1985), where the nominated significance level (0.05) is divided by the number of non-independent tests to provide added protection against Type I errors.

To standardise the differences in the developing biofilm compared with the mature biofilm on each sample day, the mean value of the parameters measured for the natural substrata were subtracted from the mean of each parameter for the dowel substrata. This described the difference for each parameter between the developing biofilm and the mature biofilm.



(a)



(b)

Figure 7.4 (a) Upper pool level (metres AHD) and (b) discharge (ML/day) for Pool 1 for the duration of submergence of the dowel substrata (Data from the South Australian Engineering and Water Supply Department).

Table 7.1 Results of one-way ANOVA for differences in periphyton parameters on natural substrata (n=5) over the seven sample days.

Parameter	
% Organic Content	$F_{2,60}$=0.104, p>0.05
Chlorophyll *a* (mg/m^2)	$F_{2,60}$=0.204, p>0.05
Acidification Ratio	$F_{2,60}$=0.319, p>0.05
% Carbon Content	$F_{2,52}$=0.614, p>0.05
Carbon: Nitrogen	$F_{2,52}$=1.949, p>0.05

7.2.3 Results

During the experiment river discharge at Lock 1 was minimal, ranging from 1140 to 3130 ML/day. Environmental conditions in the backwater for the seven sample days are given in Table 7.2. Both discharge and stage, measured 30 km downstream at Lock 1, decreased slightly over the sampling period (Figure 7.4). The decrease in stage over the 14 weeks was minimal (maximum 10 cm), and unlikely to have had any impact on biofilm development. The slight decrease in discharge after Day 52 may explain the observed increase in the Secchi depth (cf. Table 7.2).

Table 7.2 Instantaneous environmental data for Scotts Creek backwater on the seven sample days.

Day	Oxygen (% Saturation)	Salinity (mg/L)	Temperature ^{0}C	Secchi Depth (cm)	Total Depth (cm)
9	90	463	21	15	38
24	90	437	26	16	35
38	100	481	22	17	37
52	100	503	20	20	31
69	100	503	20	25	30
80	100	499	17	30	30
99	100	536	15	30	30

The community composition of the developing biofilm on the dowel substrata for the sampling period is summarised in Table 7.3. Initially the proportion of amorphous organic detritus was high compared with living algal forms. The percentage of diatoms in the assemblage increased until approximately Day 52. After this filamentous algae, such as *Spirogyra* sp., dominated. The proportion of inorganic detritus remained constant, while the abundance of unicellular algae and blue-green algae was low.

Table 7.3 Estimated abundance of the seven food groups in periphyton scrubbed from dowel (n=9) substrata over the seven sample days.

Group	Day 9	Day 24	Day 38	Day 52	Day 69	Day 80	Day 99
Inorganic detritus	25%	25%	25%	20%	20%	20%	20%
Organic detritus	60%	50%	45%	35%	30%	35%	25%
Diatoms	10%	15%	20%	30%	30%	30%	30%
Filamentous Algae	<5%	5%	<10%	10%	15%	25%	25%
Other Algae	<5%	<5%	<10%	<5%	<5%	<5%	<5%
Blue-green Algae	<5%	<5%	<5%	<5%	<5%	<5%	<5%
Animal Material	<5%	<5%	<5%	<5%	<5%	<5%	<5%

Values for organic content were transformed by $\arcsin\sqrt{p}$ where p is the proportional organic content of the sample. Means (SE) for organic content of periphyton from dowel substrata and natural substrata for each sampling date are given in Table 7.4a. Periphyton on natural substrata did not differ in organic content among the 7 sample days ($F_{6,27}$=1.007, p>0.01).

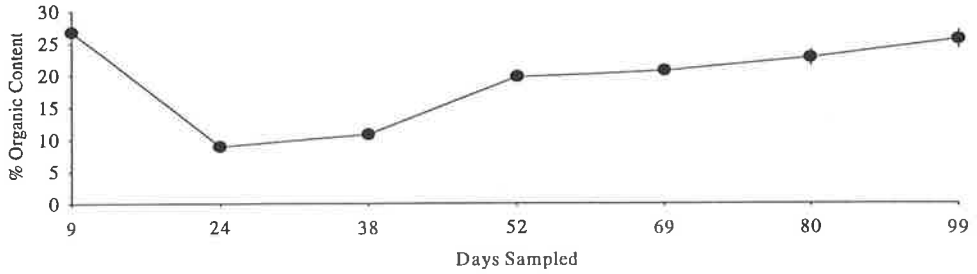
On dowel substrata the organic content of periphyton varied with time since initial inundation (Figure 7.5a). Nine days after substrata were submerged the organic content was high, although not different to that on natural substrata (Figure 7.5b). Community composition of the periphyton at this stage showed little algal material and a dominance of organic matter (Table 7.3). At sample dates 24 and 38 the dowel periphyton had a lower organic content than did periphyton on natural substrata (t=5.61, df=12, p<0.001 and t=4.31, df=12, p<0.001 respectively). This may be attributed to an increase in the amount of inorganic material trapped within the periphyton and, therefore, a decrease in total organic content. From day 52 until day 80 periphyton on dowel substrata had a higher organic content than that on natural

substrata (Figure 7.6b), corresponding to an increase in biomass of filamentous green algae (Day 52: t=3.06, df=12, p<0.01; Day 69: t=5.05, df=12 p<0.01; Day 80: t=3.05, df=12, p<0.01). At day 99 there had been an increase in the organic content of periphyton on natural substrata, corresponding to a slight increase in the photic depth of the water (cf. Table 7.3), there was no difference in organic content of periphyton between the two substrata (t=1.51, df=12, p>0.01).

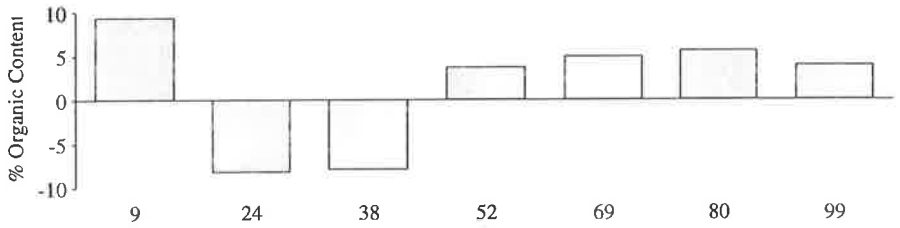
Means (SE) for chlorophyll *a* concentration (mg/m^2) of periphyton from dowel substrata and natural substrata for each sample date are given in Table 7.4b. The chlorophyll *a* content of periphyton on natural substrata differed among the 7 sample days ($F_{6,27}$=4.135, p<0.01). Differences existed between Day 9 and Days 80 and 99. This corresponds to the increase in Secchi depth, and therefore light penetration, after Day 69 and an increase in algal biomass.

The chlorophyll *a* concentration of the periphyton growing on dowel substrata changed with increasing time after inundation (Figure 7.6a). On Day 9 there was no difference in chlorophyll *a* between natural and dowel substrata (Figure 7.6b). Examination of the composition of the periphyton at this stage showed diatoms comprised 50% of the algal biomass on the dowel substrata compared with nearly 100% filamentous green algae on the natural substrata (cf. Table 7.3). From Day 24 until the last sampling on Day 99 the periphyton on the dowel substrata had a higher chlorophyll *a* concentration (mg/m^2) than did that growing on the natural substrata. In both cases filamentous greens were the most abundant algal type.

The acidification ratio gives an indication of the amount of living compared with decaying algal material in the periphyton. Means (SE) of this ratio for periphyton from both substrata are given in Table 7.4c. The ratio for periphyton on natural substrata did not differ during the sampling period ($F_{6,27}$=1.238, p>0.01). On the dowel substrata the ratio was variable with no trend of change with time since inundation of the dowel (Figure 7.7a). The ratio of dowel periphyton does not differ from that of periphyton on natural substrata for any of the sample days (Figure 7.7b). This suggests that the periphyton on both snags and dowel is predominantly living algal material with little or no senescent material.

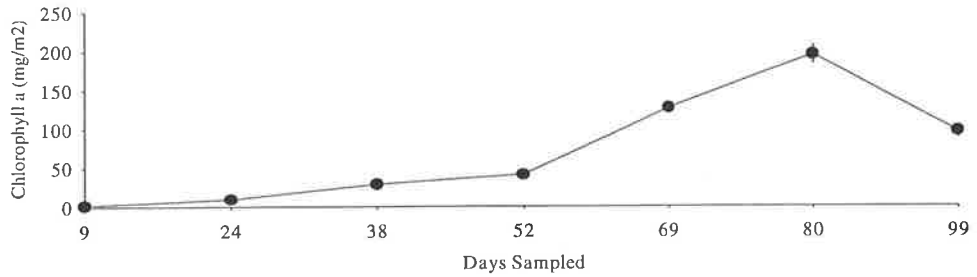


(a)

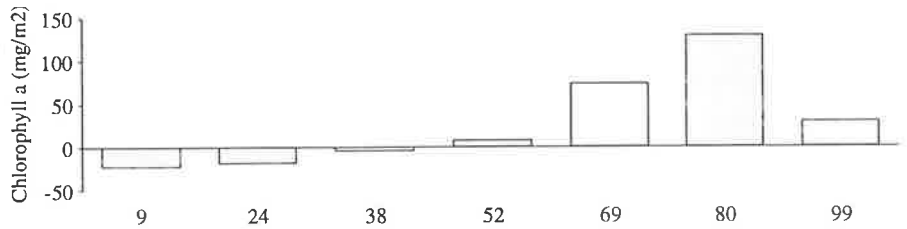


(b)

Figure 7.5
(a) Percent organic content of periphyton developing on dowel substrata over the sampling period.
(b) Difference in percent organic content of periphyton developing on dowel substrata compared with that on background natural substrata.



(a)



(b)

Figure 7.6
(a) Chlorophyll *a* concentration (mg/m^2) of periphyton developing on dowel substrata over the sampling period.
(b) Difference in chlorophyll *a* concentration (mg/m^2) of periphyton developing on dowel substrata compared with that on background natural substrata.

The ratio of carbon to nitrogen (C:N) in periphyton indicates the food quality value of that sample (Russell-Hunter, 1970; McMahon *et al.,* 1974). Samples with a higher ratio have more carbon than nitrogen per unit weight and thus, a lower food quality. Means (SE) of C:N for all sample days are given in Table 7.4d and means (SE) for percentage carbon in Table 7.4e. Statistical tests could not be applied for C:N between dowel and natural substrata on Day 9, as the biomass of periphyton at this stage was low and samples from all dowel substrata were combined in order to provide a sufficient volume for the estimation of total carbon and nitrogen. There was no difference in C:N of periphyton from natural substrata between the sample days ($F_{6,27}$=3.19, p>0.01).

The ratio of C:N of dowel periphyton declined with increasing time since inundation (Figure 7.8a). Initially the ratio was low indicating periphyton of a relatively high food quality. By Day 38 the C:N of dowel periphyton was not different to that on natural substrata (Figure 7.8b). This trend corresponds with the percent carbon content of the periphyton (Figure 7.9a and 7.9b).

Although it cannot be confirmed statistically, owing to the insufficient volumes obtained for replication, there appears to be no difference in the carbon content of periphyton samples from either substrata on Day 9. If so, the observed differences in C:N may be attributed to a higher nitrogen content on dowel substrata. After Day 38 there was no difference in food quality, in terms of carbon and nitrogen content, of periphyton from dowel and natural substrata.

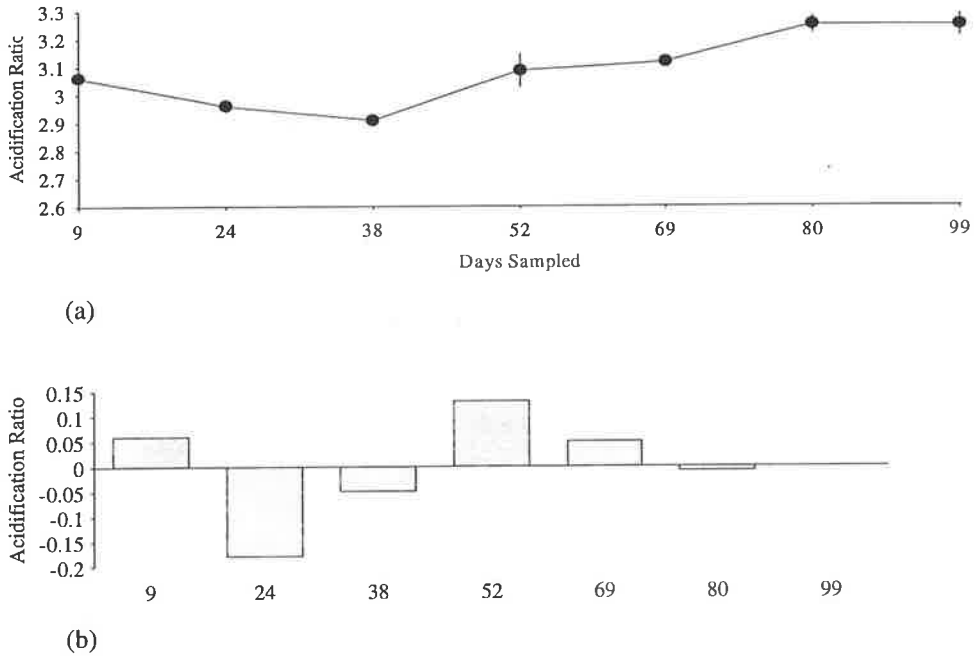


Figure 7.7
(a) Acidification ratio of periphyton developing on dowel substrata over the sampling period.
(b) Difference in acidification ratio of periphyton developing on dowel substrata compared with that on background natural substrata

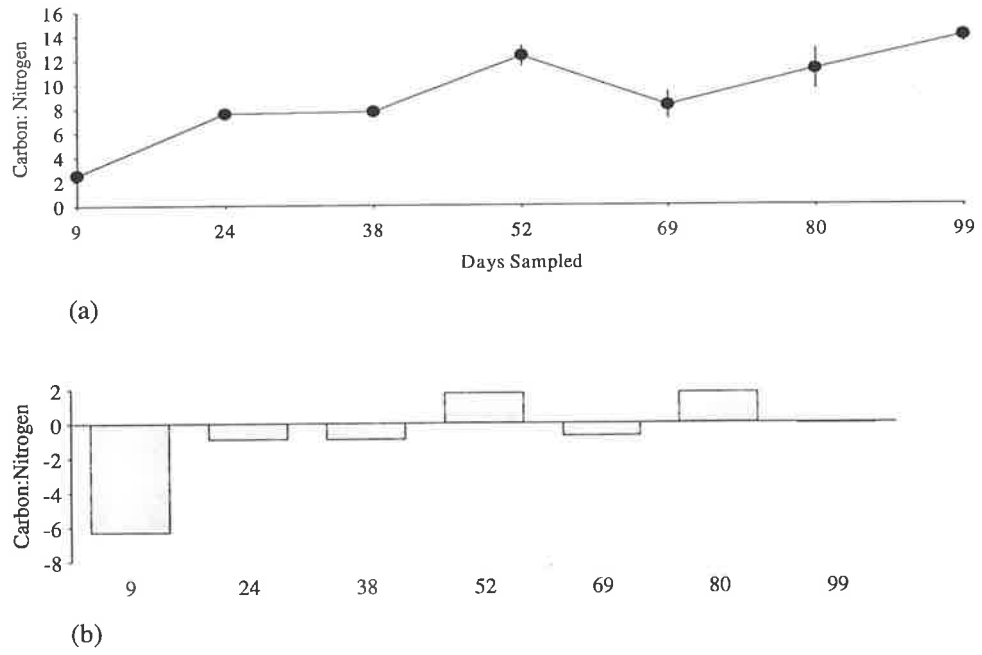


Figure 7.8
(a) Carbon to nitrogen ratio of periphyton developing on dowel substrata over the sampling period.
(b) Difference in carbon to nitrogen ratio of periphyton developing on dowel substrata compared with that on background natural substrata

Table 7.4 Mean *(SE)* for (a) % organic content, (b) chlorophyll *a* concentration (mg/m^2), (c) acidification ratio, (d) carbon:nitrogen ratio and (e) % carbon content of periphyton from dowel (n=9) and natural (n=5) substrata. Value for Student's *t* on transformed data. A Bonferroni-corrected significance level of 0.01 is applied as a threshold for statistical significance.

(a)

Day	Dowel	Natural	Student's *t*
9	26.81 *(2.46)*	17.39 *(2.06)*	2.59, p>0.01
24	8.91 *(0.81)*	17.15 *(0.89)*	5.61, p<0.001
38	10.83 *(0.79)*	18.75 *(2.09)*	4.31, p<0.001
52	19.95 *(0.76)*	16.31 *(0.38)*	3.06, p<0.01
69	20.85 *(0.64)*	15.66 *(0.78)*	5.05, p<0.001
80	22.96 *(1.34)*	17.21 *(0.93)*	3.05, p<0.01
99	25.81 *(1.44)*	21.36 *(3.31)*	1.51, p>0.01

(b)

Day	Dowel	Natural	Student's *t*
9	1.43 *(0.2)*	6.05 *(1.78)*	3.52, p<0.01
24	9.22 *(0.85)*	6.98 *(0.62)*	1.81, p>0.01
38	28.85 *(1.05)*	8.31 *(2.12)*	9.78, p<0.001
52	40.86 *(2.76)*	8.32 *(0.71)*	7.62, p<0.001
69	126.44 *(7.79)*	13.24 *(0.99)*	10.61, p<0.001
80	194.79 *(12.23)*	16.37 *(3.99)*	10.52, p<0.001
99	95.74 *(8.17)*	16.58 *(2.63)*	6.99, p<0.001

(c)

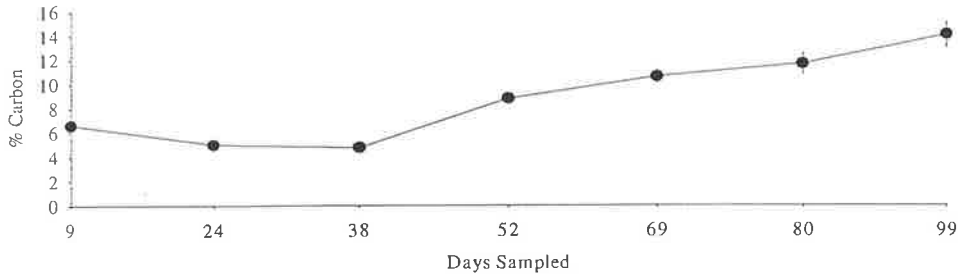
Day	Dowel	Natural	Student's *t*
9	3.06 *(0.23)*	2.9 *(0.12)*	0.18, p>0.01
24	2.96 *(0.02)*	3.21 *(0.24)*	1.43, p>0.01
38	2.91 *(0.02)*	2.97 *(0.09)*	0.73, p>0.01
52	3.09 *(0.06)*	2.96 *(0.04)*	1.41, p>0.01
69	3.12 *(0.02)*	3.07 *(0.06)*	0.87, p>0.01
80	3.25 *(0.03)*	3.26 *(0.06)*	0.23, p>0.01
99	3.25 *(0.04)*	3.25 *(0.06)*	0.004, p>0.01

(d)

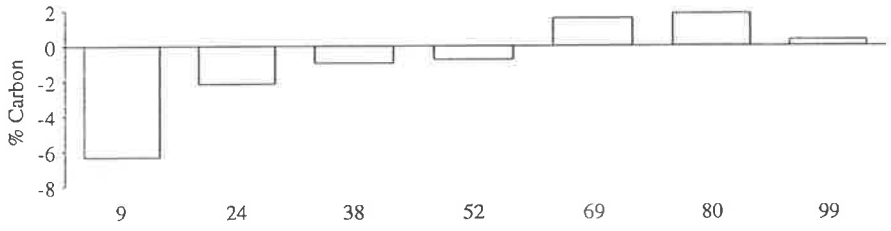
Days	Dowel	Natural	Student's *t*
9	2.5	8.86 *(1.57)*	
24	6.33 *(0.36)*	8.51 *(0.71)*	3.08, p<0.01
38	7.68 *(0.32)*	8.67 *(0.31)*	2.04, p>0.01
52	10.51 *(0.28)*	11.29 *(1.2)*	0.89, p>0.01
69	10.32 *(0.48)*	8.73 *(0.96)*	1.66, p>0.01
80	11.28 *(0.46)*	9.43 *(0.93)*	2.03, p>0.01
99	14.39 *(0.55)*	14.03 *(1.71)*	0.27, p>0.01

(e)

Days	Dowel	Natural	Student's *t*
9	6.6	6.61 *(0.86)*	
24	5.01 *(0.26)*	6.84 *(0.55)*	3.45, p<0.01
38	4.73 *(0.41)*	6.98 *(0.84)*	2.71, p>0.01
52	8.83 *(0.36)*	7.47 *(0.71)*	1.95, p>0.01
69	10.66 *(0.62)*	5.72 *(1.51)*	2.76, p>0.01
80	11.72 *(0.94)*	8.09 *(0.75)*	2.71, p>0.01
99	14.12 *(1.11)*	12.36 *(2.09)*	0.85, p>0.01



(a)



(b)

Figure 7.9
(a) Percent carbon content of periphyton developing on dowel substrata over the sampling period.
(b) Difference in percent carbon content of periphyton developing on dowel substrata compared with that on background natural substrata.

7.2.4 Discussion

The biofilm on the dowel substrata (cf. Figures 7.5 to 7.9) changed with time after initial submergence in a manner similar to that previously described for biofilms on river red gum blocks (Sholtz and Boon, 1993). Initially, the dowel biofilm had a high organic content, low algal biomass and a relatively low ratio of carbon to nitrogen, suggesting an assemblage with minimal cellulose supporting structures. At this stage the biofilm had a high food quality (low C:N). After initial colonisation there is a rapid increase in the biomass of filamentous algae and an increase in the ratio of carbon to nitrogen. This corresponds with the accumulation of algal types with a high content of cellulose supporting structures. Periphyton during this stage showed a trend of decreasing food quality (increasing C:N).

The biofilm developing on the dowel substrata attained a much higher algal biomass (cf. Table 7.4b) than that present on the natural substrata, despite both having come from the same water depth. Periphyton colonisation patterns on wood may be influenced by surface area to volume ratios, making it difficult to directly compare biofilms on different substrata (Golladay and Sinsabaugh, 1991). Differences in the total biomass on the two substrata may also be attributed to their chemical composition. Woody substrata with a high initial nitrogen content decay much faster than substrata with initially high lignin and low nitrogen (cf. Melillo *et al.,* 1983). Red gum is a relatively dense wood and the depth of oxygen penetration, and thus decay rates, may be less than for other types of wood (cf. O'Connor, 1992).

Chlorophyll *a* levels for biofilms on natural substrata in this study are similar to those reported by Scholtz and Boon (1993) for redgum blocks in billabongs from the middle reaches of the River Murray (approximately 20 mg/m^2). Welsh *et al.* (1988) suggested that a periphyton assemblage dominated by filamentous species could be expected when benthic chlorophyll *a* levels exceed 100 mg/m^2. Filamentous forms are most likely to occur at sites of high nutrient concentration. Thus, the larger algal biomass developing on the dowel substrata may be related to an increased availability of nutrients in dowel compared with red gum.

Differences did not exist in the acidification ratio of the biofilm developing on the two substrata, despite the much higher algal biomass on the dowel substrata. The acidification ratio gives some indication of the proportion of living compared with decaying pigment in the biofilm. We would expect therefore, that periphyton on natural substrata would have accumulated a larger biomass of detritus and decaying algal matter, and therefore have a lower ratio, than the newly developing biofilm on the dowel substrata. The similar values for the acidification ratio could be explained if the detritus portion of the biofilm was being continually removed by animal grazers and/or collectors. Other studies support this notion, as even when living algal biomass is greatest, invertebrate diets may still be dominated by detritus (Fisher *et al.,* 1978).

It appears that the nutritional quality of periphyton growing in the stable photic zone of the lower Murray littoral begins to decline after 24 days of submergence, with maximum deterioration after 52 days (Figures 7.5 to 7.9). The change is associated with enhanced autotrophic production and a marked increase in the biomass of high carbon filamentous species. Similar situations have been observed in other rivers. During periods of low flow in the Ogoochee River (USA) an increase in the photic depth, owing to low flows, shifted the usually microbial, heterotrophic, biofilm towards one of increased algal production (Findlay *et al.,* 1986). In some large New Zealand rivers algal biomass has been observed to be highest during periods of low flow, with increased water velocity correlated with low biomass (Biggs and Gerbeaux, 1993).

Unregulated lowland rivers do not spend prolonged periods at a stable water level. Rather, the level moves continually, either flooding new surfaces as the water level rises or bringing deep surfaces into the photic zone as the water level falls (cf. Junk *et al.,* 1989). This suggests that in large lowland rivers littoral movement may be important for maintaining biofilms in a perpetual state of early succession, and therefore high nutritional quality. This may have been the case in the unregulated lower Murray (Figure 7.10) where river levels showed sustained rises and falls throughout the year, with stable levels only apparent for short periods (weeks). Flow regulation, however, has virtually eliminated the movement of the littoral zone, creating conditions where a stable stage is maintained in both upper and lower pools for months to years.

Figure 7.10 River height (metres AHD) at Lock 3 (Overland Corner) for the period prior to construction of the Lock. Based on daily records from the Engineering and Water Supply Department, South Australia.

Water level stability is demonstrated in Figure 7.11, which shows daily stage data in the upper pool of Pool 3 and lower pool of Pool 2 (Overland Corner) from 1921 until 1989. After the construction of Lock 3 in 1925 the weir is topped occasionally by seasonal floods, such as in the 1930's, as well as by large flood events (e.g. 1956/57 and 1974), otherwise levels in the upper pool have remained relatively constant. Levels in the lower pool immediately downstream of the weir are more variable. The presence of Lock 2 further downstream, however, creates a base level of approximately 6 mAHD, below which river levels cannot fall (Chapter 1). Thus, during periods of low flow the level of the littoral zone, even in lower pools, remains extremely stable.

This study suggests that the length of time substrata remain within the photic zone is a critical factor in determining the type of biofilm that will develop. The longer substrata are within the photic zone, the greater the biomass of high carbon containing, late successional taxa, within the biofilm. This suggests a link between increasing stability in river stage associated with flow regulation, and a change in the nature of riverine biofilms.

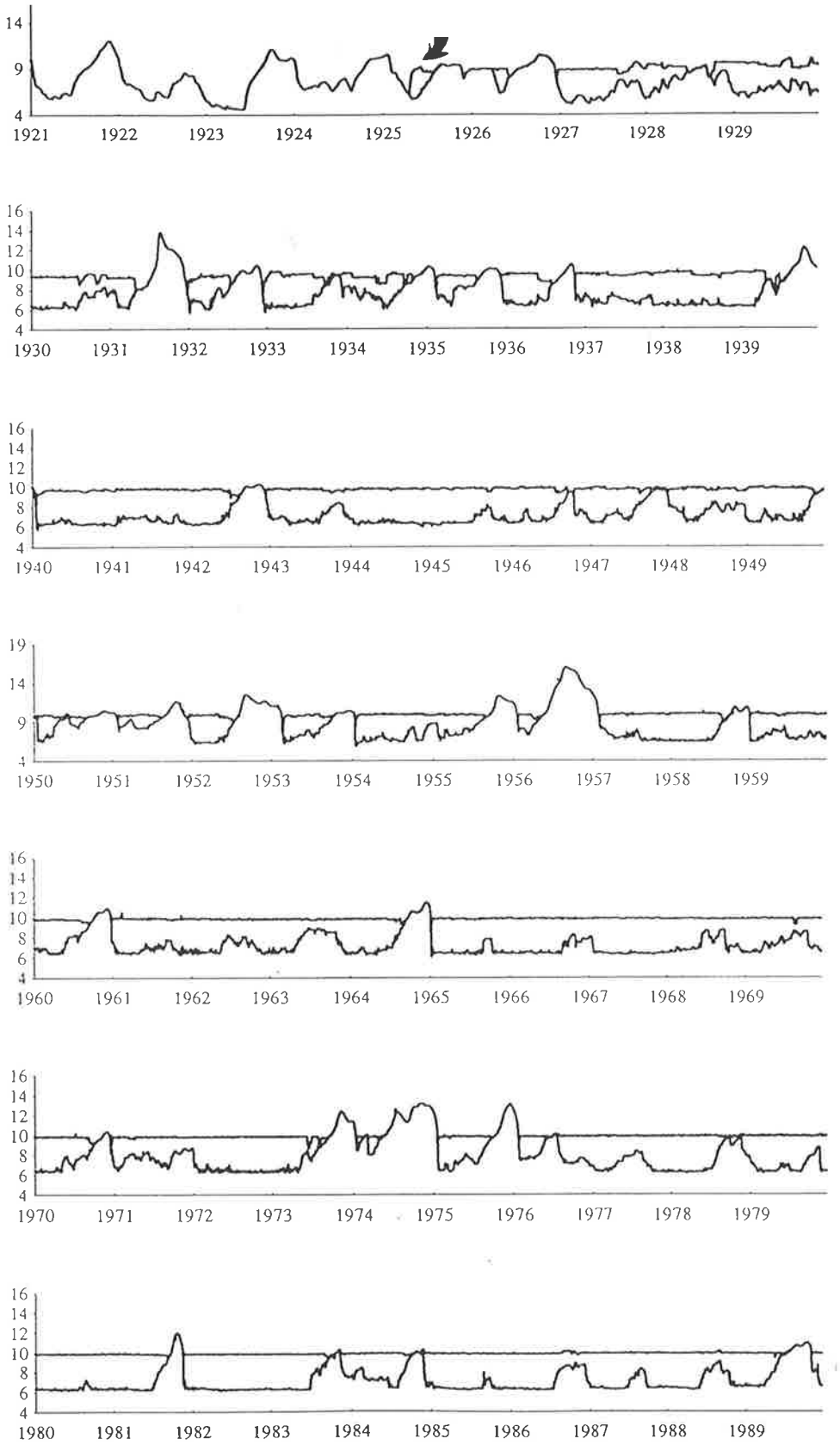


Figure 7.11 Daily river heights (mAHD) in the upper pool of Pool 3 and lower Pool of Pool 2 from 1921 until 1989. The construction of Lock 3 is indicated by the arrow. Modified from Walker and Thoms (1993).

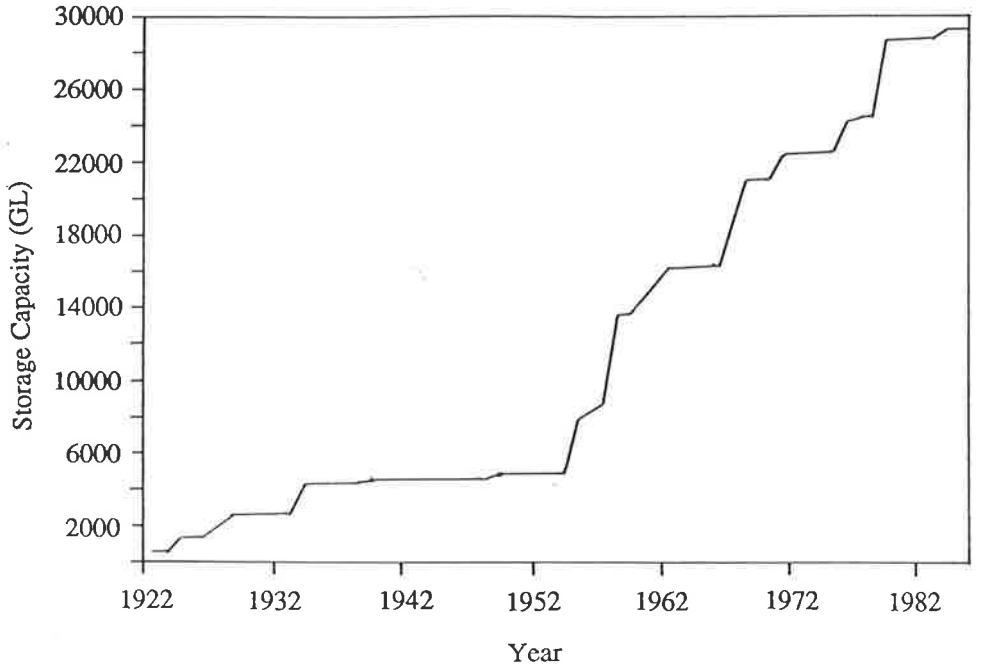
7.3 FLOW REGULATION AND WATER LEVEL STABILISATION

7.3.1 Introduction

In the Murray-Darling Basin flow regulation began with the construction of Lock and Weir 1 in 1922 and control over flows has increased continually since (Close, 1990; Chapter 1). The development of flow regulation can be subdivided into eight stages (cf. Maheshwari *et al.,* 1993) corresponding to the construction of various regulators (Table 7.5).

The process of flow regulation within the Murray-Darling Basin must be considered in stages, as the cumulative construction of the various regulators is likely to have had different impacts on the pattern of flow. Figure 7.12a shows the cumulative regulated storage capacity of the Murray-Darling Basin since construction of the first weir in 1922. The volume of stored water has increased markedly since the mid-1950's, as has the volume of water diverted for irrigation (Figure 7.12b). The period since the 1950's corresponds to the construction of a number of regulators with large storage capacities, including the enlargement of Hume Dam (1961), Menindee Lakes (1968) and, most recently (1979), the construction of Dartmouth Dam on the Mitta Mitta River (cf. Table 7.5). These storages have further altered the pattern of flows in the lower River Murray by increasing the volume of water stored in the upper catchment during the wet winter and spring months and releasing this water over the dry summer and autumn. This pattern of flow management has reduced the frequency of small and moderate floods and increased flows during periods of drought (cf. Close, 1990; Walker and Thoms, 1993).

In a large lowland rivers, such as the River Murray, it may be the magnitude and variability of river levels (movement of the littoral), rather than variability in discharge, that is the dominant influence on ecological processes. Prior to regulation the average daily rate of water level change in the lower Murray was 36 mm/day (Maheshwari *et al.,* 1993); thus, river levels would have taken roughly 10 days to undergo a change equivalent to the average photic depth , 300 mm (cf. Walker *et al.,* 1992).



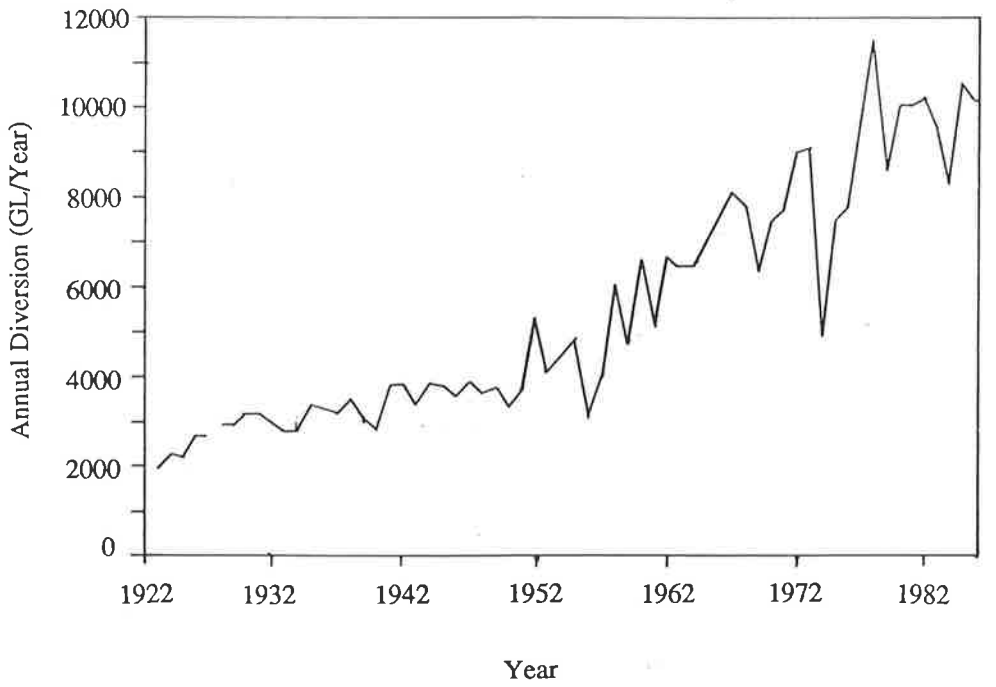


Figure 7.12
(a) Total installed storage capacity in the Murray-Darling Basin since 1922 (from Close, 1990),
(b) Annual diversions from the rivers of the Murray-Darling Basin, excluding those in the Queensland portion of the Darling River catchment (from Close, 1990).

This section examines the average number of days taken for the river in the lower pool of Pool 2, below Lock 3, pre- and post-regulation, to undergo stage changes from 10 cm to 100 cm. A limit of 100 cm was chosen as it represents the average maximum depth of light penetration, approximately three times the measured Secchi depth (cf. Cole, 1983). Differences in pre-regulation and recent post-regulation data for years with similar total and average discharge are initially considered. The impact of different regulatory structures on the stability of river stage is then examined by subdividing the data into the eight 'stages' outlined in Table 7.5. The difference in the stability of river levels along the gradient created by the presence of low-level weirs is then examined using stage data from the 1980's.

Table 7.5 Stages of regulation in the Murray-Darling Basin, from Maheshwari *et al.* (1993).

Stage			
Stage 1	Natural	-1921	Natural flow regime, no storage or diversions.
Stage 2	Pre-Lake Victoria	1922-1927	Some irrigation from Murray and tributaries; weir construction on Murray; Goulbourn Weir and Eildon Dam (Goulbourn R).
Stage 3	Pre-Hume Dam	1928-1935	Lake Victoria Regulator.
Stage 4	Post-Hume Dam	1936-1940	Hume Dam; more weirs constructed on Murray; increased irrigation.
Stage 5	Post-Yarrawonga	1940-1960	Yarrawonga Weir, river mouth barrages in operation; increased irrigation.
Stage 6	Post-Hume Weir	1961-1967	Hume Weir; increased irrigation; changes in operating rules.
Stage 7	Post Menindee Lakes	1968-1978	Menindee Lakes; diversions from Snowy to Murray; increased irrigation.
Stage 8	Post-Dartmouth Dam	1979-	Dartmouth Dam in operation (Mitta Mitta R).

7.3.2 Data Analysis

Daily stage data for the lower River Murray in the lower pool of Pool 2 were used for all analyses. The number of days taken for the river to undergo stage changes from 10 cm to 100 cm were calculated from these using a "macro" (Appendix H) written for Microsoft Excel v. 4.0 (Microsoft, 1992). For all data the average number of days taken for the river to undergo a given stage change is plotted against that change in stage.

7.3.3 Level Stabilisation: Pre-regulation versus Post-regulation

Daily records for pre-regulation water levels at Lock 3 extend for only 4 years (1921-24). To examine stabilisation three years of pre-regulation data (1921, 1922 and 1923) were compared with three years of post-regulation data of similar total discharge from the 1980's (Table 7.6).

For all years there was an increase in the average number of days taken for river levels to change from 10 cm to 100 cm (Figure 7.13). There was no apparent difference in the trend for the unregulated years of the 1920's and the post-regulation years 1984 and 1989. The years 1921 and 1923 are years of comparatively high discharge (cf. Table 7.6) and comparing them with similar years from the post-regulation period may mask impacts of regulation. At high discharges the river is under little or no regulatory control, at least until the later stages of flood recession.

By comparing the one pre-regulation year in which total discharge is low (1922) with a similar year from the post-regulation period (1981) there is an obvious difference in the number of days taken for river level changes. In 1981 it took an average of 54 days for a change of 30 cm, the average Secchi depth, compared with 17 days in 1922 (Table 7.7). This suggests, that at least for 1981, river levels in the lower pool of Pool 2 took on average twice as many days to undergo depth changes of up to 100 cm compared with the unregulated river.

Table 7.6 Total discharge (GL) and average monthly discharge (GL) *(SE)* of the lower River Murray for years from the pre-regulation and post-regulation period.

		Total Discharge (GL)	Monthly Discharge (GL)
Pre-regulation	**1921**	116706	1392.17 *(348.64)*
	1922	8034	669.5 *(96.54)*
	1923	12450	1037.5 *(299.46)*
Post-regulation	**1981**	9743	811.96 *(287.62)*
	1984	9679	806.59 *(164.85)*
	1989	14559	1213.25 *(250.11)*

Table 7.7 Means (SE) for average number of days taken for river levels to change from 10cm to 100cm or pre-regulation and post-regulation years of similar annual discharge.

				Pre-Regulation		
River Level (cm)	**n**	**1921**	**n**	**1922**	**n**	**1923**
10	361	6.88 *(0.26)*	362	7.84 *(0.29)*	349	11.21 *(0.57)*
20	360	12.1 *(0.55)*	359	12.2 *(0.42)*	345	18.01 *(0.87)*
30	358	17.34 *(0.8)*	357	16.67 *(0.54)*	304	26.59 *(1.51)*
40	356	21.94 *(0.99)*	355	20.93 *(0.65)*	301	36.65 *(2.04)*
50	354	27.71 *(1.21)*	353	24.68 *(0.74)*	299	43.14 *(2.29)*
60	353	35.08 *(1.6)*	352	28.98 *(0.93)*	297	49.45 *(2.46)*
70	351	38.46 *(1.64)*	351	34.44 *(1.17)*	295	53.3 *(2.52)*
80	349	41.99 *(1.68)*	350	39.74 *(1.35)*	293	56.85 *(2.57)*
90	347	45.2 *(1.68)*	347	44.95 *(1.47)*	291	62.84 *(2.82)*
100	345	48.48 *(1.72)*	346	53.07 *(1.61)*	288	66.44 *(2.91)*

				Post-Regulation		
River Level (cm)	**n**	**1981**	**n**	**1984**	**n**	**1989**
10	361	16.55 *(1.03)*	363	8.29 *(0.34)*	358	10.19, *(0.45)*
20	347	35.56 *(2.23)*	362	14.45 *(0.7)*	356	20.37 *(1.01)*
30	330	54.17 *(3.16)*	361	24.78 *(1.33)*	354	28.09 *(1.25)*
40	329	56.9 *(3.17)*	360	31.13 *(1.49)*	353	33.29 *(1.35)*
50	329	58.53 *(3.18)*	345	34.54 *(1.53)*	352	37.26 *(1.38)*
60	329	60.91 *(3.22)*	344	36.68 *(1.54)*	352	40.52 *(1.44)*
70	327	63.35 *(3.19)*	343	39.42 *(1.64)*	350	45.39 *(1.53)*
80	327	65.3 *(3.21)*	342	52.55 *(2.32)*	349	49.18 *(1.56)*
90	326	67.69 *(3.21)*	342	63.04 *(2.81)*	348	52.57 *(1.59)*
100	325	69.9 *(3.24)*	342	71.89 *(3.04)*	348	65.56 *(1.64)*

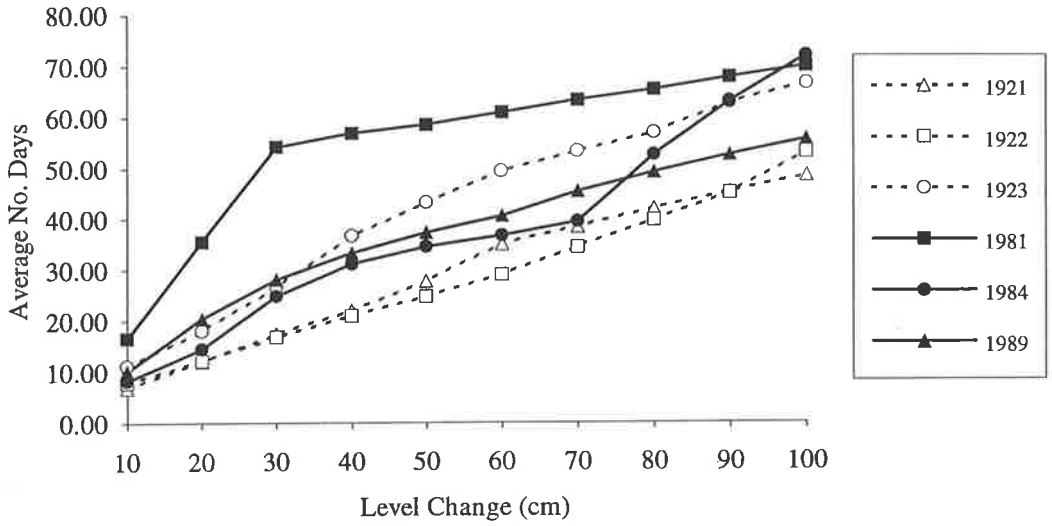


Figure 7.13 Average number of days taken for river levels to change from 10cm to 100cm, for pre-regulation (1921, 1922 and 1923) and post-regulation (1981, 1984 and 1989) years of similar annual discharge.

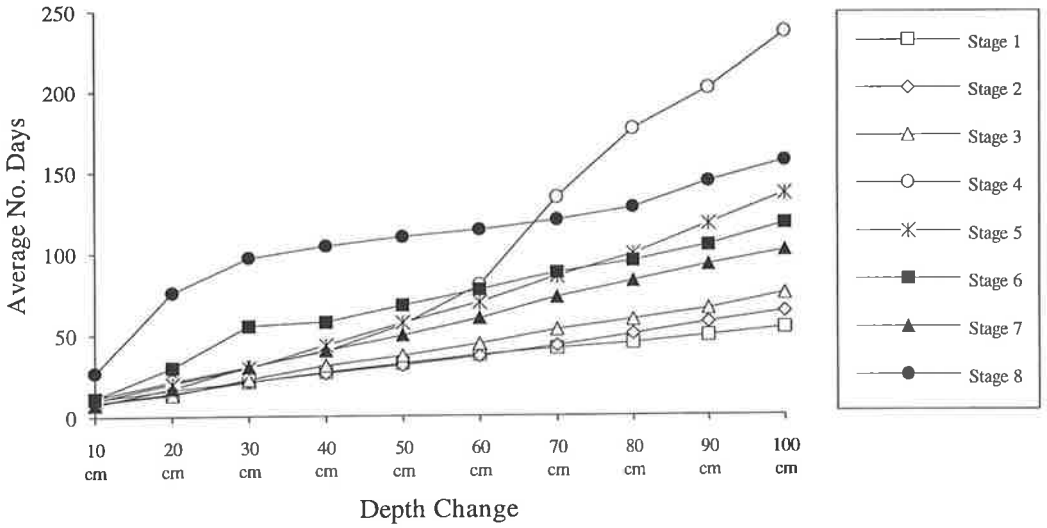
7.3.4 Level Stabilisation: Stages of increasing regulatory control

Daily stage data for the period of record (1921 to 1989) were divided into 8 periods by Maheshwari *et al.* (1993) (cf. Table 7.5). For each period, means (SE) for the number of days river stage takes to undergo a depth change of a given magnitude, are given in Table 7.8. When level changes were plotted against the average number of days taken for each change there was a distinct pattern (Figure 7.14a and b). Stages 1 to 3 corresponded to the pre-Hume Dam years and showed similar trends, with a gradual increase in the average number of days taken for changes, approximately 21 days for a 30 cm change and 30 to 40 days for a 50 cm change (cf. Table 7.8).

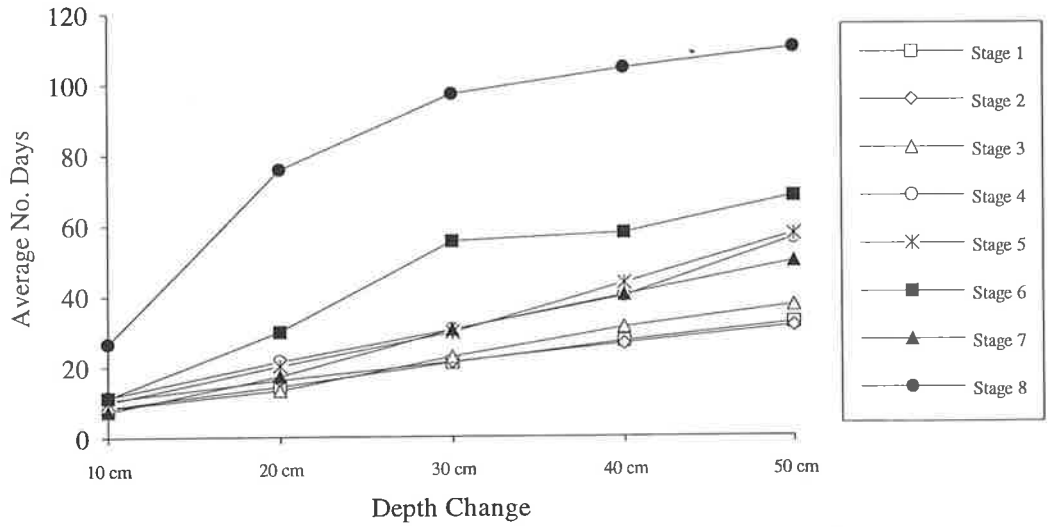
After 1935, and the completion of the first stage of Hume Dam (1936), there was an increase in the average number of days river levels take to change 30 cm. Stages 4, 5 and 7 showed a similar pattern of approximately 30 days for a 30 cm change, whereas data for Stage 6 showed, on average, more days for all stage changes greater than 10 cm, 50 days for a 30 cm change (cf. Table 7.8). This may be an artefact, however, of natural flow variability. Stage 6, which corresponded to an increase in the storage capacity of Hume Dam, also covered a series of dry (low flow) years (cf. Figure 7.11) and during this time natural stability of river levels may have enhanced the stability caused by flow regulation.

The major change in the behaviour of the river occurred after construction of Dartmouth Dam, Stage 8. From 1978 to 1990 there was a noticeable increase in the average number of days river stage took to change through all levels. For all Stages prior to 1978 a river level change of 10 cm took approximately 10 days, compared with 25 days since the construction of Dartmouth Dam (cf. Table 7.8). A river level change of 50 cm now takes on average over 100 days compared with less than 40 days for the early stages of regulation.

The construction of Dartmouth Dam, on the Mitta Mitta River, has had a marked impact on the distribution of river flows. Dartmouth Dam has a capacity of 4000 GL (cf. Table 1.2) and thus, has substantially increased the volume of water held in the upper Murray catchment during the high rainfall winter and spring. This water is then released over the drier months of summer and autumn to maintain flows along the middle and lower Murray. Dartmouth has given water managers a greater insurance against drought and increased control over the distribution of river flows. This has further reduced the frequency of small to moderate floods and increased the frequency of bankfull low flows.



(a)



(b)

Figure 7.14 Average number of days taken for river levels below Lock 3 (Overland Corner), on the lower River Murray, to change from (a) 10cm to 100cm and (b) 10cm to 50cm.

Table 7.8 Means *(SE)* for average number of days taken for river levels to change from 10cm to 100cm for the eight stages of regulation given in Table 7.5.

River Level (cm)	n	Stage 1	n	Stage 2	n	Stage 3	n	Stage 4
10	1204	8.53 *(0.22)*	1343	10.57 *(0.37)*	2919	8.29 *(0.15)*	1454	11.45 *(0.34)*
20	1201	14.31 *(0.36)*	1342	16.19 *(0.46)*	2916	13.29 *(0.23)*	1450	21.46 *(0.71)*
30	1201	21.08 *(0.54)*	1341	21.28 *(0.53)*	2916	22.7 *(0.49)*	1445	30.35 *(0.85)*
40	1199	27.06 *(0.69)*	1339	26.43 *(0.59)*	2913	31.01 *(0.64)*	1441	39.79 *(1.03)*
50	1172	32.15 *(0.81)*	1337	31.28 *(0.69)*	2912	37.07 *(0.74)*	1437	56.06 *(1.68)*
60	1158	37.46 *(0.91)*	1336	36.47 *(0.83)*	2912	44.12 *(0.84)*	1436	79.95 *(2.61)*
70	1144	41.31 *(0.96)*	1335	43 *(0.96)*	2912	52.75 *(0.92)*	1433	134.13 *(4.1)*
80	1119	44.49 *(1.01)*	1334	49.9 *(1.11)*	2912	58.91 *(0.97)*	1432	175.83 *(5.2)*
90	1116	48.88 *(1.08)*	1332	57.27 *(1.25)*	2912	65.32 *(1.01)*	1430	200.74 *(5.7)*
100	1115	53.65 *(1.12)*	1331	63.7 *(1.33)*	2911	74.79 *(1.26)*	1429	235.51 *(6.3)*

River Level (cm)	n	Stage 5	n	Stage 6	n	Stage 7	n	Stage 8
10	7667	9.96 *(0.13)*	2549	11.23 *(0.25)*	4012	7.36 *(0.11)*	4011	26.57 *(0.6)*
20	7667	20.15 *(0.29)*	2506	29.87 *(0.96)*	4005	17.28 *(0.38)*	4009	75.72 *(1.55)*
30	7667	29.57 *(0.43)*	2395	55.32 *(1.62)*	4004	30.37 *(0.67)*	4007	97.05 *(1.83)*
40	7667	43.46 *(0.65)*	2217	57.7 *(1.47)*	4001	40.12 *(0.79)*	4006	104.29 *(1.9)*
50	7667	57.19 *(0.86)*	2217	67.97 *(1.5)*	4000	49.48 *(0.93)*	4005	109.96 *(1.9)*
60	7667	69.61 *(1.02)*	2217	77.44 *(1.51)*	3992	59.77 *(1.11)*	4005	114.19 *(1.9)*
70	7667	85.45 *(1.23)*	2217	87.83 *(1.54)*	3987	72.83 *(1.3)*	4003	120.07 *(1.9)*
80	7667	98.95 *(1.41)*	2216	94.83 *(1.55)*	3988	82.45 *(1.4)*	4002	127.74 *(1.9)*
90	7667	117.5 *(1.63)*	2215	104.42 *(1.7)*	3987	92.41 *(1.5)*	4001	143.53 *(2.2)*
100	7667	136.14 *(1.8)*	2215	117.55 *(1.8)*	3987	100.9 *(1.57)*	4001	156.1 *(2.3)*

7.3.5 Level Stabilisation: Regulated Conditions, differences within Pools.

The above analyses were conducted on data from the lower pool region of Pool 2. The river level immediately upstream of a weir, however, is more stable than that below the weir (Chapters 1 and 4). Upper pools are held at levels previously only reached during minor floods and therefore fluctuate only when flows are higher than these levels, less than 20% of the time (Close, 1990). In this section the stability in river levels at five sites between Lock 4 (Bookpurnong) and Lock 3 (Overland Corner) (cf. Figure 1.7) is examined for the years 1983 and 1985.

The average number of days taken for level changes in lower pool regions of Pools 2 and 3, for both years, is less than in any other region of the river (cf. Table 7.9). In both 1983 and 1985 lower pools are more reflective of the pattern expressed by the unregulated river (Figure 7.15a and 7.15b). The data for Loxton, approximately 30 km further downstream from the lower pool of Pool 3, show a similar pattern to that seen in lower pools, but levels take nearly twice as long to undergo all changes (Table 7.9). Cobdogla, 30 km further downstream, begins to show the affects of increased level stabilisation in association with Lock 3. The upper pool region of Pool 3 is the most stable and in 1985 did not show a change in level greater than 20 cm for the entire year. In 1983 changes of greater than 60 cm did not occur for the entire year. Daily stage hydrographs for both upper and lower pools for 1983 and 1985 demonstrate the stability of the upper pools (Figure 7.16).

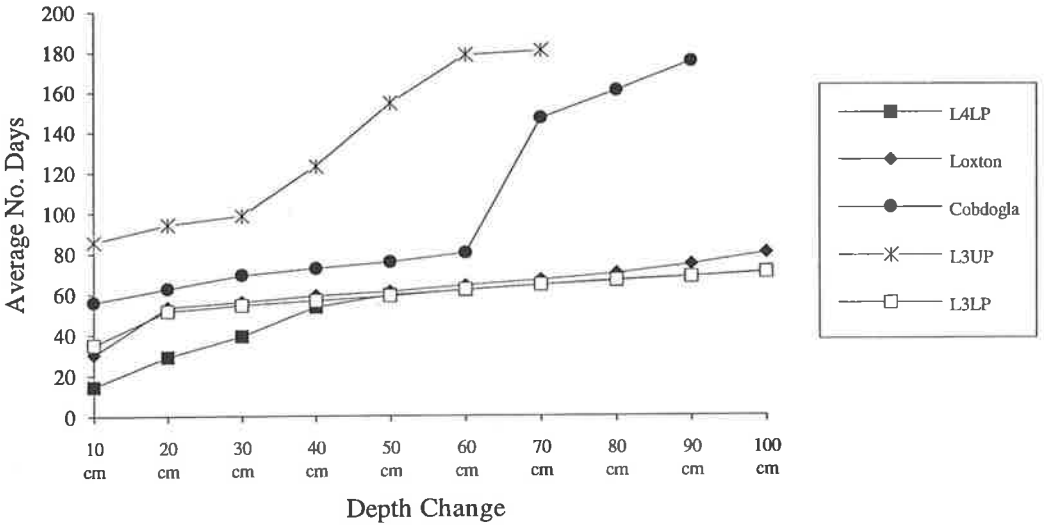
Table 7.9 (a) Means *(SE)* for average number of days taken for river levels to change from 10cm to 100cm for sites between the Lower Pool of Lock 4 and the Lower Pool of Lock 3 for 1983.
(b) Means *(SE)* for average number of days taken for river levels to change from 10cm to 100cm for sites between the Lower Pool of Lock 4 and the Lower Pool of Lock 3 for 1985.

(a)

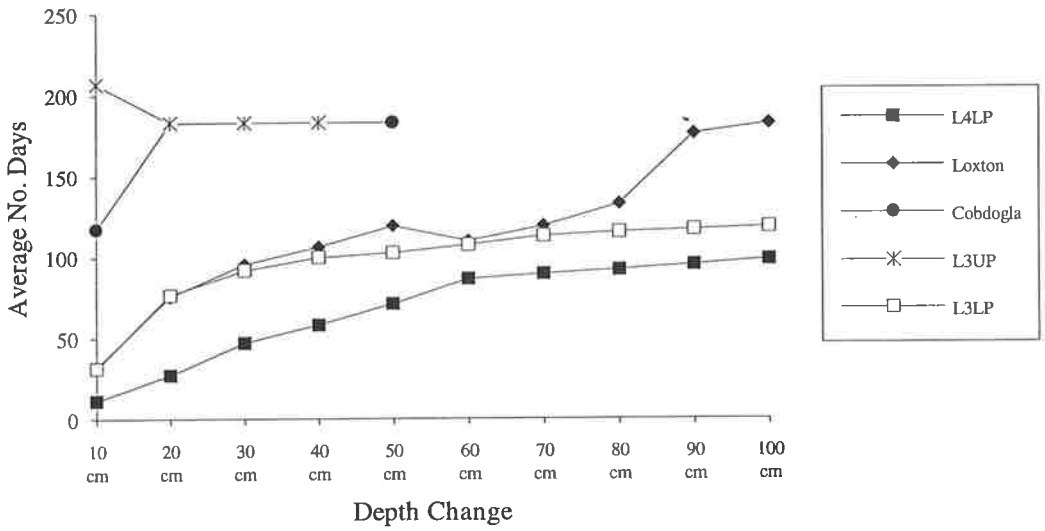
River Level (cm)	n	L4 Lower Pool	n	Loxton	n	Cobdogla	n	L3 Upper Pool	n	L3 Lower Pool
10	352	14.54 *(0.71)*	347	30.1 *(1.78)*	334	55.87 *(3.11)*	365	85.64 *(4.15)*	353	34.99 *(2.37)*
20	348	29.03 *(1.66)*	339	53.37 *(3.02)*	332	62.52 *(2.92)*	365	94.12 *(4.15)*	349	51.42 *(3.02)*
30	334	39.08 *(1.87)*	333	55.97 *(3.03)*	322	69.07 *(2.84)*	365	98.71 *(4.14)*	336	54.21 *(3.1)*
40	330	53.32 *(2.79)*	330	58.93 *(2.98)*	320	72.42 *(2.75)*	365	122.98 *(4.52)*	335	56.57 *(3.03)*
50	329	59.38 *(2.89)*	328	60.96 *(2.94)*	319	75.54 *(2.69)*	365	154.26 *(5.38)*	334	58.79 *(2.97)*
60	327	61.65 *(2.87)*	325	63.95 *(2.91)*	318	79.92 *(2.64)*	365	178.26 *(5.77)*	330	61.77 *(2.94)*
70	324	64.14 *(2.83)*	323	66.57 *(2.86)*	315	146.59 *(4.39)*	365	180.43 *(5.66)*	329	64.2 *(2.89)*
80	322	66.07 *(2.79)*	322	69.68 *(2.87)*	315	160.31 *(4.08)*			327	66.44 *(2.83)*
90	322	68.05 *(2.73)*	321	74.17 *(2.92)*	312	174.97 *(4.04)*			327	68.04 *(2.78)*
100	321	70.44 *(2.69)*	320	79.82 *(2.98)*	184	272.98 *(4.02)*			325	70.13 *(2.75)*

(b)

River Level (cm)	n	L4 Lower Pool	n	Loxton	n	Cobdogla	n	L3 Upper Pool	n	L3 Lower Pool
10	356	11.27 *(0.52)*	328	31.87 *(1.56)*	293	117.41 *(4.17)*	247	206.65 *(5.84)*	348	31.39 *(1.54)*
20	355	27.09 *(1.27)*	293	75.8 *(3.25)*	365	182.74 *(5.51)*	365	183 *(5.52)*	328	76.75 *(3.43)*
30	332	46.94 *(2.11)*	281	95.51 *(4.05)*	365	183 *(5.52)*	365	183 *(5.52)*	296	91.85 *(4.15)*
40	332	57.96 *(2.23)*	279	106.24 *(4.34)*	365	183 *(5.52)*	365	183 *(5.52)*	282	99.8 *(4.31)*
50	294	70.98 *(3.04)*	278	119.18 *(4.26)*	365	183 *(5.52)*			282	102.77 *(4.34)*
60	294	86.51 *(3.83)*	365	109.75 *(4.14)*					281	107.41 *(4.38)*
70	283	89.59 *(3.98)*	365	119.17 *(4.37)*					280	112.97 *(4.47)*
80	282	92.16 *(3.96)*	365	132.66 *(5.02)*					279	115.46 *(4.38)*
90	282	95.13 *(3.89)*	365	175.89 *(5.6)*					276	116.8 *(4.39)*
100	280	98.47 *(3.91)*	365	182.24 *(5.54)*					276	118.52 *(4.3)*



(a)



(b)

Figure 7.15 Average number of days taken for river levels to change from 10cm to 100cm for five sites between Lock 4 and Lock 3 for the years (a) 1983 and (b) 1985.

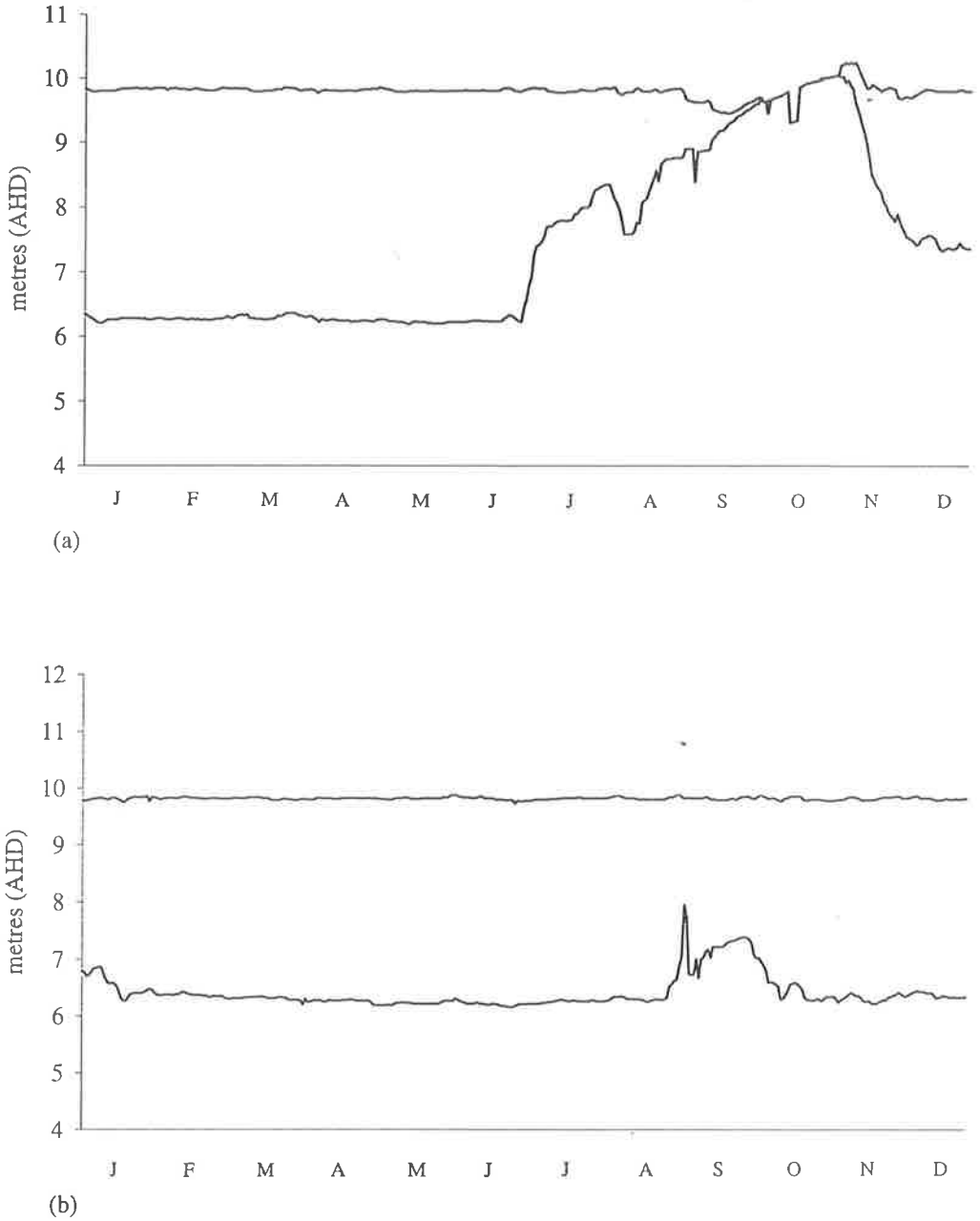


Figure 7.16 Daily data for upper pool (Lock 3) and lower pool (Lock 2) river levels for the years (a) 1983 and (b) 1985. Based on daily records from the Engineering and Water Supply Department, South Australia.

7.3.6 Discussion

Flow regulation in the Murray-Darling Basin has had a profound impact on the 'microtime' (cf. Chapter 2) stability of river levels in the lower River Murray. The trend shows an increase in the number of days taken for levels to change. This is most evident in years in which flows are low and the river is under maximum control and less obvious during high flow years where the river is essentially unregulated.

There appear to be two major changes in the pattern of increasing river level stability in association with the development of flow regulation in the Murray-Darling Basin. The first change occurs after construction of Hume Dam (Stage 3; Table 7.5), with river levels taking at least twice as long to undergo stage changes of less than 100 cm compared with the period prior to regulation. The major change in the pattern of river flows has occurred since the completion of Dartmouth Dam in 1978. Since then, there has been an increase in the number of days river levels take to make even small changes of 10 cm (Figure 7.14a and 7.14b). The time taken for changes of greater magnitudes, such as 40 or 50 cm, are nearly twice as great as was the case in the lower river prior to regulation (cf. Table 7.10). This increasing stability of river levels corresponds to an increase in the control of river flows by water managers. There has also been an increase in level of "entitlement" flows to South Australia which maintains river flows at 1850 GL per year.

7.4 Flow Regulation and Implications for Changes in the Composition of Biofilms

In small streams floods are the major resetting mechanism for periphyton assemblages on benthic substrata (Fisher *et al.,* 1978; Webster *et al.,* 1983; Biggs and Gerbeaux, 1993). Floods prevent dominance by late successional taxa through scouring, this resets succession. In large rivers most small and moderate floods will be insufficient to remove attached periphyton. In these rivers the magnitude of littoral zone water level movements, in association with floods, may act as the disturbance, disrupting the process of succession.

Odum (1969) suggests that assemblages in the early stages of development will be dominated by small organisms with rapid simple life cycles, whereas larger organisms, with more complex life cycles, will characterise the latter stages. The post flood succession of periphyton assemblages in Sycamore Creek (Arizona)

reflects this pattern, with a transition from diatoms and unicellular green to larger filamentous green and blue-green algae (cf. Fisher *et al.,* 1978). For periphyton, the disturbance created by the movement of the littoral zone in a large river, however, is not comparable to that created by a flash flood in a small stream. Flash floods are reset succession as a majority of the biomass is removed, whereas the movement of littoral water levels essentially prevent assemblages from reaching latter stages of succession. Substrata are either moved into deeper waters and out of the photic zone, or are exposed as waters recede.

Section 7.2 demonstrates how the length of time substrata are maintained within the photic zone influences the composition of the biofilm. The initial assemblage, during the first weeks of inundation, has a high organic content comprising mostly organic detritus and microbial biomass. Although low in abundance, diatoms are the most common algae. With increasing time in the photic zone the composition of the assemblage changes, diatoms increase in dominance until filamentous algae eventually comprise the majority of the biomass (cf. Figure 7.17).

These changes are associated with a shift in the food quality of the biofilm, measured as the ratio of C:N. Food quality is initially high but declines most rapidly after 52 days of submergence, coinciding with an increase in the biomass of filamentous algal forms. Although published data on the temporal succession of periphyton assemblages are few, the time of approximately 52 days of submergence within the photic zone for maximum biomass to be attained is comparable to that recorded in Sycamore Creek, a desert stream in Arizona (USA). In the absence of scouring floods a maximum biomass of benthic periphyton was attained after 63 days of submergence (Fisher *et al.,* 1982). Thus, the length of the disturbance free period, either the interval between floods or the time remaining in the zone of light penetration, may be the single most important factor in determining both the level of periphyton biomass and the composition of the resulting assemblage (cf. Lohman *et al.,* 1992).

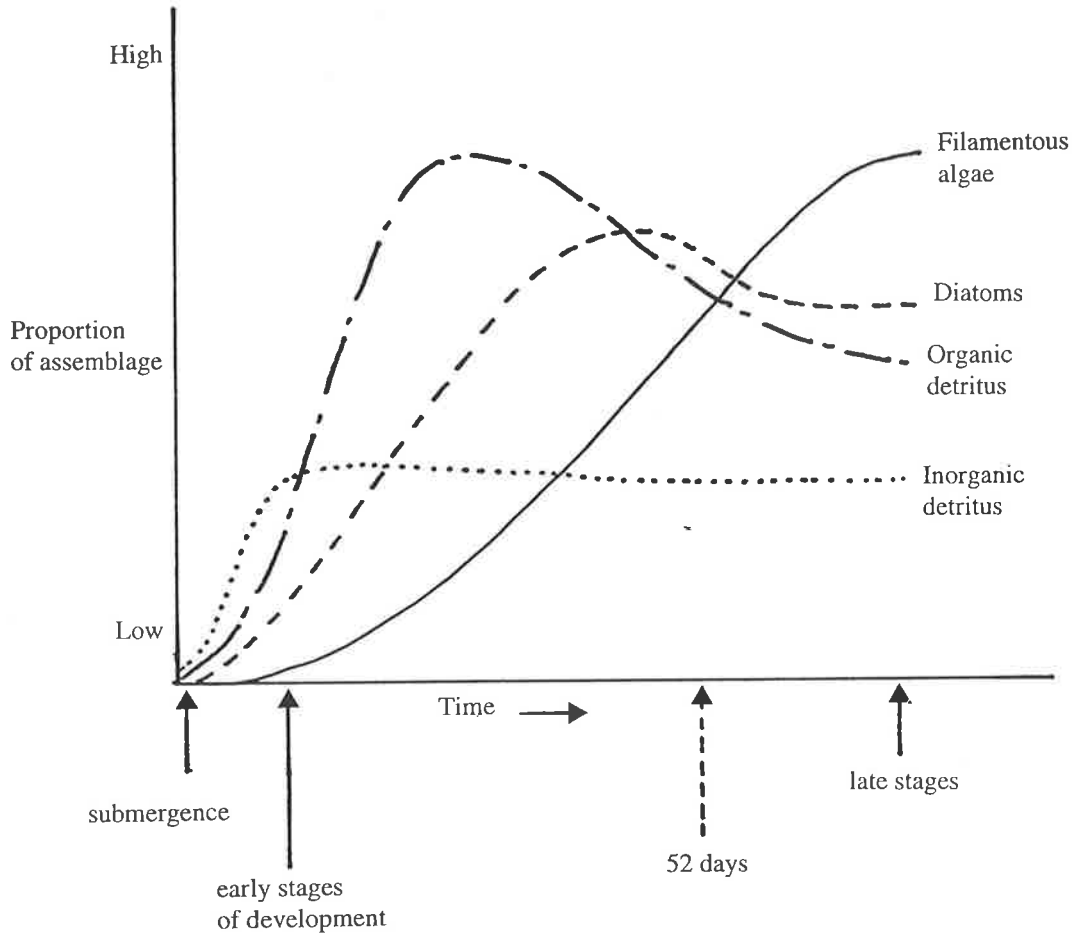


Figure 7.17 Changes occurring in periphyton assemblages with increasing time in the photic zone after submergence of substrata.

Flow regulation can influence the length of time littoral substrata spend in the photic zone. The unregulated lower Murray was characterised by seasonal water level movements, with sustained rises and falls (Maheshwari *et al.,* 1993). Regulation has changed the scale of these movements. In the regulated river of the 1980's we see an increase in the frequency of small short-term (daily) fluctuations (see Chapter 5; Maheshwari *et al.,* 1993), water levels move erratically up and down around a stable base level, with an average daily magnitude of <20 cm (cf. Walker *et al.,* 1992). There has also been a decrease in the larger seasonal changes in water level, owing to successive weirs along the lower river, as well as the maintenance of comparatively high "entitlement" flows during periods of naturally low discharge (see Chapter 1)

The above changes in littoral zone water level movement did not occur simultaneously with the construction of the first weir; rather, they have been cumulative, with the larger storages, Hume Dam and Dartmouth Dam, exerting most influence. Prior to regulation river levels took around 10 days to undergo depth changes that were equivalent to the average Secchi depth, approximately 30 cm, which suggests an average light penetration in the range of one metre (cf. Cole, 1983). After the construction of Hume Dam, however, this increased to an average of 30 days for the same change and after the completion of Dartmouth Dam, and the increase in entitlement flows to the lower Murray, levels now take over 90 days to undergo comparable depth changes.

To predict the impact of regulation on the composition of periphyton assemblages we can combine the times taken for water levels in the regulated lower Murray to undergo specific changes in stage with the time required for a decrease in the food quality of periphyton. With an average minimum of 30 days required for a change of 30 cm, biofilms developing within the photic zone of the regulated river will reach a late successional stage before water levels move sufficiently to either expose the substrata, or limit light availability (cf. Figure 7.17). Given that this is the situation in lower pool regions, which have the most variable water levels (Chapter 1), assemblages in middle and upper pool regions will be subjected to stable levels for longer periods and periphyton assemblages would be further dominated by filamentous algal forms. For a majority of time the food quality of periphyton will be low, owing to the high biomass of filamentous algae.

The increasing stability of the littoral zone in all regions of the lower Murray has been cumulative, with the periods of most change occurring after the 1950's (increase in irrigation diversions) and during the 1970's (completion of Dartmouth Dam) (see Table 7.5). These periods of change in littoral zone stability, and therefore biofilm food quality, coincide with the time-frame suggested for the disappearance of many faunal groups, including the prosobranch gastropods. Dietary evidence suggests that the gastropods, *T. balonnensis* and *Notopala* spp., consume organic matter, even when algae are present (Chapter 6). It is reasonable to suggest, therefore, that these gastropods have been eliminated from the lower river through changed food resources, the result of the long term stability of water levels in the littoral zone caused by flow regulation. This highlights a role for moving water levels in the dynamics of riverine littoral zones. This is explored further in Chapter 8.

Chapter 8

Conclusion

8.1 SUMMARY

The riverine littoral zone is the boundary between a lotic aquatic environment and the adjacent terrestrial environment. It corresponds to the "wetted perimeter" of the river when it is within its banks, and to the advancing or receding water's edge in times of flood. The zone exhibits physical complexity over a range of scales in space (macro-, meso- and micro-habitats) and time (macro-, meso- and micro-time). Spatial complexity reflects floodplain geomorphology, and temporal complexity is evident in the timing, duration and other features of the flood pulse (cf. Chapter 2).

Flow regulation changes the scale of littoral habitat patches. Spatially, it can decrease lateral (channel-floodplain) gradients and enhance longitudinal (upstream-downstream) gradients, isolating floodplain habitats from the channel. Regulation also modifies the flood pulse: reductions in the frequency, amplitude or duration of flooding decrease water-level changes at 'micro-time' (seasonal or flood-pulse) scales, whilst management operations may increase the frequency of fluctuations at smaller scales, creating daily or weekly water-level changes (Chapter 2).

Changes of this nature are readily apparent in the River Murray, a dryland river in south-eastern Australia. Flows are regulated by storages on the upper Murray and its tributaries, and by low-level weirs in the middle and lower tracts of the river. The modified regime includes increased summer-autumn flows, increased flow constancy due to regulated releases from upstream storages, and short-term flow fluctuations associated with weir operations. The changes include:

- modified meso-habitat structure, whereby some temporary habitats have become permanent and others are isolated from flooding
- modified micro-habitat diversity through changes in erosion, deposition and the magnitude and duration of floods
- changed features of the flood-pulse at a micro-time scale, through reduction in the frequency of low and moderate flows, leading to a more stable hydrograph

- more frequent short-term flow fluctuations, hence littoral water level changes, at daily and weekly time scales.

This thesis explores the impacts of these changes on the ecology of the littoral zone of the Murray in South Australia. Macroinvertebrate assemblages were examined with regard for spatial patterns in macro-, meso- and micro-habitats and longitudinal changes in the composition of assemblages, determined by water-level gradients associated with weir operations. Special attention is given to the large prosobranch gastropods *Thiara balonnensis* and *Notopala* spp., taxa that were abundant in the unregulated lower Murray, but are now approaching local extinction. The analysis considers whether changed flow fluctuations in the littoral zone may have contributed to the decline of these species.

Littoral zone habitats of the lower Darling and lower Murray, sampled in summer 1990, supported 103 macroinvertebrate taxa. Assemblages were dominated by insects and crustaceans, but with an uneven distribution of individuals amongst taxa (Appendices B-D). In both floodplain and channel habitats of the lower Murray the shrimp *Paratya australiensis* was extraordinarily abundant, comprising 68% of the total macroinvertebrate organisms in main-channel habitats (Chapters 3 and 4).

The littoral zones of each river contained a wide diversity of mesohabitats and microhabitats. The mesohabitats reflected the geomorphology of the particular river reach (macrohabitat). The lower Murray with a broad, well-watered floodplain contains diverse mesohabitats (billabongs, backwaters, slow and fast flowing anabranches and main channel) with predominantly vegetation microhabitats. In contrast, the lower Darling flows in a 10-m trench and has a less often inundated floodplain; it was dominated by channel habitats, supporting less vegetation, with 'snag' and 'open littoral' microhabitats. Distinct assemblages were apparent at all three scales, but microhabitat structural complexity appeared likely to be a major factor, with microhabitat composition influencing mesohabitat patterns and the same at the macrohabitat scale (Chapter 3).

The FFG composition of assemblages in all habitats reflected the utilisation of diverse resources of organic detritus. Generalist collector-gatherers were commonest, with comparatively few filterers and scrapers. This argues for the significance of organic inputs from floodplain environments, rather than ultrafine particulate and dissolved organic matter, in the lowland reaches of large rivers (cf. RCC: Vannote *et al.,* 1980).

In large rivers regulation may decrease the extent of lateral water movements, imposing a longitudinal gradient on the littoral zone. This gradient may be further disrupted by dams or weirs (cf. SDC: Ward and Stanford, 1983). The weirs on the lower Murray create sequential water-level and trophic gradients, and disrupt the distribution of vegetation microhabitats (Chapter 4; Walker *et al.*, 1994). The gradients are reflected in the formation of upper, middle and lower pool sections along the main channel.

The distribution of microhabitats between the pool sections is a key factor in determining invertebrate assemblage composition. In upper, middle and lower pools snags and the emergent macrophyte *Phragmites australis* are common microhabitats with assemblages that include the abundant shrimps *Paratya australiensis* and *Caridina mccullochi*, the prawn *Macrobrachium australiense* and a number of chironomids. The submerged macrophyte *Vallisneria spiralis* is common in upper pools and provides habitat for rarer taxa, including the baetid mayfly *Cloeon* sp., the amphipod *Austrochiltonia australis* and the gastropod *Ferrissia* sp., that may utilise filamentous algae on *V. spiralis* leaves. In lower pools unvegetated littoral areas and the sedge *Cyperus gymnocaulos* are common habitats for the isopod *Austroargathona picta*, the ceratopogonid *Forcipomyia* sp. and the chironomids *Cladotanytarsus* sp. and *Tanytarsus* sp.

Analyses of the spatial patterns of macroinvertebrate assemblages in the littoral zone showed that lateral connections between the main channel and floodplain may enhance diversity by increasing the number of available habitats, and that flow regulation may impose gradients in resources and habitat availability, potentially modifying assemblage composition.

These analyses do not, however, explain the recent extinction of groups such as the aquatic gastropods (Chapter 1). To do this, specific features of the biology of the prosobranch gastropods were examined.

In the lower Murray regulation has changes the scale of water level movements in the littoral zone. Increases in the rate and magnitude of daily and weekly water level changes in the lower weir pools (Chapters 1 and 5) may have contributed to gastropod decline through stranding when water levels fall suddenly, or through habitat modification. Experiments demonstrated that *Notopala sublineata* and *Thiara balonnensis*, and the pulmonate *Physa acuta,* were able to respond to sudden

changes of magnitudes greater than normally occur in the regulated river (Chapter 5). It is also unlikely that regulation has modified microhabitat composition in a manner that affects gastropods. Both, *Notopala sublineata* and *Thiara balonnensis,* are found in the rivers of the Lake Eyre basin associated with microhabitats that are also abundant in the regulated lower Murray.

Regulation has also decreased the magnitude of water level changes over a flood-pulse, which may contribute to gastropod decline by modifying available food resources. Studies of the diets of *Notopala* spp. and *T. balonnensis* show that they are detritivores, utilising the bacterial portion of the detritus even when algae are available (Chapter 6). Both taxa are also viviparous, requiring a rich supply of nitrogen in their diets to satisfy the breeding requirements and growth of females. The food quality of microbial biofilms has a lower ratio of carbon to nitrogen (C:N), and therefore a higher food quality, than does algal periphyton (Chapter 6). When exposed to a food resource dominated by filamentous algae, *N. hanleyi* is unable to select organic detritus over algae (Section 6.6). Thus, faced with a food resource consisting entirely of algae, the gastropods may actively consume it but be unable to obtain enough nitrogen for growth and survival. This may account for the decline of these species in the lower Murray. In environments where the food resources is rich in nitrogen, like the irrigation pipelines in the South Australian Riverland, both species are abundant (Chapter 6; Sheldon and Walker, 1993b).

In the regulated lower Murray, algal biofilms are prevalent in all pool sections. Algal periphyton, however, may not have always dominated biofilms in the lower Murray. Increased stability of the photic zone, associated with changes in water-level fluctuations at seasonal or flood-pulse scales ('microtime'), may have enhanced the growth of benthic algae. In unregulated, turbid rivers the continual movement of littoral zone water levels would be reflected in a continually moving photic zone, preventing prolific algal growth (cf. Chapter 7). Production in these systems would have been predominantly heterotrophic (bacterial/microbial). The shift from bacterial-microbial towards algal food sources, corresponding with the change from unregulated to regulated flows, may have affected the food sources for many aquatic invertebrate species.

The degree of water level stability in the littoral zone has changed since regulation commenced. The greatest changes occurred after the construction of Hume Dam (1930's), with increases in water diversions (1950's), and after construction of Dartmouth Dam (1979) (cf. Figure 1.8). Under present levels of regulation water

levels in the lower Murray remain stable within the average photic depth for at least 100 days, well within the time for prolific algal growth and food deterioration to occur (Chapter 7). The period in which major increases in stability occurred (late 1950's to 1979), coincides with the population decline of the prosobranch gastropods.

These changes may have affected other groups. The survey of lower Murray invertebrate assemblages (cf. Bennison *et al.,* 1989) suggested that the similar diversity but lower abundance of lower Murray assemblages, compared with upstream assemblages, was caused by a physical stressor such as high turbidity. From the present study, such a stressor may be the scarcity of the right type of food. Thus, although a diverse assemblage can survive in the river, individual abundances are low because of food limitation. This may also explain why the shrimp *Paratya australiensis* has been able to dominate the invertebrate assemblage. Its high mobility may make it better at utilising a patchy or scarce food resource. The affect littoral zone stability may be having on the fauna presently inhabiting the Murray poses a new question.

8.2 PERSPECTIVE

Neither the River Continuum Concept (RCC: Vannote *et al.,* 1980) nor the Flood Pulse Concept (FPC: Junk *et al.,* 1989) adequately explain ecological processes observed in river systems; a combination of these concepts is more realistic (Chapter 2). Rivers exist as cascading habitat patches linked in space and time by the actions of the flood-pulse and the flow of water. The relative significance of spatial linkages (lateral, longitudinal, vertical) will vary with river distance from the headwaters to the mouth, depending on stream gradient and degree of floodplain development (cf. Section 2.3; Figure 2.8).

Most large rivers have well developed floodplains and low gradients, therefore, lateral connections between floodplain and channel habitats will be significant in driving ecological processes. The moving water's edge of the littoral zone during flooding connects the channel and floodplain habitats. Its cyclic fluctuations, within the channel and across the floodplain, increase physically habitat complexity and contribute to biotic diversity. Lateral movements of the littoral also enhance organic matter cycling and contribute to nutrient fluxes (cf. Figure 8.1). In dryland rivers variability in the amplitude and frequency of floods suggests that the movement of the littoral zone, within the channel and occasionally across the floodplain will be vital in maintaining these ecological processes, as the frequency of floodplain inundation is highly variable (Section 2.2).

Rising water levels within the channel can be as significant as larger overbank flows (Figure 8.2). As the littoral zone rises within the channel nutrients are released from newly flooded sediments, terrestrial allochthonous detritus is inundated and there is increased growth of vegetation and associated food and habitat for animals. The recession of the flood-pulse triggers aquatic production via an increase in nutrient input and an increase in aerobic decomposition of organic matter (cf. Section 2.2). The only period of significant autochthonous production in such systems would occur when water levels were stable within the channel.

In river-floodplain systems "disturbances" are not necessarily harmful events as they can reset late successional stages to earlier stages and thus, increase habitat and species diversity (Sparks *et al.,* 1990). Continual movement of littoral water-levels may, therefore, be likened to a small, repeated, disturbance. Such movements can continually disrupt the photic zone and prevent late successional taxa, such as filamentous algae from dominating periphytic biofilms.

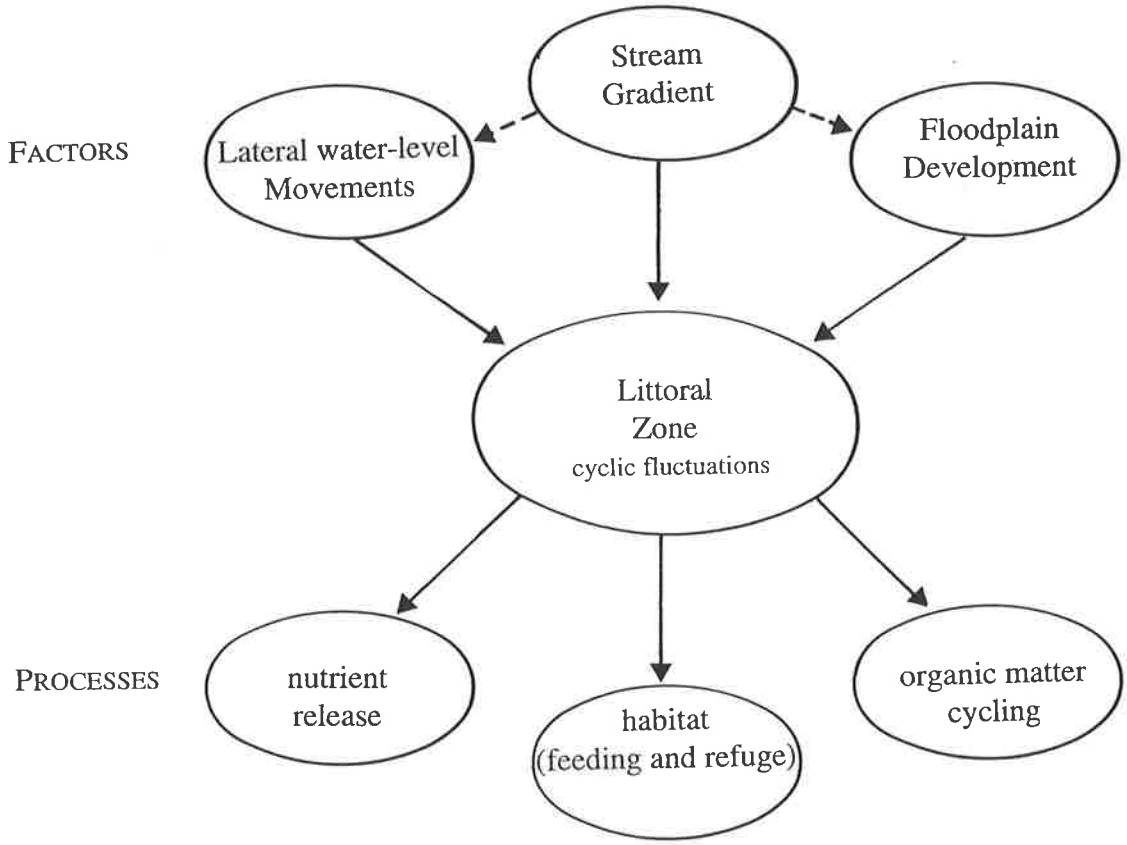


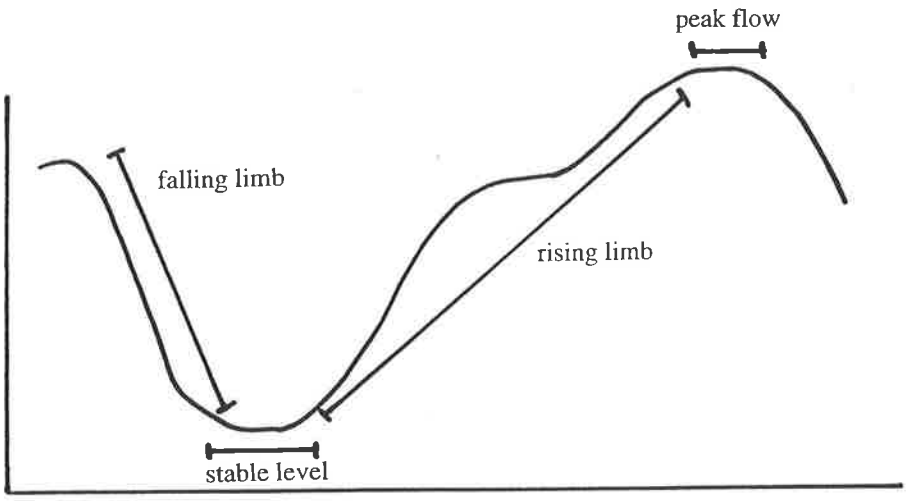
Figure 8.1 Ecological interactions occurring in the littoral zone of a large floodplain river.

In large rivers flow regulation may exert its greatest impact on the littoral zone by changing the scale of water-level movements in space and time. This is demonstrated in Figure 8.3 for three flood-pulse events of different magnitudes in the lower River Murray, South Australia. Actual regulated data are used along with simulated data for unregulated conditions (River Murray Model, Murray-Darling Basin Commission). During a large unregulated flood pulse (Figure 8.3a) water levels move continually, both within the channel and across the floodplain. Regulation of this pulse decreases the magnitude of the water-level rises and falls and increases the duration of stable water levels. A smaller flood pulse (Figure 8.3b) displays the same pattern, however, the duration of stable flow has increased. For small 'within-channel' flood pulses (Figure 8.3c) regulation has eliminated the natural rises and falls of littoral water levels within the channel and water levels remain stable for the duration of the pulse.

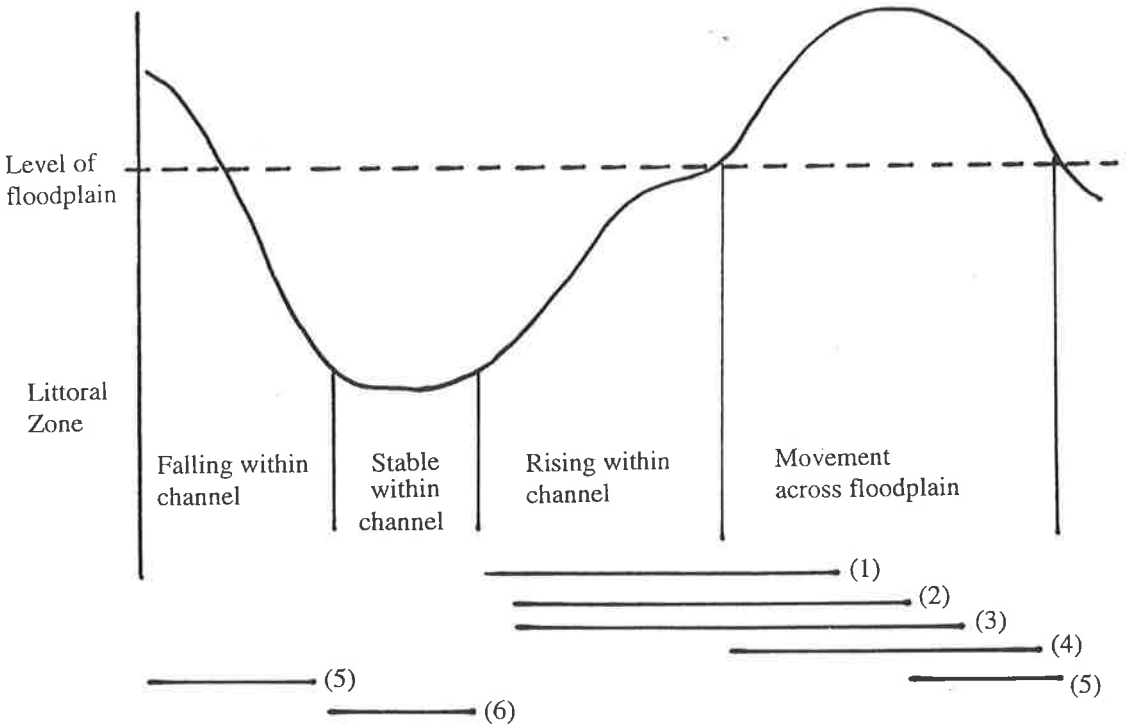
Under regulated conditions the ecological processes occurring within the littoral zone that will be most affected will be those concentrated in the rising and falling limbs of a flood pulse. The processes unaffected, or enhanced, will be those within periods of stable water levels, including autochthonous production.

This thesis began with the observation that the littoral communities of large rivers have been neglected by ecologists. Clearly, the littoral zone is a significant for the ecology of the lower Murray, but as the Murray is distinctive in many respects, not least because it is a dryland river, the ideas discussed need to be generalised. Studies of the littoral ecology of large rivers elsewhere in the world may yield other insights, and so contribute to the now fast-growing conceptual framework for large-river ecology.

Figure 8.2 (a) Various stages of a flood pulse
(b) Idealised changes in littoral zone water levels in a large river. Numbered horizontal bars indicate characteristic littoral zone interactions as follows: (1) nutrients released as littoral water's edge rises within the channel and across the floodplain, (2) inundation of allochthonous terrestrial detritus accumulated on the dry channel banks and floodplain, (3) growth of aquatic plants in advancing water's edge, (4) major period of detrital processing on floodplain, (5) organic matter exported from the floodplain to the river, (6) maximum plankton and autochthonous production in river and floodplain habitats. After Ward (1989b), modified for application to within channel littoral zone movements.

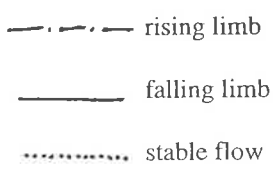

peak flow
falling limb
rising limb
stable level

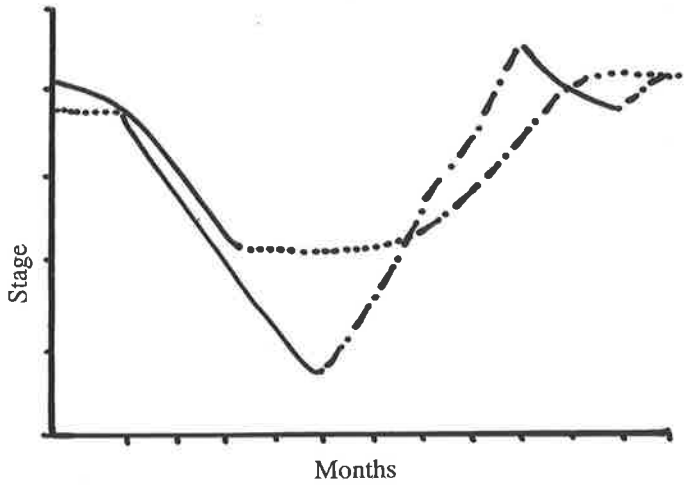
(a)

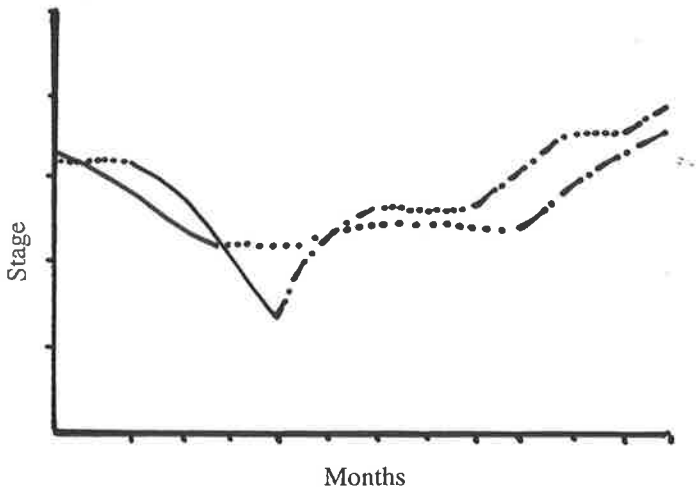

Level of floodplain
Littoral Zone
Falling within channel
Stable within channel
Rising within channel
Movement across floodplain
(1)
(2)
(3)
(4)
(5)
(5)
(6)

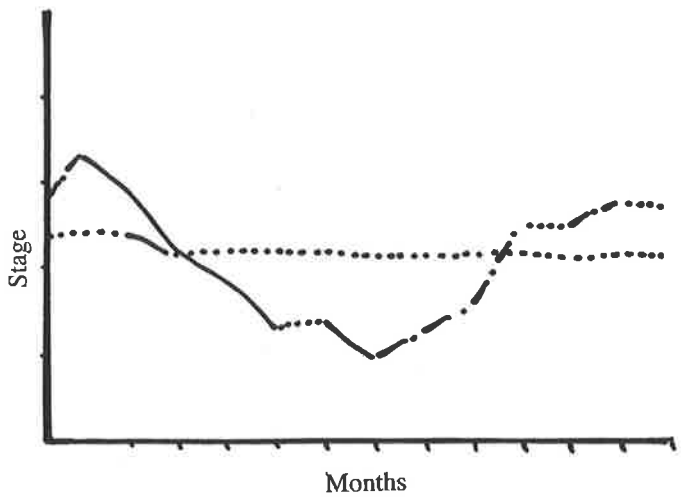
(b)

Figure 8.3 Simulated flow data for flood-pulse events of different magnitudes, (a) large overbank flood, (b)small flood, (c) within channel flood-pulse. Overlay shows the actual regulated flows for the same events and highlights the changes associated with flow regulation




Stage
Months


Stage
Months


Stage
Months

Chapter 9

Recommendations for Management

The Murray-Darling Basin Environmental Resources Study (MDBMC, 1987) suggested that "*a legislative mandate for the allocation of water for in-stream uses*" in the Murray and Darling Rivers was required, but "*before water allocations can be made for in-stream needs, further research will be needed ... to quantify environmental requirements and establish optimum timings for water supply*". Based on the results of this thesis, the following three 'broad' options are suggested for the management of flows in the lower Murray. Each option is considered from an ecological viewpoint, being concerned with river system function. Consideration for the implications of each option on flow conditions and water supply is briefly suggested. It is not within the scope of this study to explore the social implications of each option, however, an indication of ecological "success" and other associated problems is suggested.

9.1 Management Options for the Lower River Murray

Option 1 Remove All Weirs

Effects on Flow Conditions:
Removing weirs would eliminate short-term flow fluctuations and allow water levels to recede in a manner reflecting natural conditions. Flows over the summer, however, would still be increases, compared with unregulated conditions, owing to releases from upstream dams. This option would reinstate water level movements at a 'microtime' scale.

Effects on Water Supply:
Such changes are likely to be detrimental to irrigation, as base water levels would be lower than presently in the river.

Success Rating and Other Problems:
A high degree of ecological success in restoring some cyclic fluctuations to the littoral zone would be expected. Associated problems may include increased salt loads to the channel owing to locally raised groundwater, this may inadvertently affect biota.

Option 2 Change the Distribution of Entitlement Flows

Effects on Flow Conditions:
One impact of flow regulation is stable water levels over a natural flood pulse. Such stability is partly caused by the release of "entitlement" (cf. Chapter 1; Appendix A) flows to the lower Murray. In 1993 the "entitlement" flow was 1850 GL. Modifications to the way such flows are distributed to the lower Murray may reinstate a more 'natural' hydrograph and allow littoral water levels to fluctuate within the channel. This may be done by releasing entitlement flows in small pulses. These changes would increase the amplitude of fluctuations at a 'microtime' scale.

Effects on Water Supply:
This option may require some modification to existing irrigation pumps, allowing use over a broad range of water levels.

Success Rating and Other Problems:
Some success would be expected, depending on the amplitude of water-level changes adopted. The optimum change would be a sustained rise or fall in levels, of at least 30 cm every 50 days, preventing the proliferation of benthic algae and subsequent deterioration in food quality (cf. Chapter 7).

Option 3 Increase Base Level Variability

Effects on Flow Conditions:
Through structural modifications to weirs, variability in base water levels may be increased. Modifications would need to allow sustained rises and falls in levels, rather than a series of stepwise falls or rises between set levels.

Effects on Water Supply:
Modifications to structures to allowing variability in base levels would affect irrigation pumping, requiring some changes to pump levels. Water levels in upper pool sections would be lowered and water storage capacity would be lost.

Success Rating and Other Problems:
This option would be difficult to implement given the current structural limitations.

These options are brief examples of the changes that may be implemented in the lower Murray to restore cyclic fluctuations in littoral zone water levels.

References

Adamek, Z and I Sukop (1992) 'Invertebrate communities of former southern Moravian floodplains (Czechoslovakia) and impacts of regulation', *Regulated Rivers: Research and Management* **7**:181-192.

Aldridge, D.W. (1983) 'Physiological ecology of freshwater prosobranchs', in, Russell-Hunter, W.D. (Ed), *The Mollusca*, Vol. 6, *Ecology*. Academic Press, London. pp. 330-359.

Allanson, B.R., R.C. Hart, J.H. O'Keefe and R.D. Robarts (1990) *Inland Waters of Southern Africa: an Ecological Perspective,* Monographiae Biologicae 64, Kluwer Academic Publishers.

Allen, T.F.H. and T.B. Starr (1982) *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.

Allen, T.F.H , R.V. O'Neill and T.W. Hoekstra (1984) 'Interlevel relations in ecological research and management: some working principles from hierarchy theory', *United States Forestry Technical Report* RM-100.

Aloi, J.E. (1990) 'A critical review of recent freshwater periphyton field methods', *Canadian Journal of Fisheries and Aquatic Sciences* **47**:656-670.

Amoros, C. and A.L. Roux (1988) 'Interaction between water bodies within the floodplains of large rivers: function and development of connectivity', in Schreiber, K.F. (Ed), *Connectivity in Landscape Ecology*. Proceedings of the Second International Seminar of the International Association for Landscape Ecology. pp. 125-130.

Amoros, C., A.L. Roux, J.L. Reygrobellet, J.P. Bravard and G. Pautou (1987) 'A method for applied ecological studies of fluvial hydrosystems', *Regulated Rivers: Research and Management* **1**:17-36.

Anderson, N.H. and J.R. Sedell (1979) 'Detritus processing by macroinvertebrates in stream ecosystems', *Annual Review of Entomology* **24**: 351-377.

Angel, M. (1959) 'An account of *Plagiorchis maculosus* (Rud.), its synonymy and its life history in South Australia', *Transactions of the Royal Society of South Australia* **82**:265-279.

Angradi, T.R. (1993) 'Stable carbon and nitrogen isotope analysis of seston in a regulated rocky mountain river, USA', *Regulated Rivers: Research and Management* **8**:251-270.

Armitage, P.D. (1978) 'Downstream changes in the composition, numbers and biomass of bottom fauna in the Tees below Cow Green reservoir and in an unregulated tributary Maize Beck, in the first five years after impoundment', *Hydrobiologia* **58**:145-156.

Baker, J.H. and L.A. Bradnam (1976) 'The role of bacteria in the nutrition of aquatic detritivores', *Oecologia* **24**:95-104.

Baker, B.W. and G.L. Wright (1978) 'The Murray Valley: its hydrologic regime and the effects of water development on the river', *Proceedings of the Royal Society of Victoria* **90**: 103-110.

Barbetti, M and H. Allen (1972) 'Prehistoric man at Lake Mungo, Australia, 32 000 years B.P.', *Nature* **240**:46-48.

Barnes, R.D. (1982) *Invertebrate Zoology*. Holt-Saunders, Japan. 1087 pages.

Barnese, L.E. and R.L. Lowe (1990) 'Comparative grazing efficiency of pulmonate and prosobranch snails', *Journal of the North American Benthological Society* **9**:35-44.

Battegazzore, M., R.C. Petersen Jr., G. Moretti and B. Rossaro (1992) 'An evaluation of the environmental quality of the River Po using benthic macroinvertebrates', *Archive fur Hydrobiologie* **125**:175-206.

Bayley, P.B. (1991) 'The flood pulse advantage and the restoration of river-floodplain systems', *Regulated Rivers: Research and Management* **6**:75-81.

Belbin, L. (1991) *PATN Technical Reference Manual*. CSIRO Division of Wildlife and Ecology, Canberra.

Belbin, L. (1993) *PATN Users Manual*. CSIRO Division of Wildlife and Ecology, Canberra.

Belbin, L. and C. McDonald (1993) 'Comparing three classification strategies for use in ecology', *Journal of Vegetation Science* **4**:341-348.

Bender, M.M. (1971) 'Variations in the $^{13}C/^{12}C$ ratio's of plants in relation to the pathway of photosynthetic carbon dioxide fixation', *Phytochemistry* **10**:1239-1244.

Bennison, G.L., T.J. Hillman and P.J. Suter (1989) *Macroinvertebrates of the River Murray; Survey and Monitoring 1980-1985*. Murray-Darling Basin Commission. 77 pages.

Biggs, B.J.F. (1990) 'Periphyton communities and their environments in New Zealand rivers', *New Zealand Journal of Marine and Freshwater Research* **24:**367-386.

Biggs, B.J.F. and M.E. Close (1989) 'Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients', *Freshwater Biology* **22**:209-231.

Biggs, B.J.F. and P. Gerbeaux (1993) 'Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand', *New Zealand Journal of Marine and Freshwater Research* **27**:39-53.

Biggs, B.J.F. and G.M. Price (1987) 'A survey of filamentous algal proliferations in New Zealand rivers', *New Zealand Journal of Marine and Freshwater Research* **21**:175-191.

Blinn, D.W., R.E. Truitt. and A. Pickart (1989) 'Feeding ecology and radular morphology of the freshwater limpet *Ferrissia fragilis*', *Journal of the North American Benthological Society* **8**:237-242.

Boon, P.J. (1988) 'The impact of river regulation on invertebrate communities in the U.K', *Regulated Rivers: Research and Management* **2**:389-409.

Boon, P.I. (1991) 'Bacterial assemblages in rivers and billabongs of southeastern Australia', *Microbial Ecology* **22**:27-52.

Boon, P.I. and S.E Bunn (in press) 'Methanotrophic bacteria may contribute to ^{13}C-depletion of metazoan consumers in billabong food webs', *Oecologia*

Boulton, A.J. (1988) *Composition and Dynamics of Macroinvertebrate Communities in Two Intermittent Streams*, Ph.D. Thesis, Monash University, Victoria, Australia.

Boulton, A.J. (1989) 'Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria', *Transactions of the Royal Society of South Australia* **113**:23-34.

Boulton, A.J. (1993) 'Stream ecology and surface-hyporheic hydrologic exchange: Implications, techniques and limitations', *Australian Journal of Marine and Freshwater Research* **44**:553-564.

Boulton, A.J. and P.S. Lake (1992a) 'The ecology of two intermittent streams in Victoria, Australia. II Comparisons of faunal composition between habitats, rivers and years', *Freshwater Biology* **27**:99-121.

Boulton, A.J. and P.S. Lake (1992b) 'The ecology of two intermittent streams in Victoria, Australia. III Temporal changes in faunal composition', *Freshwater Biology* **27**:123-138.

Boulton, A.J. and L.N. Lloyd (1991) 'Macroinvertebrate assemblages in floodplain habitats of the lower River Murray, South Australia', *Regulated Rivers: Research and Management* **6**:183-201.

Boulton, A.J. and L.N. Lloyd (1992) 'Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia', *Regulated Rivers: Research and Management* **7**:137-151.

Bowen, S.H. (1987) 'Composition and nutritional value of detritus', in Moriarty, D.J.W. and R.S.V. Pullin (Eds) *Detritus and Microbial Ecology in Aquaculture*, ICLARM Conference Proceedings. pp. 192-216.

Bren, L.J. (1988) 'Effects of river regulation on flooding of a riparian red gum forest on the River Murray, Australia', *Regulated Rivers: Research and Management* **2**:65-77.

Bren, L.J. (1990) 'Red gum forests' in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 231-244.

Brittain, J.E. and T.J. Eikeland (1988) 'Invertebrate drift - A review', *Hydrobiologia* **166**:77-93.

Brittain, J.E. and S.J. Saltveit (1989) 'A review of the effect of river regulation on mayflies (Ephemeroptera)', *Regulated Rivers: Research and Management* **3**:191-204.

Brown, K.M., D. Varza and T.D. Richardson (1989) 'Life histories and population dynamics of two subtropical snails (Prosobranchia: Viviparidae)', *Journal of the North American Benthological Society* **8**:222-228.

Browne, R.A. (1978) 'Growth, mortality, fecundity, biomass and productivity of four lake populations of the prosobranch snail, *Viviparus georgianus*', *Ecology* **59**:742-750.

Brusven, M. (1984) 'The distribution and abundance of benthic insects subjected to reservoir-release flows in the Clearwater River, Idaho, USA', in Lillehammer, S. and S.J. Salveit (Eds) *Regulated Rivers*, Universitetsforlaget, Oslo. pp. 167-180.

Brusven, M.A., C. MacPhee and R.C. Biggam (1974) 'Effects of water fluctuations on benthic insects', in *Anatomy of a River,* Pacific Northwest River Basins Report, Vancouver AW. pp. 67-79.

Bruwer, C.A. and P.J. Ashton (1989) 'Flow-modifying structures and their impacts on lotic ecosystems' in Ferrar, A.A. (Ed) *Ecological Flow Requirements for South African Rivers*, South African National Scientific Programmes Report no. 62. pp. 3-15.

Bunn, S.E., D.R. Barton, H.B.N. Hynes, G. Power and M. Pope (1989) 'Stable isotope analysis of carbon flow in a tundra river system', *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1769-1775.

Cadwallader, P.L. and B. Lawrence (1990) 'Fish' in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 317-336.

Calow, P. (1970) 'Studies on the natural diet of *Lymnaea pereger obtusa* (Kobelt) and its possible ecological implications', *Proceedings of the Malacological Society of London* **39**:203-215.

Calow, P. (1973) 'Field observations and laboratory experiments on the general food requirements of two species of freshwater snail, *Planorbis contortus* (Linn.) and *Ancylus fluviatilis* Mull', *Proceedings of the Malacological Society of London* **40**:483-489.

Calow, P. (1974) 'Evidence for bacterial feeding in *Planorbis contortus* Linn. (Gastropoda: Pulmonata)', *Proceedings of the Malacological Society of London* **41**:145-156.

Castella, E., M. Richardot-Coulet, P. Richoux and C. Roux (1984) 'Macroinvertebrates as 'describers' of morphological and hydrological types of aquatic ecosystems abandoned by the Rhone River', *Hydrobiologia* **119**:219-225.

Castella, E., M. Richardot-Coulet, C. Roux and P. Richoux 1991. 'Aquatic macroinvertebrate assemblages of two contrasting floodplains: the Rhône and Ain Rivers, France', *Regulated Rivers: Research and Management* **6**:289-300.

Close, A.F. (1990) 'The impact of man on the flow regime' in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 61-76.

Cole, G.A. (1983) *Textbook of Limnology*. Waveland Press, Illinois. 401 pages.

Colwell, R.K. (1974) 'Predictability, constancy and contingency of periodic phenomena', *Ecology* **55**:1148-1153.

Conners, M.E. and R.J. Naiman (1984) 'Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed', *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1473-1484.

Cooling, M.P. and A.J. Boulton (1993) 'Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream', *Australian Journal of Marine and Freshwater Research* **44**:411-426.

Corkum, L.D. (1992) 'Relationships between density of macroinvertebrates and detritus in rivers', *Archive fur Hydrobiologie* **125**:149-166.

Corrarino, C.A. and M.A. Brusven (1983) 'The effects of reduced stream discharge on insect drift and stranding of near shore insects', *Freshwater Invertebrate Biology* **2**:88-98

Cotton, B.C. (1935) 'The Australian viviparous river snails', *Victorian Naturalist* **52**:96-99

Couch, C.A. and J.L. Meyer (1992) 'Development and composition of the epixylic biofilm in a blackwater river', *Freshwater Biology* **27**:43-51.

Crome, F.H.J. and S.M. Carpenter (1988) 'Plankton community cycling and recovery after drought - dynamics in a basin on a floodplain', *Hydrobiologia* **164**:193-211.

Cuffney, T.F. (1988) 'Input, movement and exchange of organic matter within a subtropical coastal blackwater river-floodplain system', *Freshwater Biology* **19**:305-320.

Cummins, K.W. (1974) 'Structure and function of stream ecosystems' *Bioscience* **24**:631-641.

Cummins, K.W. and M.J. Klug (1979) 'Feeding ecology of stream invertebrates', *Annual Review of Ecology and Systematics* **10**:147-172.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck and V.I. Holt (1973) 'The utilisation of leaf litter by stream detritivores', *Ecology* **54**:336-345.

Cyr, H. and Downing, J.A. (1988) 'The abundance of phytophilous invertebrates on different species of submerged macrophytes', *Freshwater Biology* **20**:365-374.

Décamps, H. and R.J. Naiman (1990) 'Towards an ecotone perspective', in Naiman, R.J. and H. Décamps (Eds) *The Ecology and Management of Aquatic-Terrestrial Ecotones*, UNESCO Man and the Biosphere Series Vol. 4, Parthenon, Paris. pp. 1-5.

Dechro, A.W. and D.J.W. Moriarty (1990) 'Bacterial exopolymer utilisation by a harpacticoid copepod: a methodology and results', *Limnology and Oceanography* **35**:1039-1049.

Deniro, M.J. and S. Epstein (1978) 'Influence of diet on the distribution of nitrogen isotopes in animals', *Geochimica Cosmochimica Acta* **45**:341-351.

Dillon, R.T. and K.B. Davis (1991) 'The diatoms ingested by freshwater snails: temporal, spatial and interspecific variation', *Hydrobiologia* **210:**233-242.

Downes, B.J., P.S. Lake and E.S.G. Schreiber (1993) 'Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organisation', *Freshwater Biology* **30**:119-132.

Drake, J.A. (1984) 'Species aggregation: the influence of detritus in a benthic invertebrate community', *Hydrobiologia* **112**:109-115.

Dudgeon, D. and M.W. Yipp (1983) 'The diets of Hong Kong gastropods', in Morton, B. and D. Dudgeon (Eds) *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China*, Hong Kong University Press. pp 491-509.

Dufford, R.G., H.J. Zimmermann, L.D. Cline and J.V. Ward (1987) 'Responses of epilithic algae to regulation of Rocky Mountain streams', in Craig, J.F. and J.B. Kemper (Eds) *Regulated Streams: Advances in Ecology.* Plenum Press, New York, London. pp. 383-390.

Eastburn, D. (1990) 'The river' in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 3-16.

Edwards, R.W. and M. Brooker (1984) 'Wye' in Whitton, B.A. (Ed) *Ecology of European Rivers*, Blackwell Scientific Publications, London. pp. 51-82.

Edwards, R.T. and J.L. Meyer (1987) 'Metabolism of a sub-tropical low gradient blackwater river', *Freshwater Biology* **17**:251-263

Eisenberg, R.M. (1966) 'The regulation of density in a natural population of the pond snail *Lymnaea elodes', Ecology* **47**:889-906.

Eisenberg, R.M. (1970) 'The role of food in the regulation of the pond snail, *Lymnaea elodes', Ecology* **51**:680-684.

El-Eman, M.A. and H. Madsen (1982) 'The effect of temperature, darkness, starvation and various food types on growth, survival and reproduction of *Helisoma duryi, Biomphalaria alexandrina* and *Bulinus truncatus* (Gastropoda: Planorbidae)', *Hydrobiologia* **88**:265-275.

Elliott, J.M. (1977) *Some methods for the Statistical Analysis of samples of Benthic Invertebrates*. Freshwater Biological Association Publication No. 25. 158 pages.

Elstad, C.A. (1986) 'Macrobenthic distribution and community structure in the upper navigation pools of the Upper Mississippi River', *Hydrobiologia* **136:**85-100.

Elwood, J.W., J.D. Newbold, R.V. O'Neill and W. Van Winkle (1983) 'Resource spiralling: an operational paradigm for analysing lotic ecosystems', in Fontaine, T.D. and S.M. Bartell (Eds) *Dynamics of Lotic Ecosystems.* Ann Arbor Science, Butterworth. pp. 3-27.

Evans, D.L. (1991) 'The effect of salinity on the gastropod fauna of the lower River Murray', *Unpublished Honours Thesis*, Department of Zoology, University of Adelaide. 61 pages.

Faith, D.P. and R.H. Norris (1989) 'Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates', *Biological Conservation* **50:**77-98.

Faith, D.P., P.R. Minchin and L. Belbin (1987) 'Compositional dissimilarity as a robust measure of ecological distance', *Vegetatio* **69:**57-68.

Findlay, D. and J.L. Meyer (1984) 'Significance of bacterial biomass and production as an organic carbon source in lotic detrital systems', *Bulletin of Marine Science* **35**:318-325.

Findlay, S. and K.R. Tenore (1982) 'Nitrogen source for the detritivore polychaete Capitella capitata: detritus substrate or microbes', *Science* 218:371-372.

Findlay, S. J.L. Meyer and R. Risley (1986) 'Benthic bacterial biomass and production in two blackwater rivers', *Canadian Journal of Fisheries and Aquatic Sciences* **43**:1271-1276.

Finlayson, B.L. and T.A. McMahon (1988) 'Australia vs. the world: A comparative analysis of streamflow charactersitics', in Warner, R. (Ed) *Fluvial Geomorphology of Australia*, Academic Press, Sydney. pp. 17-40.

Fisher, S.G. and A. LaVoy (1972) 'Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam', *Journal of the Fisheries Research Board of Canada* **29:**1472-1476.

Fletcher, A.R., A.K. Morison and D.J. Hume (1985) 'Effects of carp *Cyprinus carpio* L., on communities of aquatic vegetation and turbidity of waterbodies in the lower Goulbourn River Basin', *Australian Journal of Marine and Freshwater Research* **36:**311-327.

Forman, R.T.T. and M. Godron (1981) 'Patches and structural components for a landscape ecology', *Bioscience* **31**:733-740.

Frissell, C.A. (1986) 'A hierarchical framework for stream habitat classification: Viewing streams in a watershed context', *Environmental Management* **10**:199-214.

Fruget, J.F. (1991) 'The impact of river regulation on the lotic macroinvertebrate communities of the lower Rhône, France', *Regulated Rivers: Research and Management* **6**:241-255.

Fry, B. (1984) $^{13}C/^{12}C$ ratio's and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows', *Marine Biology* **79**:11-19.

Fry, B., A. Joern and P.L. Parker (1978) 'Grasshopper food web analysis: use of carbon isotope ratio's to examine feeding relationships among terrestrial herbivores', *Ecology* **59**:498-506.

Gauch, H.G. Jr. (1982) *Multivariate Analysis in Community Ecology*, Cambridge University Press, Cambridge, U.K.

Geddes, M.C. (1990) 'Crayfish', in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 303-308.

Gerish, F.M. and M.A. Brusven (1981) 'Insect colonisation rates in near-shore regions subject to hydroelectric power peaking flows', *Journal of Freshwater Ecology* **1:**231-236.

Golloday, S.W. and R.L. Sinsabaugh (1991) 'Biofilm development on leaf and wood surfaces in a boreal river', *Freshwater Biology* **25**:437-450.

Goonan, P.M., J.A. Beer, T.B. Thompson and P.J. Suter (1992) 'Wetlands of the River Murray floodplain, South Australia I. Preliminary survey of the biota and physico-chemistry of ten wetlands from Chowilla to Mannum', *Transactions of the Royal Society of South Australia* **116**:81-94.

Gosz, J.R. (1993) 'Ecotone hierachies', *Ecological Applications* **3**:369-376.

Graf, W.L. (1988) 'Definition of the floodplains along arid region rivers', in Baker, V.R., R.C. Kochel and P.C. Patton (Eds), *Flood Geomorphology*, Wiley, New York. pp. 231-242.

Gray, L.J., J.V. Ward, R. Martinson, and E. Bergey (1983) 'Aquatic macroinvertebrates of the Piceance Basin, Colorado: community response along spatial and temporal gradients of environmental conditions', *The Southwestern Naturalist* **28:**125-135.

Gregory, S.V., F.J Swanson, W.A. McKee and K.W. Cummins (1991) 'An ecosystem perspective of riparian zones', *Bioscience* **41**:540-551.

Grubaugh, J.W. and R.V. Anderson (1989) 'Upper Mississippi River: seasonal and floodplain forest influences on organic matter transport', *Hydrobiologia* **174**:235-244.

Haag, K.H. and J.H. Thorp (1991) 'Cross-channel distribution patterns of zoobenthos in a regulated reach of the Tennessee River', *Regulated Rivers: Research and Management* **6**:225-233.

Haines, E.B. and C.L. Montague (1979) 'Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios', *Ecology* **60**:48-56.

Hamilton, S.K., W.M. Lewis Jr. and S.J. Sippel (1992) 'Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes', *Oecologia* **89**:324-330.

Hargrave, B.T. (1971) 'The utilisation of benthic microflora by *Hyalella azteca*', *Journal of Animal Ecology* **39**:427-437.

Hauer, F.R., J.A. Stanford and J.V. Ward (1989) 'Serial discontinuities in a Rocky Mountain River II: Distribution and abundance of Trichoptera', *Regulated Rivers: Research and Management* **3**:177-182.

Hawkins, S.J., D.C. Watson, A.S. Hill, S.P. Harding, M.A. Kyriakides, S. Hutchinson and T.A. Norton (1989) 'A comparison of feeding mechanisms in microphagous, herbivorous, intertidal prosobranchs in relation to resource partitioning', *Journal of Molluscan Studies* **55**:151-165.

Hellawell, J.M. (1988) 'River regulation and nature conservation', *Regulated Rivers: Research and Management* **2**:425-443.

Hickman, C.S. (1980) 'Gastropod radulae and the assessment of form in evolutionary palaeontology', *Palaeobiology* **6**:276-294.

Hickman, C.S. and T.E. Morris (1985) 'Gastropod feeding tracks as a source of data in analysis of functional morphology of radulae', *Veliger* **27**:357-365.

Hill, M.O., R.G.H Bunce and M.W. Shaw (1975) 'Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland', *Journal of Ecology* **63:**597-613.

Hill, W.R. (1992) 'Food limitation and interspecific competition in snail-dominated streams', *Canadian Journal of Fisheries and Aquatic Sciences* **49**:1257-1267.

Hill, W.R., S.C. Weber and A.J. Stewart (1992) 'Food limitation of two lotic grazers: quantity, quality and size-specificity', *Journal of the North American Benthological Society* **11**:420-432.

Howard-Williams, C. and G.M. Lenton (1975) 'The role of the littoral zone in the functioning of a shallow tropical lake ecosystem', *Freshwater Biology* **5:**445-459.

Hunt, P.C. and J.W. Jones (1972) 'The effect of water level fluctuations on a littoral fauna', *Journal of Fish Biology* **4**:385-394.

Jokinen, E.H., J. Guerette and R.W. Kortman (1982) 'The natural history of an oviviparous snail *Viviparous georgianus* (Lea), in a soft-water eutrophic lake', *Freshwater Invertebrate Biology* **1**:2-17.

Jongman, R.H.G., C.J.F. ter Braak and O.R.F. van Tongeren (1987) *Data Analysis in Community and Landscape Ecology*. Pudoc Wageningen. 295 pages.

Junk, W.J. (1984) 'Ecology of the Varzea, floodplain of Amazonian white-water rivers', in Sioli, H. (Ed) *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and its Basin*. Dr W. Junk Publishers, Dordrecht.

Junk, W.J. (1986) 'Aquatic plants of the Amazon system', in Davies, B.R. and K.F. Walker (Eds) *The Ecology of River Systems*. Dr W. Junk, Dordrecht. pp. 319-337.

Junk, W.J. (1989) 'The use of Amazonian floodplains under an ecological perspective', *Interciena* **14**:317-322.

Junk, W.J., P.B. Bayley and R.E. Sparks (1989) 'The flood pulse concept in river-floodplain systems', in Dodge, D.P. (Ed) *Proceedings of the International Large River Symposium*. Canadian Special Publications of Fisheries and Aquatic Sciences 106. pp. 110-127.

Junk, W.J. and C. Howard-Williams (1984) 'Ecology of aquatic macrophytes in Amazonia', in Sioli, H. (Ed) *The Amazon Limnology and landscape ecology a mighty tropical river and its basin*. Dr W. Junk Dordrecht. pp. 269-293.

Junk, W.J. and R.L. Welcomme (1990) 'Floodplains', in Pattern, B.C.. [eds.], *Wetlands and Shallow Continental Water Bodies* Vol 1. SPB Academic Publishing. The Hague, The Netherlands. pp. 491-524.

Kaster, J.L. and J.Z. Jacobi (1978) 'Benthic macroinvertebrates of a fluctuating reservoir', *Freshwater Biology* **8**: 283-290.

Kesler, D.H., E.H. Jokinen and W.R. Munns Jr. (1986) 'Trophic preferences and feeding morphology of two pulmonate snail species from a small New England pond, U.S.A', *Canadian Journal of Zoology* **64**:2570-2575.

King, J.M., J.A. Day, P.R. Hurly, M-P. Henshall-Howard and B.R. Davies (1988) 'Macroinvertebrate communities and environments in a southern African mountain stream', *Canadian Journal of Fisheries and Aquatic Sciences* **45**:2168-2181.

Klinge, H., W.J. Junk and C.J. Revilla (1990) 'Status and distribution of forested wetlands in tropical South America', *Forest Ecology and Management* **33/34**:81-101.

Kofoed, L.H. (1978) 'The feeding biology of *Hydrobia ventrosa* (Montagu) I. The assimilation of different components of the food', *Journal of Experimental Marine Biology and Ecology* **19**:233-241.

Kotliar, N.B. and J.A. Wiens (1990) 'Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity', *Oikos* **59**:253-260.

Kotwicki, V. (1986) *Floods of Lake Eyre*. South Australian Engineering and Water Supply Department, Adelaide.

Kruskal, J.B. and M. Wish (1978) *Multidimensional Scaling*, Sage, London

Lake, P.S., L.A. Barmuta, A.J. Boulton, I.C. Campbell and R.M. St Clair (1984) 'Australian streams and northern hemisphere stream ecology: comparisons and problems', *Proceedings of the Ecological Society of Australia* **14**:61-82.

Lake, P.S., I.A.E. Bayly and D.W. Morton (1989) 'The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession, *Archiv für Hydrobiologie* **115**:171-202.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman and K.M.S. Moore (1991) 'Stream ecosystem recovery following a catastrophic debris flow', *Canadian Journal of Fisheries and Aquatic Sciences* **48**:196-208.

Lane, J.M. (1991) 'The effect of variation in quality and quantity of periphyton on feeding rate and absorption efficiencies of the snail *Neritina reclivata* (Say)', *Journal of Experimental Marine Biology and Ecology* **150**:117-129.

Lieberman, D.M. and T.A Burke (1993) 'Particulate organic matter transport in the lower Colorado River, South-western USA', *Regulated Rivers: Research and Management* **8**:323-334.

Lloyd, L.N. and K.F. Walker (1986) 'Distribution and conservation status of small freshwater fish in the River Murray, South Australia', *Transactions of the Royal Society of South Australia* **110**: 49-57.

Lloyd, L.N., J.T. Puckridge and K.F. Walker (1990) 'The significance of fish populations in the Murray-Darling system and their requirements for survival', *Conservation in Management of the River Murray system - making conservation count.* Proceedings of the Third Fenner Conference on the Environment, Canberra.

Lloyd, L.N., K.F. Walker and T.J. Hillman (1991) *Environmental significance of snags in the River Murray*, Project Completion Report 85/45, Australian Water Research Advisory Council, Department of Primary Industries and Energy, Canberra. pp. 1-33.

Lodge, D.M. (1986) 'Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions', *Freshwater Biology* **16:**831-841.

Lowe, R.L. (1979) 'Phytobenthic ecology and regulated streams', In Stanford and Ward (Eds) *Regulated Streams* pp. 25-34.

MacArthur, J.V. (1988) 'Aquatic and terrestrial linkages: floodplain functions', in Hook, D. and R. Lea (Eds) *Proceedings of the Symposium on Forested Wetlands of the Southern USA,* USA Department of Forest Services. pp. 107-116.

Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra.

Mackay N.J., T.J. Hillman and J. Rolls (1988) 'Water quality of the River Murray. Review of monitoring, 1978 to 1986', *Water Quality Report 3*. Murray-Darling Basin Commission, Canberra.

Macumber, P. (1990) 'The salinity problem', in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 111-126.

Magurran, A.E. (1988) *Ecological Diversity and its Measurement*, Croom Helm, London. 179 pages.

Maheshwari, B.L., K.F. Walker and T.A. McMahon (1993) *The Impact of Flow Regulation on the Hydrology of the River Murray and its Ecological Implications,* Centre for Environmental Applied Hydrology, University of Melbourne, Australia. 154 pages.

Mallen-Cooper, M. and E. Edwards (1990) *Fish passage through the main weir at Menindee Lakes during the flood of September 1990.* Fisheries Research Institute NSW.

Marchant, R., L. Metzeling, A. Graesser and P. Suter (1985) 'The organisation of macroinvertebrate communities in the major tributaries of the La Trobe River, Victoria, Australia', *Freshwater Biology* **15**:315-331.

Marchant, R., P. Mitchell and R. Norris (1984) 'Distribution of benthic invertebrates along a disturbed section of the La Trobe River, Vic. An analysis based on numerical classification', *Australian Journal of Marine and Freshwater Research* **35**:793-806.

McMahon, R.F., R.D. Hunter and W.D. Russell-Hunter (1974) 'Variation in aufuchs at six freshwater habitats in terms of carbon biomass and of carbon:nitrogen ratio', *Hydrobiologia* **45**:391-404.

McMahon, T.A. and B.A. Finlayson (1991) 'Australian surface and groundwater hydrology - regional characteristics and implications', in Pigram, J.J. and B.P. Hooper (Eds) *Water Allocation for the Environment*, Proceedings of an International Seminar and Workshop, Centre for Water Policy Research, University of New England, Armidale. pp. 21-40.

MDBC (1991) *Annual Report 1991*, Murray-Darling Basin Commission.

MDBMC (Murray-Darling Basin Ministerial Council) (1987) *Murray-Darling Basin Environmental Resources Study*. State Pollution Control Commission, Sydney and Murray-Darling Basin Ministerial Council Canberra. 424 pages.

Minshall, G.W. (1984) 'Aquatic insect-substrate relationships' in Resh, V.H. and D. Rosenberg (Eds) *The Ecology of Aquatic Insects*, Praeger Publishers, New York. pp. 358-400.

Minshall, G.W. (1988) 'Stream ecosystem theory: a global perspective', *Journal of the North American Benthological Society* 7:263-288.

Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell and R.L. Vannote (1985) 'Development in stream ecosystem theory', *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1045-1055.

Molles, M.C., C.N. Dahm and M.T. Crocker (1992) 'Climatic variability and streams and rivers in semi-arid regions', in R, Roberts, R.D. and M.L. Bothwell (Eds) *Aquatic Ecosystems in Semi-arid Regions: Implications for Resource Management.* NHRI Symposium Series 7, Environment Canada, Saskatoon.

Moon, H.P. (1935) 'Flood movements of the littoral fauna of Windermere', *Journal of Animal Ecology* 4:216-228.

Moss, R. (1988) *Ecology of Fresh Waters: Man and Medium.* Blackwell Scientific Publications, London. 417 pages.

Motoda, S. (1956) 'Devices of simple plankton apparatus', *Memoirs, Faculty of Fisheries, Hokkaido University* **7**:79-94.

Mulholland, P.J. (1981) 'Organic carbon flow in a swamp-stream ecosystem', *Ecological Monographs* **51**:307-322.

Munn, M.D. and M.A. Brusven (1991) 'Benthic macroinvertebrate communities in nonregulated and regulated waters of the clearwater river, Idaho, U.S.A', *Regulated Rivers: Research and Management* **6**:1-11.

Mûnoz, I. and N. Prat (1989) 'Effects of river regulation on the lower Ebro River (NE Spain)', *Regulated Rivers: Research and Management* **3**:345-354.

Naiman, R.J. (1983) 'The influence of stream size on the food quality of seston', *Canadian Journal of Zoology* **61**:1995-2010.

Naiman, R.J., J.M. Melillo, M.A. Lock, T.E. Ford and S.R. Reice (1987) 'Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum', *Ecology* **68**:1139-1156.

Naiman, R.J., H. Décamps, J. Pastor and C.A. Johnston (1988) 'The potential importance of boundaries to fluvial ecosystems', *Journal of the North American Benthological Society* **7**:289-306.

NEC (1988) *Chowilla Salinity Mitigation Scheme: Draft Environmental Impact Statement.* Prepared for the Engineering and Water Supply Department of South Australia by National Environmental Consultancy, Adelaide.

Newbold, J.D., R.V. O'Neill, J.W. Elwood and W. van Winkle (1982) 'Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity', *American Naturalist* **120**:628-652.

Newell, R. (1965) 'The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*', *Proceedings of the Zoological Society of London* **144**:25-45.

Newell, R.C. and J.G. Field (1983) 'The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community', *Marine Biology Letters* **4**:23-56.

Neter, J., W. Wasserman and M.H. Kutner (1985) *Applied Linear Statistical Models: Regression, Analysis of Variance and Experimental Designs*. Richard D Irwin Inc., Illinois. 1127 pages.

Nicholls, N. (1989) 'How old is ENSO?', *Climate Change* **14**:111-115.

Nilsson, C. (1987) 'Distribution of stream-edge vegetation along a gradient of current velocity', *Journal of Ecology* **75**:513-522.

Nilsson, C., G. Grelsson, M. Johansson and U. Sperens (1988) 'Can rarity and diversity be predicted in vegetation along riverbanks?' *Biological Conservation* **44**:201-212.

O'Conner, N.A. (1992) 'Quantification of submerged wood in a lowland Australian stream system', *Freshwater Biology* **27**:387-395.

O'Malley, C. and F. Sheldon (1990) *Chowilla Floodplain Biological Study*, Nature Conservation Society of South Australia Inc.

Obrdlik, P. and U. Fuchs (1991) 'Surface water connection and the macrozoobenthos of two types of floodplains on the upper Rhine', *Regulated Rivers: Research and Management* **6**:279-288.

Odum, E.P. (1969) 'The strategy of ecosystem development', *Science* **164**:262-270.

Pace, G.L. and E.J. Szuch (1985) 'An exceptional stream population of the banded applesnail *Viviparus georgianus*, in Michigan', *Nautilus* **99**:48-53.

Palmer, R.W. and J.H. O'Keefe (1990) 'Downstream effects of a small impoundment on a turbid river', *Archive Hydrobiologie* **119:**457-473.

Palmer, C.G., J.H. O'Keefe and A.R. Palmer (1991) 'Are macroinvertebrate assemblages in the Buffalo River, Southern Africa, associated with particular biotypes?' *Journal of the North American Benthological Society* **10**:349-357.

Palmer, C., J. O'Keeffe, A. Palmer, T. Dunne and S. Radloff (1993a) 'Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, eastern Cape, South Africa. I Dietary variability', *Freshwater Biology* **29:**441-453.

Palmer, C., J. O'Keefe, A. Palmer (1993b) 'Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, eastern Cape, South Africa. II Functional morphology and behaviour', *Freshwater Biology* **29:**455-462.

Parker, S.J. (1989) 'The potential of Aboriginal shell middens as indicators of the River Murray's pre-impoundment ecology', *unpublished Honours Thesis*, Department of Zoology, University of Adelaide. 79 pages.

Perry, S.A. and W.B. Perry (1991) 'Organic carbon dynamics in two regulated rivers in northwestern Montana, USA', *Hydrobiologia* **218**:193-203.

Petelle, M., B. Haines and E. Haines (1979) 'Insect food preferences analysed using $^{13}C/^{12}C$ ratios', *Oecologia* **38**:159-166.

Peterjohn, W.T. and D.L. Correll (1984) 'Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest', *Ecology* **65**:1466-1475.

Petersen, B.J. and B. Fry (1987) 'Stable isotopes in ecosystem studies' *Annual Review of Ecology and Systematics* **18**:293-320.

Petersen, B.J. J.E. Hobbie, A.E. Hershey, M.A. Lock, T.E. Ford, J.R. Vestal, V.L. McKinley, M.A.J. Huller, M.C. Miller, R.M. Ventullo and G.S. Volk (1985) 'Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorous', *Science* **229**:1383-1386.

Petersen, C.G. (1987) 'Influences of flow regime on development and dessication response of lotic diatom communities', *Ecology* **68**:946-954.

Petts, G.E. (1984) *Impounded Rivers: Perspectives for Ecological Management.* John Wiley and Sons, Chichester. 326 pages.

Petts, G.E. (1989) 'Regulated rivers in the UK', *Regulated Rivers: Research and Management* **2**:201-220.

Pickett, S.T.A. and P.S. White (1985) *The Ecology of Natural Disturbances and Patch Dynamics,* Academic Press, New York.

Pieczynska, E. (1990) 'Lentic aquatic-terrestrial ecotones: Their structure, functions and importance', in Naiman, R.J. and H. Décamps (Eds) *The Ecology and Management of Aquatic-Terrestrial Ecotones*, UNESCO Man and the Biosphere Series Vol. 4, Parthenon, Paris. pp. 103-135.

Pinay, G., H. Décamps, E. Chauvet and E. Fustec (1990) in Naiman, R.J. and H. Décamps (Eds) *The Ecology and Management of Aquatic-Terrestrial Ecotones*, UNESCO Man and the Biosphere Series Vol. 4, Parthenon, Paris. pp. 141-164.

Ploeger, S. and A.S.H. Breure (1977) 'A rapid procedure for preparation of radulae for routine research with the Scanning Electron Microscope', *Basteria* **41**:47-52.

Poff, N.L. and J.V. Ward (1990) 'Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity'. *Environmental Management* **14**:629-645.

Pringle, C.M., R.J. Naiman, G. Breteshko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme and M.J. Winterbourn (1988) 'Patch dynamics in lotic systems: the stream as a mosaic', *Journal of the North American Benthological Society* **7**:503-524.

Puckridge, J.T., F. Sheldon, A.J. Boulton and K.F. Walker (Unpublished MS) 'Flow variability and the Flood Pulse Concept'.

Rader, R.B. and J.V. Ward (1988) 'Influence of regulation on environmental conditions and the macroinvertebrate community in the upper Colorado River', *Regulated Rivers: Research and Management* **2**:597-618.

Rader, R.B. and J.V. Ward (1989) 'Influence of impoundments on mayfly diets, life histories and production', *Journal of the North American Benthological Society* **8**:64-75.

Raefaelli, D. (1985) 'Functional feeding groups of some intertidal molluscs defined by git contents analysis', *Journal of Molluscan Studies* **51**:233-239.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schafer and I.R. Kaplan (1983) 'Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs', *Ecology* **64**:1314-1318.

Reid, J.R.W and J. Gillen (1988) *The Coongie Lakes Study*. Department of Environment and Planning, Adelaide, South Australia.

Reid, J.R.W. and J.T. Puckridge (1990) 'Coongie Lakes' in Tyler, M.J., C.R. Twidale, M. Davies and C.B. Wells (Eds) *Natural History of the North East Deserts*. Royal Society of South Australia, Inc. pp. 119-131.

Ribi, G. and M. Gebhardt (1986) 'Age specific fecundity and size of offspring in the prosobranch snail *Viviparous ater', Oecologia* **71**:18-24.

Richardson, J.S. (1991) 'Seasonal food limitation of detritivores in a montane stream: an experimental test', *Ecology* **72**:873-887.

Richardson, T.D. and K.M. Brown (1989) 'Secondary production of two subtropical snails (Prosobranchia: Viviparidae)', *Journal of the North American Benthological Society* **8**:229-236.

Risser, P.G. (1990) 'The ecological importance of land-water ecotones' in Naiman, R.J. and H. Décamps (Eds) *The Ecology and Management of Aquatic-Terrestrial Ecotones*, UNESCO Man and the Biosphere Series Vol. 4, Parthenon, Paris. pp. 7-18.

Roberts, J. and J.A. Ludwig (1990) 'Aquatic macrophyte communities', in O'Malley, C. and F. Sheldon (Eds) *Chowilla Floodplain Biological Study*, Nature Conservation Society of South Australia Inc. pp. 137-154

Roberts, J. and J.A. Ludwig (1991) 'Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray, Australia', *Journal of Ecology* **79**:117-127.

Ropelewski, C.F. and M.S. Halpert (1987) 'Global and regional scale precipitation patterns associated with the El Nino/ Southern Oscillation', *Monthly Weather Review* **115**:1606-1626.

Rounick, J.S. and M.J. Winterbourn (1986) 'Stable carbon isotopes and carbon flow in ecosystems', *Bioscience* **36**:171-177.

Rounick, J.S., M.J. Winterbourn and G.L. Lyon (1982) 'Differential utilisation of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study', *Oikos* **39**:191-198.

Russel-Hunter, W.D. (1970) *Aquatic Productivity*, Macmillan, New York.

Salo, J. (1990) 'External processes influencing origin and maintenance of inland water-land ecotones', in Naiman, R.J. and H. Décamps (Eds) *The Ecology and Management of Aquatic-Terrestrial Ecotones*, UNESCO Man and the Biosphere Series Vol. 4, Parthenon, Paris. pp. 37-59.

Scarsbrook, M.R. and C.R. Townsend (1993) 'Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams', *Freshwater Biology* **29:**395-410.

Scholtz, O. and P.I. Boon (1993a) 'Biofilms on submerged River Red Gum (*Eucalyptus camaldulensis* Dehnh. Myrtaceae) wood in billabongs: an analysis of bacterial assemblages using phospholipid profiles', *Hydrobiologia* **259**:169-178.

Scholtz and Boon (1993b) 'Alkaline phosphatase, aminopeptidase and β-D glucosidase activities associated with billabong periphyton', (in press).

Sedell, J.R. and J.L. Froggatt (1984) 'Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal', *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* **22**:1828-1834.

Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford and C.P. Hawkins (1990) 'Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems', *Environmental Management* **14**:711-724

Sedell, J.R., J.E. Richey and F.J. Swanson (1989) 'The river continuum concept: a basis for the expected ecosystem behaviour of very large rivers?' in D.P. Dodge (Ed) *Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Sciences*, **106**. pp. 49-55.

Sheldon, F. and L.N. Lloyd (1990) 'Physical limnology and aquatic habitats', in O'Malley, C. and F. Sheldon (Eds) *Chowilla Floodplain Biological Study*, Nature Conservation Society of South Australia Inc. pp. 119-136.

Sheldon, F. and K.F. Walker (1989) 'Effects of hypoxia on oxygen consumption by two species of freshwater mussel (Unionacea: Hyriidae) from the River Murray, *Australian Journal of Marine and Freshwater Research* **40**:491-499.

Sheldon, F. and K.F. Walker (1993a) 'Pipelines as a refuge for freshwater snails', *Regulated Rivers: Research and Management* **8**:295-299.

Sheldon, F. and K.F. Walker (1993b) 'Shell variation in Australian Notopala (Gastropoda: Prosobranchia: Viviparidae)', *Journal of the Malacological Society of Australia* **14**:59-71.

Sherr, E.B. (1988) 'Direct use of high molecular weight polysaccharides by heterotrophic flagellates', *Nature* **335**:348-351.

Skelton, P.H. (1986) 'Fish of the Orange-Vaal system', in Davies, B.R. and K.F. Walker (Eds) *The Ecology of River Systems*, Dr W, Junk Publishers, Dordrecht. pp. 143-162.

Smith, B.J. (1978) 'Molluscs of the Murray-Darling river system', *Proceedings of the Royal Society of Victoria* **90**:203-209.

Smith, B.J. (1992) *Zoological Catalogue of Australia*, vol 8. *Non-Marine Mollusca.* Australian Government Publishing Service, Canberra, 399 pages.

Smith, B.N. and S. Epstein (1971) 'Two categories of $^{13}C/^{12}C$ ratio's for higher plants', *Plant Physiology* **47**:380-384.

Smith, B.J. and R.C. Kershaw (1979) *Field Guide to the Non-Marine Molluscs of South Eastern Australia.* Australian National University Press, Canberra, 285 pages.

Sparks, R.E., P.B. Bayley, S.L. Kohler and L.L Osbourne (1990) 'Disturbance and recovery of large floodplain rivers', *Environmental Management* **14**:699-709.

Spence, J.A. and H.B.N Hynes (1971) 'Differences in the benthos upstream and downstream of an impoundment', *Journal of the Fisheries Research Board of Canada* **28**:35-43.

Stanczykowska, A., E. Magnin and A Dumouchel (1971) 'Etude de trois populations de *Viviparus malleatus* (Reeve) (Gastropoda, Prosobranchia) de la region de Montreal I. Croissance, fecondite, biomasse et production annuelle', *Canadian Journal of Zoology* **49:**1413-1441.

Stanczykowska, A., M. Plinski and E. Magnin (1972) 'Etude de trois populations de *Viviparus malleatus* (Reeve) (Gastropoda, Prosobranchia) de la region de Montreal II. Etude qualitative et quantitative de la nourriture', *Canadian Journal of Zoology* **50:**1617-1624.

Stanford, J.A. and J.V. Ward (1989) 'Serial discontinuities in a Rocky Mountain river I. Distribution and abundance of Plecoptera', *Regulated River: Research and Management* **3**:169-175.

Statzner, B., J.A. Gore and V.H. Resh (1988) 'Hydraulic stream ecology: observed patterns and potential applications', *Journal of the North American Benthological Society* **7**:307-360.

Steneck, R.S. and L. Watling (1982) 'Feeding capabilities and limitation of herbivorous molluscs: a functional group approach', *Marine Biology* **68**:299-319.

Stoddart, J.A. (1985a) 'Western Australian Viviparids (Prosobranchia: Mollusca)' *Journal of the Malacological Society of Australia* **5**:167-173.

Stoddart, J.A. (1985b) 'Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept', *Journal of the Malacological Society of Australia* **7**:7-16.

Suberkropp, K. and M.J. Klug (1976) 'Fungi and bacteria associated with leaves during processing in a woodland stream', *Ecology* **57**:707-719.

Suren, A.M. and M.J. Winterbourn (1992) 'The influence of periphyton, detritus and shelter on invertebrate colonisation of aquatic bryophytes', *Freshwater Biology* **27**:327-339.

Swales, S. (1982) 'Environmental effects of river channel works used in land drainage improvement', *Journal of Environmental Management* **14:**103-126.

Sweeney, B.W. and R.L. Vannote (1986) 'Growth and production of a stream stonefly: influences of diet and temperature', *Ecology* **67**:1396-1410.

Taki, A. (1981) 'The fecundity of a mud snail, *Cipangopaludina japonica', International Association of Theoretical and Applied Limnology* **21**:1637-1639.

Tashiro, J.S. and S.D. Colman (1982) 'Filter-feeding in the freshwater prosobranch snail *Bithynia tentaculata*: Bioenergetic partitioning of ingested carbon and nitrogen', *American Midland Naturalist* **107**:114-125.

Tett, P., M.G. Kelly and G.M. Hornberger (1975) 'A method for the spectrophotometric measurement of chlorophyll a and pheophytin a in benthic microalgae', *Limnology and Oceanography* **20**:887-896.

Thomas, D.S.G. (1989) 'The nature of arid environments', in Thomas, D.S.G (Ed) *Arid Zone Geomorphology*, Belhaven Press, London and Halsted Press, New York. pp. 1-10.

Thomas, J.D. (1990) 'Mutualistic interactions in freshwater modular systems with molluscan components', *Advances in Ecological Research* **20**:125-178.

Thompson, M.B. (1986) *River Murray Wetlands: Their Characteristics, Significance and Management.* Department of Environment and Planning, Adelaide.

Thoms, M.C. and Walker, K.F. (1989) 'Preliminary observations of the environmental effects of flow regulation on the River Murray, South Australia'. *South Australian Geographical Journal* **89**:1-14.

Thoms, M.C. and K.F. Walker (1992) 'Channel changes related to low-level weirs on the River Murray, South Australia', in Carling, P.A. and G.E. Petts (Eds) *Lowland Floodplain Rivers: Geomorphological Perspectives*. John Wiley & Sons Ltd.

Thoms, M.C. and K.F. Walker (1992) 'Channel changes related to low-level weirs on the River Murray, South Australia', in Carling, P.A. and G.E. Petts (Eds) *Lowland Floodplain Rivers: Geomorphological Perspectives*, John Wiley & Sons, Ltd. pp. 235-249.

Thoms, M.C. and K.F. Walker (1993) 'Channel changes associated with two adjacent weirs on a regulated lowland alluvial river', *Regulated Rivers: Research and Management* **8**:271-284.

Urban, D.L., R.V. O'Neill and H.H. Shugart Jr. (1987) 'Landscape Ecology', *Bioscience* **37**:119-127.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing (1980) 'The river continuum concept'. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.

Voelz, N.J. and J.V. Ward (1990) 'Macroinvertebrate responses along a complex regulated stream environmental gradient', *Regulated Rivers: Research and Management* **5**:365-374.

Walker, K.F. (1979) 'Regulated streams in Australia: The Murray-Darling River System', in Ward, J.V. and J.A. Stanford (Eds) *The Ecology of Regulated Streams*. Plenum Press, New York.

Walker, K.F. (1981) *Ecology of freshwater mussels in the River Murray*, Australian Water Resources Council Technical Paper 63.

Walker, K.F. (1986) 'The Murray-Darling river system' in Davies, B.R. and K.F. Walker (Eds) *The Ecology of River Systems,* Junk, Dordrecht. pp. 631-659

Walker, K.F. (1990) 'Mussels', in Mackay, N. and D. Eastburn (Eds) *The Murray*, Murray-Darling Basin Commission, Canberra. pp. 309-316.

Walker, K.F. (1992) 'The River Murray, Australia: A semi-arid lowland river', in Calow, P.A. and G.E. Petts (Eds) *The Rivers Handbook, volume 1*, Blackwell Scientific, Oxford. pp. 472-492.

Walker, K.F. and T.J. Hillman (1976) *Limnological Survey of the River Murray in relation to Albury-Wodonga, 1973-1976.* Albury-Wodonga Development Corporation, Albury.

Walker, K.F., T.J. Hillman and W.D. Williams (1978) 'Effects of impoundments on rivers: an Australian case study', *International Association of Theoretical and Applied Limnology* **20**:1695-1701.

Walker, K.F. and M.C. Thoms (1993) 'Environmental effects of flow regulation on the River Murray, Australia', *Regulated Rivers: Research and Management* **8**:103-119.

Ward, J.V. (1976a) 'Effects of flow patterns below large dams on stream benthos: a review', *Instream Flow Needs Symposium* Vol II. *American Fisheries Society.* pp. 235-253.

Ward, J.V. (1976b) 'Comparative limnology of differentially regulated sections of a Colorado mountain river', *Archive Hydrobiologia* **78**:319-342.

Ward, J.V. (1989a) 'The four dimensional nature of lotic ecosystems', *Journal of the North American Benthological Society* **8**:2-8.

Ward, J.V. (1989b) 'Riverine-wetland interactions', in Sharitz, R.R. and J.W. Gibbons (Eds) *Freshwater Wetlands and Wildlife,* USDOE Office of Scientific and Technical Information Oak Ridge, Tennessee. pp 385-400.

Ward, J.V. (1992) *Aquatic Insect ecology: Biology and habitat* John Wiley & Sons Ltd.

Ward, G.M. and K.W. Cummins (1979) 'Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae)', *Ecology* **60**:57-64.

Ward, J.V. and R.A. Short (1978) 'Macroinvertebrate community structure of four special lotic habitats in Colorado, USA', *International Association of Theoretical and Applied Limnology* **20**:1382-1387.

Ward, J.V. and J.A. Stanford (1983) 'The serial discontinuity of lotic ecosystems', in Fontaine, T.D. and S.M. Bartell (Eds) Dynamics of Lotic Ecosystems. Ann Arbor Scientific Publications, Michigan. pp. 29-42.

Welcomme, R.L. (1977) 'Some general and theoretical considerations on the fish yield of African Rivers', *Journal of Fish Biology* **8**:351-364.

Welcomme R.L. (1979) *Fisheries Ecology of Floodplain Rivers*, Longman, London and New York.

White, D.C., W.M. Davis, J.S. Nickels, J.D. King and R.J. Bobbie (1979) 'Determination of the sedimentary microbial biomass by extractable lipid phosphate', *Oecologia* **40**:51-62.

White, T.C.R. (1978) 'The importance of a relative shortage of food in animal ecology', *Oecologia* **33**:71-86.

Whitton, B.A. and D.T. Crisp (1984) 'Tees', in Whitton, B.A. (Ed) *Ecology of European Rivers*, Blackwell Scientific Publications, London. pp.145-178.

Wiens, J.A., C.S. Crawford and J.R. Gosz (1985) 'Boundary dynamics: a conceptual framework for studying landscape ecosystems' *Oikos* **45**:421-427.

Wilkinson, L. (1990) *SYSTAT: The System for Statistics*. SYSTAT Inc., Evanston, Il.

Williams, D.D. and N.E. Williams (1993) 'The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a welsh mountain stream', *Freshwater Biology* **30**:199-218.

Williams, R.D., and R.N. Winget (1979) 'Macoinvertebrate response to flow manipulation in the Strawberry River, Utah (USA)', in Ward, J.V. and J.A. Stanford (Eds) *The Ecology of Regulated Streams*, Plenum Press, New York. pp. 365-376

Winterbourn, M.J., J.S. Rounick and B. Cowie (1981) "Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* **15**:321-328.

Winterbourn, M.J. and J.S. Rounick (1985) 'Benthic faunas and food resources of insects in small New Zealand streams subjected to different forestry practices', *International Association of Theoretical and Applied Limnology* **22**:2148-2152.

Winterbourn, M.J., J.S. Rounick and A.G. Hildrew (1986) 'Patterns of carbon resource utilisation by benthic invertebrates in two British river systems: a stable carbon isotope study', *Archive fur Hydrobiologie* **107**:349-361.

Woodyer, K.D. (1978) 'Sediment regime of the Darling River', *Proceedings of the Royal Society of Victoria* **90**:139-147.

Woodyer, K.D., G. Taylor and K.A.W. Crook (1979) 'Depositional processes along a very low-gradient, suspended-load stream: the Barwon River, New South Wales', *Sedimentary Geology* **22**:97-120.

Woolford, T. (1984) 'A fouling bivalve, *Corbiculina australis* (Deshayes, 1830), in the Renmark irrigation pipelines: its biology and control options for the Renmark Irrigation Trust', *Unpublished Honours Thesis*, Department of Zoology, University of Adelaide, 103 pages.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd Edition. Prentice-Hall, New Jersey.

Zwolinski, Z. (1992) Sedimentology and geomorphology of overbank flows on meandering river floodplains', *Geomorphology* **4**:367-379.

Appendices

A. River Murray Waters Agreement (1990)

B. Species list, Darling River floodplain, January 1990

C. Species list, lower Murray floodplain, January 1990

D. Species list, Pool 2 and Pool 3, lower Murray, February 1990.

E. Embryo numbers in *Notopala hanleyi* and *N. sublineata*

F. Estimation of surface area of wooden substrata

G. Solutions for phospholipid analysis

H. Microsoft Excel v. 4.0 'Macro' for calculating time taken for river level changes.

Appendix A

Part of the "River Murray Waters Agreement" (1990), pages 44-48, from the **River Murray Waters Act.**

DIVISION 1 - STATE ENTITLEMENTS TO WATER

South Australia's monthly entitlement

86. South Australia is entitled to receive -

(a) the following monthly quantities of River Murray water -

July	50 500 megalitres
August	66 000 megalitres
September	77 000 megalitres
October	112 500 megalitres
November	122 000 megalitres
December	159 000 megalitres
January	159 000 megalitres
February	136 000 megalitres
March	128 000 megalitres
April	77 000 megalitres
May	35 000 megalitres
June	32 000 megalitres

except as provided in clause 127; and

(b) 58,000 megalitres per month for dilution and losses, unless the Commission determines otherwise; and

(c) such additional quantities for dilution as the Commission determines from time to time.

Measurement of South Australia's entitlement

87.(1) Each month South Australia is deemed to receive the sum of the water flowing in that month in -

(i) the River Murray between the confluences of the Rufus and Lindsay Rivers with the River Murray, and

(ii) the Lindsay River near its confluence with the River Murray.

(2) The Commission must determine the flows referred to in sub-clause 87(1) in such manner as it sees fit.

Variation of South Australia's entitlements

88. The Commission may from time to time, at the request of a Commissioner for South Australia, vary for a specified sequence of months any of the monthly quantities which that State is entitled to receive under clause 86 without increasing the total of those quantities for that sequence.

Use of Lake Victoria

89. If the Commission decides that the flow or prospective flow of the River Murray downstream of its junction with the Great Darling Anabranch is, or will be for any month in excess of the sum of -

(a) the quantities which South Australia is entitled to receive in that month under clause 86 or 88;

(b) any quantities which, in the opinion of the Commission, ought to be and can be impounded in Lake Victoria during that month with the object of filling that storage at some time before the end of the next ensuing month of May; and

(c) any quantities required for use by New South Wales and Victoria, downstream of the junction of the River Murray and the Great Darling Anabranch,

South Australia may receive that excess in addition to the quantity of water which it is entitled to receive under clause 86 or 88.

Surplus flow to South Australia

90. The quantity of water that South Australia is entitled to receive in any month shall not be reduced if it has received a greater quantity than it was entitled to receive under clause 86 or 88 in any previous month.

Entitlements of New South Wales and Victoria

91.(1) Except as otherwise expressly provided in Division 3 of this Part and subject to South Australia's entitlement under clause 86 or 88, New South Wales and Victoria are each entitled to use -

(a) all the water in tributaries of the upper River Murray downstream of Doctors Point within its territory, before it reaches the River Murray,

(b) half the water in the upper River Murray upstream of Doctors Point, including any water diverted thereto by the Authority,

(c) half the water entering the Menindee Lakes from the Darling River, subject to the prior entitlement of New South Wales to use water from the Menindee Lakes Storage as provided in clause 92; and

(d) subject to paragraph 91(1)(c), an amount of water from the upper River Murray equivalent to any water contributed by any tributary or any outfall approved by the Commission entering the upper River Murray from its territory downstream of Doctors Point.

(2) Entitlements under sub-clause 91(1) shall not be affected by the declaration of a period of special accounting except as specifically provided in Division 4 of this Part.

New South Wales' entitlement to water from Menindee Lakes

92.(1) Whenever water in the Menindee Lakes Storage falls below 480 000 megalitres, New South Wales may use the stored water as it requires until the volume next exceeds 640 000 megalitres.

(2) Whenever sub-clause 92(1) does not apply, New South Wales may -

(a) divert from -

(i) the Menindee Lakes Storage; or

(ii) the Darling River below the Menindee Lakes Storage; or

(iii) the River Murray, below its junction with the Darling River; or

(b) release from the Cawndilla outlet regulator,

a total of up to 100,000 megalitres in any 12 month period commencing on 1 April.

(3) Whenever the Commission determines that -

(a) releases from the Menindee Lakes Storage exceed the water required for storage in Lake Victoria and to supply South Australia's entitlement; or

(b) water in the Menindee Lakes Storage exceeds 1 680 000 megalitres and the amount of the excess plus the estimated water currently in the River Murray and Darling River below the Menindee Lakes Storage is sufficient to supply South Australia's entitlement and to fill Lake Victoria,

any of that water used by New South Wales or released to provide for the retention of floodwaters shall not be deemed to be part of its entitlement under sub-clause 92(2).

New South Wales' and Victoria's supply to South Australia

93. New South Wales and Victoria must provide, in equal proportions, South Australia's entitlement under clause 86 or 88 from the water available to them under clauses 91 and 92.

Limitations on use by New South Wales and Victoria

94. Unless the Commission determines otherwise, New South Wales or Victoria must not use water from the upper River Murray to an extent which may result in less than half the minimum reserve determined under clause 100 being held in upper River Murray storages and allocated to that State at the end of the following May.

DIVISION 2 - CONTROL BY COMMISSION

Commission's role in operation of storages

95.(1) The Commission may give directions for the release of water from upper River Murray storages and water must be released in accordance with any such directions.

(2) The Commission may give directions under sub-clause 95(1) in the form of standing procedures, which it may amend or suspend at any time, except as provided in clause 97.

(3) In giving directions under this clause the Commission must have regard to -

(i) maintaining supply to South Australia of the quantities of water which that State is entitled to receive,

(ii) maintaining a minimum reserve of water as provided for in clause 100, and

(iii) facilitating the exercise by New South Wales and Victoria of their respective rights to use water from the upper River Murray, as they require.

(4) In giving directions under this clause the Commission may also have regard to -

(i) the improvement or maintenance of water quality in the River Murray (including the upper River Murray);

(ii) other water management and environmental objectives consistent with this Agreement.

Limitation on Menindee Lakes operation

96.(1) The Commission must not direct that water be released from Menindee Lakes Storage after its volume falls below 480 000 megalitres and before it next exceeds 640 000 megalitres.

(2) Subject to sub-clause 96(1), a direction to release water from Menindee Lakes Storage may be given by a majority vote of the Commission or, if the Commission is equally divided, by the casting vote of the presiding member.

Procedures for Dartmouth Dam operation

97. The Commission must not amend or, except in an emergency, suspend any standing procedures affecting the release of water through the power station of Dartmouth Reservoir without first consulting the State Electricity Commission of Victoria and the Constructing Authority for Victoria.

Water estimated to be under the control of the Commission

98. "Water estimated to be under the control of the Commission" means the aggregate of -

(a) water stored in the Hume and Dartmouth Reservoirs above their minimum operating levels;

(b) water stored in Lake Victoria above its minimum operating level;

(c) water available for release from the Menindee Lakes Storage at the direction of the Commission in accordance with clause 96, after allowing for New South Wales' prior entitlements under clause 92;

(d) the estimated runoff from the catchment of the upper River Murray above Doctors Point before the end of the following May, excluding water diverted from the Tooma River to the Eucumbene Storage and the Tumut River and from the Geehi River to the Snowy River;

(e) water estimated to be diverted to the upper River Murray above Doctors Point by works of the Authority before the end of the following May;

(f) the difference between the estimated amount of water in transit in the upper River Murray and the estimated amount of water in transit at the end of the following May.

Available water

99. From time to time the Commission must -

(a) determine the minimum amount of water estimated to be under the control of the Commission;

(b) determine the allowance to be made until the end of the following May for

(i) losses by evaporation and other means in the upper River Murray; and

(ii) the entitlements of South Australia under paragraphs 86(b) and 86(c);

(c) having regard to its determinations under paragraphs 99(a) and 99(b) determine the water available -

(i) for distribution to New South Wales, Victoria and South Australia before the end of the following May;

(ii) for holding in reserve at the end of the following May.

Minimum Reserve

100.(1) From time to time the Commission must determine the minimum reserve to be held at the end of the following May.

(2) Unless the Commission determines otherwise, the minimum reserve shall be the lesser of -

(a) One third of the water available determined under paragraph 99(c)

less

The sum of the monthly entitlements of South Australia under paragraph 86(a) up to the end of the following May

plus

The sum of any imbalance of use during a period of special accounting calculated under clause 125;

and

(b) 835,000 megalitres.

(3) If the minimum reserve determined under paragraph 100(2)(a) is less than zero, then the minimum reserve shall be deemed to be zero.

(4) Unless the Commission determines otherwise, the first 250,000 megalitres of any minimum reserve shall be held in Lake Victoria.

Use of State works to convey Murray water

101. The Commission may arrange for water to be conveyed from one part of the upper River Murray to another via works under the control of a State Contracting Government, on such terms as may be agreed between the Commission and that State Contracting Government.

Appendix B

Species, total abundance and relative FFG for samples collected from habitats on the Darling River floodplain, January 1990

No.		Species	Total	FFG
	MOLLUSCA			
	BIVALVIA			
2		*Sphaerium* sp.	25	Collector
	GASTROPODA			
3	Ancylidae	*Ferrissia* spp.	534	Scraper
4	Planorbidae	*Isidorella* sp.	8	Scraper
5		*Physa acuta*	168	Scraper
6	**OLIGOCHAETA**	Oligochaeta spp.	130	Collector
	CRUSTACEA			
	ISOPODA			
9	Corallanidae	*Austroargathona picta*	326	Collector
	DECAPODA			
11	Aytidae	*Caridina mccullochi*	153	Collector
12		*Paratya australiensis*	74	Collector
13	Palaemonidae	*Macrobrachium australiense*	1939	Collector
14	Parastacidae	*Cherax destructor*	21	Collector
7	**ARACHNIDA**	Hydracarina sp. 1	2	Predator
	INSECTA			
	EPHEMEROPTERA			
15	Caenidae	*Tasmanocoenis arcuata*	410	Collector
17	Leptophlebiidae	*Atalophlebia australis*	7	Collector
18	Baetidae	*Cloeon* sp.	744	Collector
	ODONATA			
19	Gomphidae	*Austrogomphus* sp.	6	Predator
20	Coenagrionidae	*Xanthagrion erythroneurum*	48	Predator
21		*Austragrion watsoni*	64	Predator
22		*Calagrion billinghursti*	1	Predator
24		Tiny Zygoptera	201	Predator
	HEMIPTERA			
25	Veliidae	*Microvelia* sp.	24	Predator
26	Mesoveliidae	*Mesovelia* sp 1	96	Predator
28	Gerridae	Gerridae sp.	25	Predator
29	Corixidae	*Agraptocorixa* sp.	143	Collector
30		*Sigara* sp.	13	Collector
31		*Micronecta* spp.	6557	Collector
34	Notonectidae	*Anisops* spp.	183	Predator

Appendix B

	COLEOPTERA			
35	Dytiscidae	*Antiporus femoralis*	18	Predator
36		*Antiporus gilberti*	2	Predator
37		*Megaporus* sp.	11	Predator
38		*Allodessus* sp.	21	Predator
39		*Liodessus* sp.	2	Predator
40		*Paroster* sp.	31	Predator
41		*?Eretes* sp. (larvae)	1	Predator
42	Gyrinidae	*Macrogyrus* sp. (larvae)	1	Predator
43	Hydrophilidae	*Paracymus* sp.	27	Colletor
44		*Enochrus* sp.	4	Scraper
45		*Berosus* sp.	1	Scraper
46		Hydrophilidae (larvae) sp 1	3	Predator
47	Hydraenidae	*Ochthebius* sp.	3	Scraper
48		Hydraena sp.	29	Scraper
49	Elmidae	*Coxelmis* sp. (larvae)	7	Predator
	DIPTERA			
53	Chironomidae: Tanypodinae	*Ablabesmyia* sp.	63	Predator
55		*Coelopynia* sp.	624	Predator
56		*Procladius* sp.	253	Predator
57	Chironomidae: Chironominae	*Cladotanytarsus* sp.	134	Colletor
59		*Tanytarsus* spp.	168	Colletor
61		*Virgatanytarsus* sp.	1	Colletor
62		*Chironomus* sp.	11	Colletor
63		*Chironomus cloacalis*	30	Colletor
64		*Cryptochironomus* sp.	68	Colletor
65		*Stenochironomus* sp.	45	Colletor
66		*Parachironomus* sp.	201	Predator
67		*Polypedilum* spp.	185	Colletor
68		*Dicrotendipes conjunctus*	301	Colletor
69		*Dicrotendipes* sp.	1932	Colletor
70		*Paratendipes* sp.	38	Colletor
71		*Cladopelma* sp.	207	Colletor
72		*Harnishia??* sp.	1	Colletor
74		*Kiefferulus martini*	6	Colletor
75	Chironomidae: Orthocladiinae	*Parakiefferiella* sp.	72	Colletor
76		*Cricotopus* spp.	362	Colletor
80		Tiny Chironomids	43	Colletor
81	Culicidae	Culicinae sp.	6	Colletor
82	Ceratopogonidae	*Bezzia* sp.	459	Predator
84	Empididae	Empididae sp.	28	Predator
85	Tabanidae	Tabanidae sp. 1	2	Predator
86	Muscidae	Muscidae sp. 1	1	Predator
	TRICHOPTERA			
88	Ecnomidae	*Ecnomus* sp.	202	Predator
89	Leptoceridae	*Triplectides australis*	185	Colletor
91		*Triplectidina* sp.	1	Colletor
92		*Oecetis* sp.	603	Predator
93	Hydropsychidae	*Cheumatopsyche* sp.	8	Colletor

Appendix C

Species, total abundance and relative FFG for samples collected from habitats on the lower Murray floodplain, January 1990.

No.	Species	Total	FFG
	MOLLUSCA		
	BIVALVIA		
2	*Sphaerium* sp.	87	Collector
	GASTROPODA		
3 Ancylidae	*Ferrissia* spp.	5	Scraper
5 Planorbidae	*Physa acuta*	1	Scraper
6 **OLIGOCHAETA**	Oligochaeta spp.	50	Collector
	CRUSTACEA		
	ISOPODA		
9 Corallanidae	*Austroargathona picta*	5	Collector
	AMPHIPODA		
10 Ceinidae	*Austrochiltonia australis*	15	Collector
	DECAPODA		
11 Aytidae	*Caridina mccullochi*	1475	Collector
12	*Paratya australiensis*	6579	Collector
13 Palaemonidae	*Macrobrachium australiense*	541	Collector
14 Parastacidae	*Cherax destructor*	16	Collector
	INSECTA		
	EPHEMEROPTERA		
15 Caenidae	*Tasmanocoenis arcuata*	80	Collector
18 Baetidae	*Cloeon* sp.	11	Collector
	ODONATA		
95 Coenagrionidae	*Ishnura heterosticta*	368	Predator
102	*Pseudagrion aureofrons*	1	Predator
22	*Calagrion billinghursti*	12	Predator
Corduliidae	*Hemicordulia tau*	14	Predator
	HEMIPTERA		
25 Veliidae	*Microvelia* sp.	8	Predator
26 Mesoveliidae	*Mesovelia* sp.	2	Predator
29 Corixidae	*Agraptocorixa* sp.	301	Collector
30	*Sigara* sp.	1	Collector
31	*Micronecta* spp.	3291	Collector
33 Naucoridae	*Naucoris* sp.	14	Predator
100 Belostomatidae	*Diplonychus eques*	1	Predator
34 Notonectidae	*Anisops* spp.	71	Predator
101 Saldidae	*Saldura* sp.	2	Collector

Appendix C

	COLEOPTERA			
35	Dytiscidae	*Antiporus femoralis*	5	Predator
38		*Allodessus* sp.	1	Predator
40		*Paroster* sp.	3	Predator
103		*Eretes australis*	1	Predator
43	Hydrophilidae	*Paracymus* sp.	2	Collector
44		*Enochrus* sp.	9	Scraper
97		*Limnoxenus* sp.	1	Collector
96		*Berosus* sp. (larvae)	18	Predator
46		Hydrophilidae sp. (larvae)	23	Predator
47	Hydraenidae	*Ochthebius* sp.	3	Scraper
48		Hydraena sp.	10	Scraper
49	Elmidae	*Coxelmis* sp. (larvae)	7	Predator
	DIPTERA			
50	Tupulidae	Tipulidae sp.	8	Predator
53	Chironomidae: Tanypodinae	*Ablabesmyia* sp.	70	Predator
55		*Coelopynia* sp.	11	Predator
56		*Procladius* sp.	334	Predator
57	Chironomidae: Chironominae	*Cladotanytarsus* sp.	712	Collector
59		*Tanytarsus* spp.	271	Collector
62		*Chironomus* sp.	1647	Collector
63		*Chironomus cloacalis*	234	Collector
64		*Cryptochironomus* sp.	195	Collector
65		*Stenochironomus* sp.	9	Collector
66		*Parachironomus* sp.	22	Predator
68		*Dicrotendipes conjunctus*	19	Collector
69		*Dicrotendipes* sp.	443	Collector
70		*Paratendipes* sp.	38	Collector
71		*Cladopelma* sp.	9	Collector
74		*Kiefferulus martini*	47	Collector
76	Chironomidae: Orthocladiinae	*Cricotopus* spp.	467	Collector
81	Culicidae	Culicinae sp.	1	Collector
82	Ceratopogonidae	*Bezzia* sp.	575	Predator
83		*Forcipomyia* sp.	57	Collector
84	Empididae	Empididae sp.	21	Predator
98	Stratiomyidae	Stratiomyidae sp.	1	Collector
	TRICHOPTERA			
88	Ecnomidae	*Ecnomus* sp.	29	Predator
89	Leptoceridae	*Triplectides* sp.	47	Collector
92		*Oecetis* sp.	1	Predator

Appendix D

Species, total abundance, abundance status and relative FFG for samples collected from habitats in Pool 2 and Pool 3, lower Murray, February 1990.

No.	Species	Total	Abundance	FFG
	MOLLUSCA			
	BIVALVIA			
2	*Sphaerium* sp.	122	Common	Collector
	GASTROPODA			
3 Ancylidae	*Ferrissia* spp.	14	Moderate	Scraper
5 Planorbidae	*Physa acuta*	1	Rare	Scraper
6 **OLIGOCHAETA**	Oligochaeta spp.	138	Common	Collector
	ARACHNIDA			
8 Hydracarina	*Peza ops*	2	Rare	Predator
	CRUSTACEA			
	ISOPODA			
9 Corallanidae	*Austroargathona picta*	165	Common	Collector
	AMPHIPODA			
10 Ceinidae	*Austrochiltonia australis*	134	Moderate	Collector
	DECAPODA			
11 Aytidae	*Caridina mccullochi*	1126	Abundant	Collector
12	*Paratya australiensis*	20101	Abundant	Collector
13 Palaemonidae	*Macrobrachium australiense*	3193	Abundant	Collector
14 Parastacidae	*Cherax destructor*	10	Moderate	Collector
	INSECTA			
	EPHEMEROPTERA			
15 Caenidae	*Tasmanocoenis arcuata*	56	Moderate	Collector
18 Baetidae	*Cloeon* sp.	129	Common	Collector
	ODONATA			
23 Protoneuridae	*Nosostica solida*	1	Rare	Predator
24	Tiny Zygoptera	3	Rare	Predator
	HEMIPTERA			
26 Mesoveliidae	*Mesovelia* sp. 1	2	Rare	Predator
	Mesovelia sp. 2	10	Rare	Predator
28 Gerridae	Gerridae sp.	2	Rare	Predator
30 Corixidae	*Sigara* sp.	1	Rare	Collector
31	*Micronecta* spp.	115	Common	Collector
32 Ochteridae	*Octherus* sp.	2	Rare	Collector
33 Naucoridae	*Naucoris* sp.	1	Rare	Predator
34 Notonectidae	*Anisops* spp.	8	Rare	Predator

Appendix D

	COLEOPTERA				
35	Dytiscidae	*Antiporus femoralis*	5	Rare	Predator
38		*Allodessus* sp.	5	Rare	Predator
44	Hydrophilidae	*Enochrus* sp.	2	Rare	Scraper
46		Hydrophilidae sp. (larvae)	20	Moderate	Predator
47	Hydraenidae	*Ochthebius* sp.	3	Rare	Scraper
49	Elmidae	*Coxelmis* sp. (larvae)	2	Rare	Predator
	DIPTERA				
50	Tipulidae	Tipulidae sp.	3	Rare	Predator
52	Psychodidae	Psychodidae sp.	1	Rare	Collector
53	Chironomidae: Tanypodinae	*Ablabesmyia* sp.	23	Moderate	Predator
54		*Pentaneura* sp.	2	Rare	Predator
56		*Procladius* sp.	2	Rare	Predator
57	Chironomidae: Chironominae	*Cladotanytarsus* sp.	1743	Abundant	Collector
58		*Paratanytarsus* sp.	77	Moderate	Collector
59		*Tanytarsus* spp.	477	Common	Collector
60		*Tanytarsus fuscithorax*	2	Rare	Collector
63		*Chironomus cloacalis*	17	Moderate	Collector
64		*Cryptochironomus* sp.	182	Common	Collector
65		*Stenochironomus* sp.	5	Rare	Collector
66		*Parachironomus* sp.	29	Moderate	Predator
67		*Polypedilum* sp.	59	Moderate	Collector
68		*Dicrotendipes conjunctus*	7	Rare	Collector
69		*Dicrotendipes* sp.	46	Moderate	Collector
73		*Kiefferulus sp.*	5	Rare	Collector
75		*Parakiefferiella sp.*	31	Moderate	Collector
76	Chironomidae: Orthocladiinae	*Cricotopus* sp. 1	766	Abundant	Collector
77		*Cricotopus* sp. (Black)	18	Moderate	Collector
78		*Limnophyes* sp.	16	Moderate	Collector
79		EWS sp. 31	59	Moderate	Collector
82	Ceratopogonidae	*Bezzia* sp.	7	Rare	Predator
83		*Forcipomyia* sp.	117	Common	Collector
84	Empididae	Empididae sp.	3	Rare	Predator
86	Muscidae	Muscidae sp.	10	Rare	Predator
	TRICHOPTERA				
88	Ecnomidae	*Ecnomus* sp.	8	Rare	Predator
89	Leptoceridae	*Triplectides australis.*	1	Rare	Collector
90		*Triplectides elongatus*	6	Rare	Collector

Appendix E

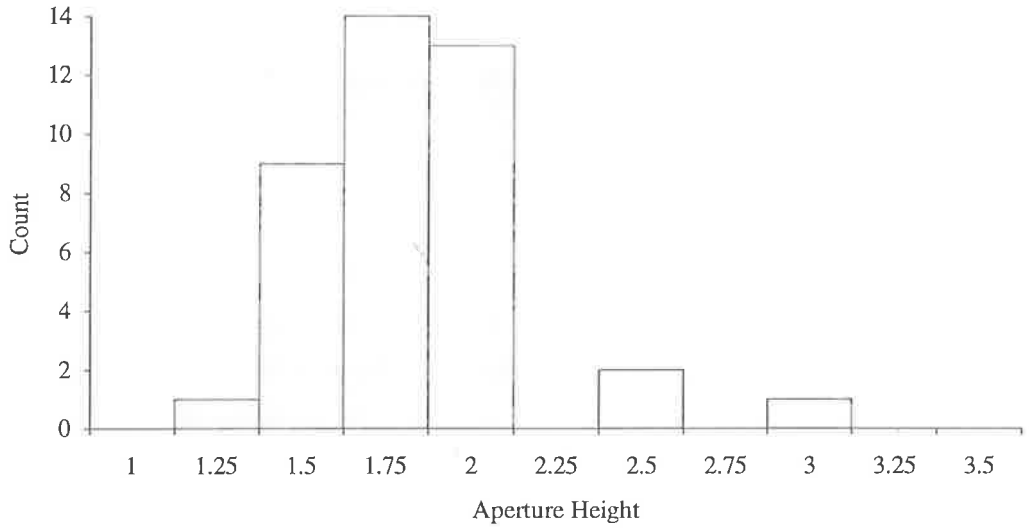
Embryo Numbers in *Notopala hanleyi* and *N. sublineata*

Female *Notopala hanleyi* were collected from the Kingston Irrigation pipeline, South Australian Riverland, in August 1992 and female *N. sublineata* from Cooper Creek, north-eastern South Australia, in December 1991 (cf. Figure 6.3). Individuals were frozen, later thawed, the bodies removed from the shells, embryo's dissected from the oviducts and counted. Aperture height was used as a measure for embryo size (cf. Sheldon and Walker, 1993b).

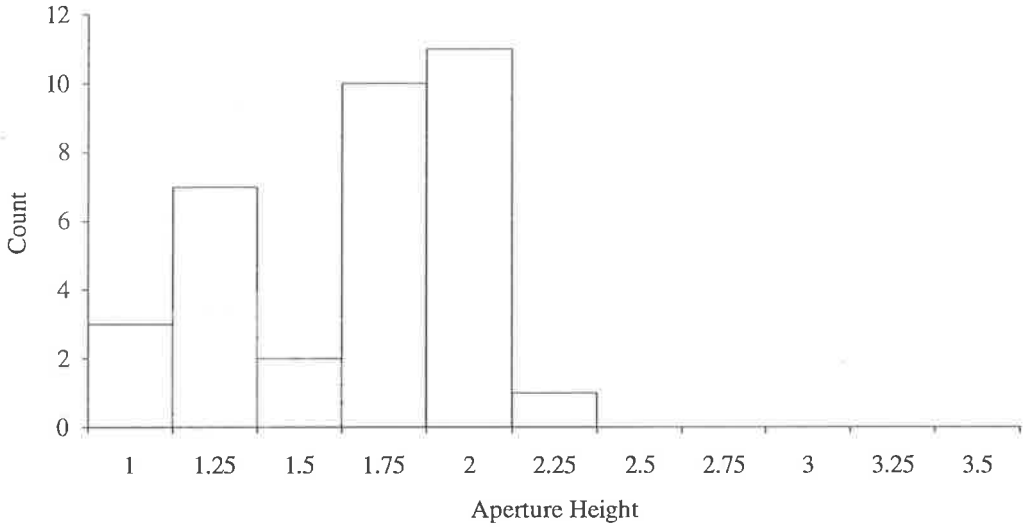
Females of both species had similar numbers of embryos (Table E.1). In *N. hanleyi* numbers ranged from 12 to 6, and in *N. sublineata* from 14 to 4. The size range of embryo's in both species was similar (cf. Figure E.1a and E.1b).

Table E.1 Mean (SE) of the number and size of embryos dissected from female *N hanleyi* and *N. sublineata* collected from the Kingston Irrigation pipeline (August 1992) and Cooper Creek (December 1991) respectively.

	n	No.	n	Size
Notopala hanleyi	5	9 *(1.14)*	40	1.89 *(0.05)*
Notopala sublineata	4	8.5 *(2.1)*	34	1.77 *(0.06)*



(a)



(b)

Figure E.1 Size distribution of embryo's in (a) *Notopala hanleyi* and (b) *Notopala sublineata*.

Appendix F

Estimation of Surface Area

A. PLASTIC FILM

The weight of plastic film "Glad Wrap" was used to estimate the surface area of wooden natural substrata. An equation for the relationship was determined by weighing "Glad Wrap" squares of known surface area (Figure F.1). The relationship was significant ($r = 0.98$, $df = 14$, $p<0.001$).

Equation: $\text{Area} = 0.09054 \times \text{Weight}$

where: 'area' is measured in metres squared (m^2)
'weight' is measured in grams (g)

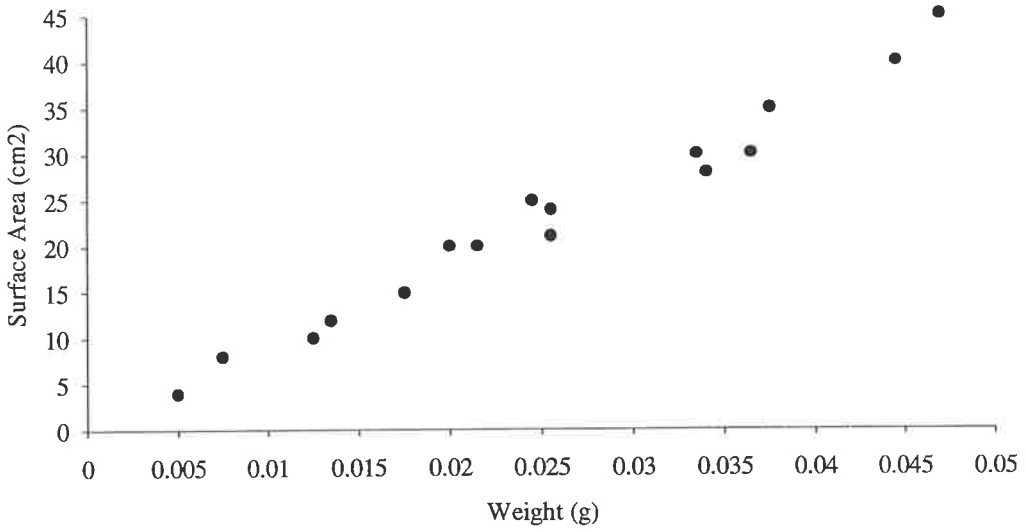


Figure F.1 Relationship of weight (g) to surface area (cm^2) for the plastic film "Glad Wrap".

B. DETERGENT DISPLACEMENT

The volume of liquid detergent displaced from a known volume was used to estimate the surface area of natural wooden substrata. The equation for the relationship was determined by measuring the volume of detergent displaced after immersing objects of known surface area (Figure F.2). The relationship was significant ($r = 0.98$, $df = 6$, $p<0.001$).

Equation: $Area = (0.0009 \times (Volume)) + 0.0011$

where: 'area' is in metres squared (m^2)
'volume' is in millilitres (mL)

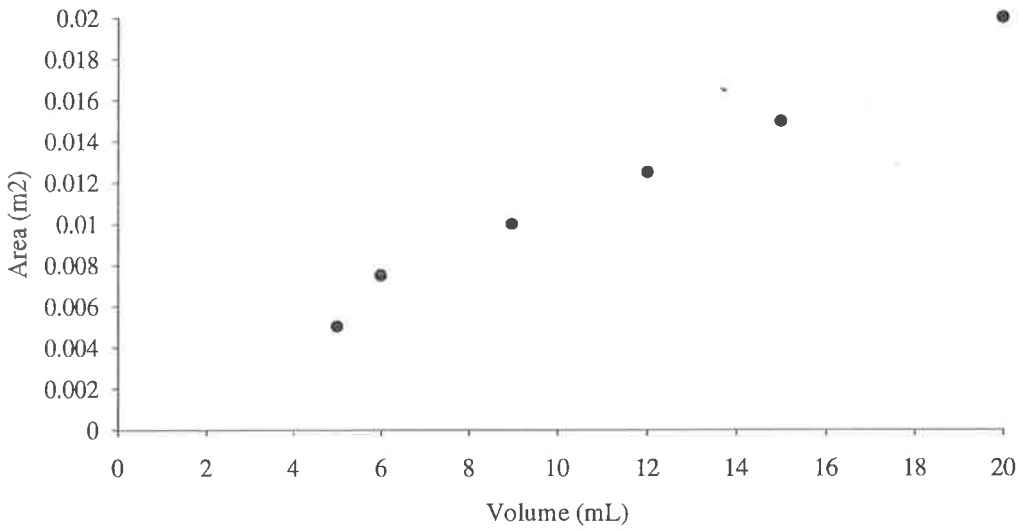


Figure F.2 Relationship of volume displaced (mL) to surface area (cm^2) for calculating surface area of complex wooden substrata.

Appendix G

Solutions for Phosopholipid Analysis

A. Phosphate Buffer

8.7 g di-potassium hydrogen orthophosphate (K_2HPO_4) dissolved in 1-L distilled water and neutralised to pH 7.4 with 1 N hydrochloric acid (HCl).

B. Molybdate Reagent

4.4 g ammonium molybdate and 14 mL concentrated sulphuric acid (H_2SO_4) dissolved in 1-L of distilled water.

C. ANSA Reagent

30 g sodium bisulfite, 2 g sodium sulfite and 0.5 g 1-amino-2-naphthol-4-sulfonic acid dissolved in 200 mL of distilled water.

This solution is stored in the dark at 4°C and diluted 1:12 with distilled water before use.

Appendix H

"Macro" written in Microsoft Excel v. 4.0 (Microsoft, 1992) for calculating the number of days taken for the river to undergo stage changes from 10 cm to 100 cm. Daily stage data are supplied in an Excel worksheet "junk.xls".

```
=ECHO(FALSE)
=ACTIVATE("junk.xls")
=DEFINE.NAME("Start")
=SELECT("r[1]c")
=DEFINE.NAME("End")
=FORMULA("=Start-End",!$A$1)
=IF(ABS(!$A$1)>1,GOTO(B14),GOTO(B11))
=IF(ABS(!$A$1)<=1,GOTO(B12),)
=IF(!$A$2=0,GOTO(B26),GOTO(B13))
=GOTO($B$7)
=FORMULA.ARRAY("=COUNT(Start:End)",!$A$2)
=SELECT(!$A$2)
=COPY()
=ACTIVATE("days.xls")
=PASTE.SPECIAL(3,1,FALSE,FALSE)
=SELECT("r[1]c")
=ACTIVATE("junk.xls")
=SELECT("Start")
=SELECT("r[1]c")
=DELETE.NAME("Start")
=DELETE.NAME("End")
=GOTO($B$6)
=RETURN()
```

Papers Bound in Support

- Walker, K.F., M.C. Thoms and F. Sheldon (1992) 'Effects of weirs on the littoral environment of the River Murray, South Australia', In *River Conservation and Management* (Eds: P.J. Boon, P. Calow and G.E. Petts), pp. 271-292, John Wiley and Sons.

- Sheldon, F. and K.F. Walker (1993) 'Pipelines as a refuge for freshwater snails', *Regulated Rivers: Research and Management* **8:**295-299.

- Sheldon, F. and K.F. Walker (1993) 'Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae)', *Journal of the Malacological Society of Australia* **14:** 59-71

- Walker, K.F. and F. Sheldon (1994) 'The ecological importance of floodplains', In *Ecotones at the river basin scale-global land/water interactions*: proceedings of Ecotones Regional Workshop, Barmera, South Australia, 12-15 October 1992. (Ed: A. Jensen), pp. 21-27, UNESCO Ecotones Research Project, 'Role of land/inland water ecotones in landscape management and restoration'.

- Walker, K.F., A.J. Boulton, M.C. Thoms and F. Sheldon (1994) 'Effects of water-level changes induced by weirs on the distribution of littoral plants along the River Murray', South Australia, *Australian Journal of Marine and Freshwater Research*. Submitted.

- Puckridge, J.T., F. Sheldon, A.J. Boulton and K.F. Walker (1994) 'Flow variability and the Flood Pulse Concept', Unpublished MS.

Walker, K.F., Thoms, M.C., and Sheldon, F., (1992) Effects of weirs on the littoral environment of the River Murray, South Australia.
In Boon, P.J., Calow, P., and Petts, G.E., (eds.), *River Conservation and Management*, John Wiley & Sons, pp. 271-292.

Sheldon, F., and Walker, K.F., (1993) Short communication. Pipelines as a refuge for freshwater snails.
Regulated Rivers: Research and Management, v. 8 (3), pp. 295-299.

Sheldon, F., and Walker, K.F., (1993) Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae).
Journal of the Malacological Society of Australia, v. 14 (1), pp. 59-71.

Sheldon, F., and Walker, K.F., (1994) The ecological importance of floodplains and wetlands.
In Jensen, A., (ed.), *Ecotones at the River Basin Scale – Global Land/Water Interactions*, Proceedings of Ecotones Regional Workshop, Barmera, South Australia, 12-15 October 1992, pp. 21-27.

Walker, K.F., Boulton, A.J., Thomas, M.C., and Sheldon, F., (1994) Effects of water-level changes induced by weirs on the distribution of littoral plants along the River Murray, South Australia.
Australian Journal of Marine and Freshwater Research, v. 45 (8), pp. 1421-1438.

FLOW VARIABILITY AND THE FLOOD PULSE CONCEPT

J.T.PUCKRIDGE[1], F. SHELDON[1], A.J. BOULTON[2] AND K.F. WALKER[2]

River Murray Laboratory,
Department of Zoology, University of Adelaide, South Australia 5005

ABSTRACT

The Flood Pulse Concept proposes that the flood pulse (the fluctuation of river discharge) is the key variable structuring the biota of large rivers, but it understates the significance of temporal and spatial variation and their biological implications. Comparisons of the hydrographs of large rivers from temperate, tropical and arid regions suggest that flow variability is multi-faceted, and distinctive both for individual rivers and for temporal and spatial scales within rivers. We extend the concept to accomodate the scale and complexity of flow variation, and propose a framework to relate hydrological and geomorphic features to biological features, processes and responses. We redefine the flood pulse as an eight-phase alternation of river stage extending into the hyporheic zone, and the floodplain to include periodically inundated areas of the river channel. We remove the term "disturbance" from the flow "habitat templet" of large rivers, and propose a templet based on flow variability. This templet is likely to be fundamentally changed by flow regulation.

KEY WORDS Flow variability Floodplain Flood Pulse Concept Habitat templet Disturbance River

---

[1]Equal senior authorship

[2]Equal junior authorship

INTRODUCTION

Floods play a vital role in rivers, particularly those with extensive floodplains. They promote exchanges of water, nutrients and biota between the main channel and the floodplain, and sustain floodplain refuges, feeding and spawning areas (e.g. Welcomme, 1979; Brinson *et al.*, 1983; Amoros and Roux, 1988; Neckles *et al.*, 1990; Bayley, 1991). The Flood Pulse Concept (FPC: Junk *et al.*, 1989) proposes that the "flood pulse" is the key variable influencing riverine biota, and focuses on the interactive roles of flooding and the floodplain in structuring lotic ecosystems. Ideas about the significance of the flood pulse, however, are based on studies in tropical and temperate regions, where there is comparatively little hydrological variability (e.g. McArthur, 1988; Junk *et al.*, 1989). These ideas tend to under-rate the ecological significance of spatial and temporal flow variability, particularly on scales relevant to rivers in arid and semi-arid regions (e.g. Farquharson *et al.*, 1992).

In this discussion paper the FPC is extended to integrate both the hydrological and the geomorphological perspectives of large-river landscapes. The extended FPC also acknowledges the range of flow patterns evident in large rivers over broad temporal and spatial scales. The "flood pulse" is redefined, and some biological implications of the extended concept are considered. The potential impacts of flow regulation on large rivers are also examined with regard for conservation and rehabilitation.

FLOW VARIABILITY IN LARGE RIVERS

To elucidate hydrological variability it is helpful to consider an idealised hydrograph depicting flow events at a given point . The hydrograph in Figure 1 depicts a sequence of *flood pulses* (alternations of river stage) which may be characterised by their amplitude and duration and the slopes of their rising and falling limbs. The sequence of pulses constitutes the *flow history* of that point on the river (cf. Fausch and Bramblett, 1991). This may then be generalised statistically to describe the *flow regime* (cf. Beckinsale, 1969; Poff and Ward, 1989), which identifies the central tendencies of flow parameters (mean pulse amplitude, duration and frequency and daily, monthly and annual flows) and the corresponding coefficients of variation.

In temperate arid and semi-arid regions (distinguished by factors like climate, runoff and temperature, *sensu* Beckinsale, 1969) rainfall varies 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 is also conspicuous, and illustrated by the effects of intense, short-lived local downpours (Farquharson *et al.*, 1992). Australian dryland rivers are hydrologically more variable than rivers elsewhere (Finlayson and McMahon, 1988; McMahon and Finlayson, 1991) and flow variability undoubtedly is an important factor in their ecology. Indeed, some form of flow variability will be significant for rivers in all climatic zones. This paper ventures a preliminary examination of its nature and extent in large rivers worldwide.

For small streams hydrological variability has been partitioned into a number of biologically-relevant components by some authors (e.g. Minshall, 1988; Poff and Ward, 1989). Parallels may exist in large rivers, and may be examined by dissecting hydrographs into components such as pulse frequency, amplitude, duration, seasonal timing and pulse shape.

Figure 2 compares 20-year hydrographs of mean monthly discharge from a number of Australian dryland rivers (from records of the Engineering and Water Supply Department, Adelaide, and the Department of Water Resources, Sydney) with rivers from tropical, temperate and arid zones world-wide (UNESCO, 1971). The data are from pre-regulation records at single gauging stations below similar-sized catchments (Table 1). To indicate changes in the components of variability after flow regulation, post-regulation hydrographs for the River Murray and Darling River were also included.

The variability within and between hydrographs at this time scale is obvious. Flows at other time scales (e.g. daily flows, or records >20 years) can also be highly variable (Erskine and Warner, 1988; McMahon and Finlayson, 1991). Here, we are considering features of the *flow regime*. For other studies, the relevance of either the flow regime, the flow history or the present flood pulse will be determined by the frame of reference (see below).

Several measures have been used previously to describe flow variability in rivers (e.g. Horwitz, 1978; McMahon, 1979; Poff and Ward, 1989). We have added to these, choosing simple indicators in preference to complex, integrative measures like flood frequency and flow duration curves (cf. Gustard, 1992). Thus, 18 measures of variability and predictability (Table 2), plus mean annual discharge, were calculated for 15 rivers. Figure 3 shows a profile of these components for each river. The profiles reflect the variation evident in the hydrographs (Figure 2), with each river showing a

distinctive pattern. Evidently, flow variability is a multi-faceted phenomenon, and resolution of its components is a necessary precursor to analyses of its biological implications.

Principal Components Analysis (PCA) was used to ordinate the foregoing measures of variability and predictability for the 15 rivers (SYSTAT version 5.0, using defaults). The first three components accounted for 80% of the total variation (Figure 4).

The first component (PC I, 48% of variation) was dominated by discharge amplitude, and clearly distinguished the two Australian arid-zone rivers (Cooper, Diamantina). The second component (PC II, 21%) was positively correlated with variation in flood duration and flood frequency, and negatively correlated with *predictability*, *contingency* (sensu Colwell, 1974) and stability in seasonal timing. This axis separated rivers approximately according to the climatic zone of their headwaters, with the Chari and Mekong being distinctly predictable and the temperate rivers less so. The third component (PC III, 11%) largely reflected Colwell's (1974) measure of *constancy*, with no climatic or regional pattern. Removing the Australian arid-zone rivers increased the separation of the remaining rivers, but did not change the associations of variability and predictability with the three principal components.

In the PCA the post-regulation hydrographs of the River Murray and Darling River were separated from their pre-regulation hydrographs. The analysis suggests that regulation has increased the variation in discharge amplitude as well as the stability of seasonal timing, the predictability and contingency of flood pulses for both rivers.

This analysis is intended only to be illustrative, but the patterns suggest some important points. Firstly, regional differences in the patterns of hydrological variability of large rivers appear to depend more on the climate of the river headwaters zone than the remainder of the river's course (cf. Rodier, 1985). Arid-zone rivers with their headwaters in semi-arid regions (Cooper, Diamantina) differ markedly from arid-zone rivers like the Chari, with headwaters in the humid tropics, or a temperate semi-arid river such as the Syr Darya, with headwaters in high-rainfall mountains (cf. Farquharson *et al.*, 1992). The Australian rivers rising in semi-arid zones differed from all other rivers analysed in the extreme variability of their flood amplitudes.

There appears to be a weak distinction between temperate and tropical rivers, based on the greater variability in frequency, duration and timing of pulses in temperate rivers, and their lower predictability. In these components, rivers with semi-arid catchments

were not consistently more variable than temperate rivers. Given the appropriate data, the differences could be explored further by comparing the periodicity of floods of different magnitude. The most biologically meaningful threshold for subdivision of flood amplitudes may be at bankfull discharge.

From this analysis it appears that, irrespective of location in climatic zone, large rivers exhibit distinctive and complex patterns of hydrological variability. An integrative measure of variability (cf. Horwitz, 1978; Finlayson and McMahon, 1988; Grossman, 1990; McMahon and Finlayson, 1991) would mask these patterns. Rivers cannot be simply summed as variable–invariant or predictable–unpredictable. The contributions of the various components of flow variability for river ecology need to be explored at appropriate temporal and spatial scales and an appropriate model for large river ecology should encompass this variability in all its forms.

CURRENT CONCEPTS

The River Continuum Concept

The River Continuum Concept (RCC) (Vannote *et al.*, 1980; Newbold *et al.*, 1981; Minshall *et al.*, 1985) supposes that there is a continuous gradient of physical conditions between the headwaters and mouth of a river, and that the composition and dynamics of biological communities along the river change in response to the gradient. The RCC overlooks the significance of floods other than as a "system reset" phenomenon (e.g. Ward and Stanford, 1983), and also overlooks the significance of river-floodplain interactions (Junk *et al.*, 1989).

The RCC is not easily applied to large rivers, particularly where there is a well-developed floodplain, or where the continuity of longitudinal gradients is interrupted by intermittency of flow and patchy local flooding. In these systems lateral linkages are likely to be more important than longitudinal linkages (MacArthur, 1988; Junk *et al.*, 1989; Sedell *et al.*, 1989). In rivers where surface waters are ephemeral, longitudinal linkages may be even less significant than vertical linkages between surface and subsurface flows (cf. Ward, 1989; Ward and Stanford, 1989). Variability in the timing and duration of flows is also likely to impede predictable longitudinal patterns of succession (Winterbourn, 1982).

The Flood Pulse Concept

The Flood Pulse Concept (FPC) (Junk *et al.*, 1989) arose partly from the perceived deficiencies of the RCC as a model for the ecology of large floodplain rivers. The FPC proposes that regular pulsing of river discharge is the key variable affecting the biota. It emphasises lateral exchanges between river and floodplain, and nutrient cycling within floodplain environments. According to the FPC, the main channel receives most of its nutrients from the floodplain, and is mainly an avenue for dispersal of biota. The flood pulse exerts an influence by imposing alternating wet and dry phases on the floodplain, maintaining it as the major site of production.

Although the FPC and subsequent interpretations (e.g. Bayley, 1991) recognise longitudinal discontinuities within river systems and accord a central role to discharge fluctuations, they do not systematically examine the scale and complexity of these fluctuations, nor pursue their implications for river function. The FPC should be extended to accomodate the following hydrological features (examples Fig. 3):

- *Variability in Pulse Timing*
  The FPC implies that the flood pulse in temperate systems may reinforce climatic seasonality (Bayley, 1991). However, the latter may be true only in rivers with regular pulse timing - where variability in pulse timing is pronounced (e.g. the Darling), the synchrony of seasonal and hydrological cycles will not be evident and the biota may be faced with conflicting seasonal and hydrological cues (Sparks *et al.*, 1990).

- *Variability in Pulse Duration*
  Where flood pulse duration is highly variable (e.g the Danube), biotic responses may differ from those proposed by the FPC. For example, use of the floodplain as a spawning, nursery and feeding ground will involve greater risk of mortality (Welcomme, 1979; Bayley, 1989) and floodplain use may be more opportunistic.

- *Variability in Pulse Amplitude*

  Rivers with highly variable pulse amplitudes (e.g. the Cooper) may experience periods of zero flow when sections will become lentic. The beginning or end of an in-channel flow event may be more significant than the overtopping of the banks, especially after long periods of drought. In these rivers 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. Rivers with extreme variability in pulse amplitude may have periods in which some reaches dry completely at the surface (Rodier, 1985; Kotwicki, 1986) and only the hyporheic zone therefore may function permanently as a "highway" (sensu Junk *et al.*, 1989) with the "main channel" functioning as part of the floodplain.

- *Long-Term Variation*

  For rivers which are relatively invariant over extended time-scales the characteristics of individual flood pulses may reflect the generalized characteristics of the flow regime and account for population and community structure. Even in these rivers, however, flow history may have pronounced effects on biotic structure (Welcomme and Hagborg, 1977; Benech *et al.*, 1983; Quiros and Cuch, 1989). In rivers which are highly variable in the long-term individual flood pulses are less likely to reflect the flow regime and single events in flow history may affect the geomorphic environment (Graf, 1988; Kresan, 1988; Pickup, 1991) and community structures (e.g. of floodplain vegetation) for decades and even centuries (Friedel *et al.* ????).

- *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 flood pulse (Schick, 1988; Fausch and Bramblett, 1991). Where it is pronounced, local hydrologic data will be important for predicting ecological features such as community structure (Horwitz, 1978; Pearson *et al.*, 1992), as floodplain location may influence patterns of inundation and physico-chemical features. In highly variable, low-gradient systems like the Cooper and Diamantina, some floods may be exhausted before reaching the drainage terminus (Kotwicki, 1986; Falkenmark, 1989), creating a downstream gradient of diminishing flood frequency with corresponding gradients in physico-chemical characteristics of the floodplains (Allan, 1988).

- *Unpredictability*
  Junk *et al.* (1989) contend that the FPC is not easily applied to rivers in which the features of the pulse are unpredictable, as the biota are unable to adapt to unpredictability. This contention suggests too narrow a perception of biotic adaptation and ecological response. Such life-history strategies as opportunism and flexibility are arguably adaptations to unpredictable hydrological regimes (Livdahl, 1979; Vogl, 1980; Kodric-Brown, 1981; Winterbourn *et al.*, 1981).

If the FPC is extended to encompass the range of patterns of variability evident in large rivers, then the definitions of a "floodplain" and of a "flood pulse" need to be broadened to accomodate this range.

NEW DEFINITIONS

Definition of "Floodplain"

Junk *et al.* (1989) acknowledge that there is essential interchange of biota between main-channel and floodplain environments, and regard the two as a unit: the river-floodplain system. In this case, the "river" appears to be synonymous with the "main channel" as distinct from the floodplain. This is confusing, and works against the intent of the river-floodplain system definition. We suggest that "river" be used to indicate a network of waterbodies connected by flow, and existing at different spatial and temporal scales. The network includes several biotopes, among them the floodplain and the main channel (Amoros and Roux, 1988).

Floodplains are usually defined as low-lying areas subject to periodic inundation by lateral overflow from fluvial channels or lakes (cf. Junk *et al.*, 1989; Junk and Welcomme, 1990). This conforms with traditional geomorphology, in which lowland fluvial systems consist of two distinct elements: *active channels* which carry flow, and *floodplains* (here designated *geo-floodplains*), formed by the deposition of sediments in marginal areas during overbank flows (cf. Gregory *et al.*, 1991).

This view lacks utility for ecological research because the critical distinction between the two elements, from a biological viewpoint, may depend on the pattern of inundation. For example, the "main channels" in rivers with high amplitude variability may be intermittently flooded, and so are functionally equivalent to floodplains. The reference to "lateral overflow" also is limiting, as floodplain flow patterns are often

more complex. For example, in large floods the geo-floodplain may be subject to longitudinal rather than lateral flows, and localised floods may involve inflow from the floodplain to the channel rather than overflow from the "main channel".

Further, floodplains are highly diverse systems (Welcomme, 1988), and processes may differ between types. They may vary in manner and degree of connection to the main channel (Amoros and Roux, 1988), and may be a drainage terminus rather than an area of lateral overflow (Rodier, 1985; Falkenmark, 1989).

Junk *et al.* (1989) venture an ecological definition of a floodplain in terms of an *Aquatic-Terrestrial Transition Zone* (ATTZ) that excludes permanent lentic and lotic habitats. It has features common to terrestrial and permanent aquatic habitats, and represents a link between them. The ATTZ is regarded as a distinct ecosystem, with physical features that are time-dependent (hence "the moving littoral"). The notion of an ATTZ emphasises the role of wetting and drying in floodplain dynamics, but oversimplifies these processes. The biota of the "aquatic" phase has characteristics (e.g. abbreviated life cycles, capabilities for aestivation and migration) that are different from those of the biota of permanent lotic or lentic habitats, and the "terrestrial" phase also is different from a terrestrial habitat not subject to flooding (e.g. water-borne seeds, strong colonising capability, tolerance of submergence). Junk *et al.* (1989) acknowledge this point, but do not pursue it. In this respect the floodplain is an *ecotone* (*sensu* Holland, 1988) rather than an ecosystem alternating between two unrelated phases.

We suggest that an *eco-floodplain*, as distinct from a *geo-floodplain*, is an area periodically inundated by the 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 floodplain may be defined by the limits of inundation in the lifetime of the longest-lived flood-dependent species.

Floodplains can also be viewed in terms of hierarchical (*sensu* Frissell *et al.*, 1986) spatial and temporal scales with spatial scales in part determined by geomorphological processes (after Salo, 1990). Floodplain macrohabitats reflect morphodynamic zones (sensu Zwolinski, 1992), determined by flow energy and patterns of sedimentation—or *macroprocesses*—which vary laterally across the floodplain. The zone closest to the channel shows the highest morphological variability and contains many *mesohabitats*. These include portions of the main channel, natural levees, chutes, anabranches, backwaters, billabongs, lakes and swamps. They correspond to "channel units" (Sedell

et al., 1990), and are created by geomorphological *mesoprocesses.* Within the mesohabitats are *microhabitats*, including fallen wood, vegetation, patches of sediment types and morphological microfeatures such as crevasse splays and sand shadows. These correspond to "micro-habitat systems" (Poff and Ward, 1990) and "particles" (Sedell *et al.*, 1990), and are created by geomorphological *microprocesses.*

This geomorphological patchiness at various spatial scales (Naiman *et al.*, 1988; Pringle *et al.*, 1988; Sedell *et al.*, 1989), is overlain by and interacts with temporal hydrological patterns. For example, macrohabitats may take on different forms at different pulse stages—a billabong at low flow may become a backwater at higher flow, and later an anabranch. Hydrological events on the floodplain can also be viewed as environmental patches, both in space and time. Flow history essentially constitutes a series of pulse patches, between which organisms may move by diapause and aestivation (cf. Southwood, 1977). Such patches are linked and dependent rather than autonomous. The dynamic diversity of these habitats (compared to the relatively unchanging environment of the main channel) promotes biodiversity and underlies the importance of the floodplain habitat to river processes.

Definition of the Flood Pulse

A "flood pulse" is best defined as an increase in river stage followed by a decrease, whereas a flood is simply an increase in river stage. "Stage" is used in preference to "discharge", as an increase in discharge may not affect water levels, depending on channel morphology, and fluctuations in stage may have greater ecological significance for floodplain-channel interactions (e.g. Grubaugh and Anderson, 1988).

The definition of the flood pulse here is tied to that of the floodplain. If eco-floodplains include parts of the river channel that are periodically inundated, then the definition of a flood pulse should include periods of zero, subsurface and within-channel 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). The flood pulse therefore consists of eight phases (Table 3; cf. Lowe-McConnell, 1987, p 14; Stanley and Fisher, 1992). A river will not go through all phases in every pulse, and regulated rivers will have an additional phase of *stable stage.*

A flood pulse is typically viewed in two dimensions (vertically in space and temporally) (cf. the hydrograph), but really is 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).

A FLOW TEMPLET FOR LARGE RIVERS

In both evolutionary and ecological time, a "physical flow templet" is likely to be the dominant influence on the biota of large rivers (Poff and Ward 1989, p. 1810; Bayley and Li, 1992). The ecological implications of hydrological variability may be incorporated into the FPC *via* a "habitat templet" (cf. Southwood, 1977; 1988). The templet suggested by Southwood (1988) has two axes, one relating to disturbance and the other to adversity.

Axis of Disturbance

In small streams, floods (or spates) are important in structuring plant and animal communities, and are termed "disturbances" (e.g. Fisher *et al.*, 1982; Fisher and Grimm, 1988; Poff and Ward, 1989). In these systems intermediate levels of flood "disturbance" (cf. Intermediate Disturbance Hypothesis; Connell, 1978) are said to be responsible for maintaining high levels of diversity and productivity (Ward and Stanford, 1983). This notion has been extrapolated, somewhat uncritically, to large rivers (cf. Resh *et al.*, 1988; Junk *et al.*, 1989; Reice *et al.*, 1990; Sparks *et al.*, 1990; Bayley, 1991), with the FPC suggesting that the flood pulse is akin to an intermediate disturbance phenomenon, promoting diversity when the pulse is "regular" rather than "unpredictable" (Junk *et al.*, 1989, p. 122).

There are difficulties with using the term "disturbance" to describe the role of flooding in large rivers. There are many definitions of the term (e.g. Sousa, 1984; Pickett and White, 1985; Resh *et al.*, 1988; Sparks *et al.*, 1990; Poff, 1992), and they differ on issues such as whether a disturbance is a discrete event, what distinguishes a disturbance from "normal" variation, and whether a disturbance is unpredictable.

If unpredictability is rejected as a criterion for distinguishing disturbance (following Poff, 1992), how is "disturbance" to be objectively delineated from environmental variation, except by reference to biological response (Rykiel, 1985)? Poff recognizes that "objective measures are needed to identify events that satisfy the criteria provided in the Sousa (1984) or Pickett and White (1985) definitions" (Poff, 1992, p. 87). He suggests specifying physical thresholds for disturbance which have the *potential* to alter specified ecological or ecosystem properties, but how is this potential to be determined,

except by reference to an ecological response? The problem is that the definitions of disturbance which Poff is attempting to satisfy are framed in terms of a biological, ecological or evolutionary response, making them inherently circular.

Used in relation to large rivers, the term "disturbance" perpetuates a misconception that flood events are discrete, and can be considered in isolation. In fact, such events are embedded in an hydrological history which strongly affects their outcome. The thresholds of biological responses to a given event will always depend on past events.

Rather than attempting to partition the hydrological variability of large rivers into "normal" and "disturbance" regimes, river ecologists might more productively begin by describing the full spectrum of components of hydrological variation, and testing biological responses to these components and their combinations (cf. Molles *et al.*, 1992). The designation of biologically significant discontinuities or thresholds may arise from such work (cf. Wiens, 1985).

In relation to the flow templet for large rivers the inclusion of an axis relating to "disturbance" is unjustified. Its inverse, *habitat durational stability* (Southwood, 1988), is also indistinguishable from environmental variability.

Axis of Adversity

Adverse habitats are "those that pose a particular cost for the maintenance of normal protoplasmic homeostasis and the integrity and normal functioning of membranes and enzymes" (Southwood, 1988, p. 12). In this physiological sense, rivers with extreme but constant flow conditions (e.g. torrential flows) and rivers with highly variable flow regimes may both be adverse. Adversity due to extreme flow variation would be incorporated in many of the components of hydrological variability, and adversity due to constant extreme flow conditions would be incorporated in components such as mean discharge, mean pulse frequency, mean pulse duration. It is therefore unnecessary to specify a separate axis of adversity in the flow templet for large rivers.

Flow Templet

In small streams, combinations of flood frequency, flood predictability and overall flow variability have been suggested as the axes of a flow templet (Minshall, 1988; Poff and Ward, 1989). Our analysis suggests that the situation may be more complex in large rivers (cf. Bayley and Li, 1992), with the flow templet being multi-faceted. Templet

axes would represent variations in flood amplitude, flood periodicity (including duration, frequency and seasonality), predictability (including Colwell's measures of "contingency" and "constancy") and some measure of central tendency (e.g. mean discharge) at spatial and temporal scales appropriate to the organisms under study.

For the templet to be predictive, the biological implications of aspects of flow variability need to be established. Hydrological features of flow variability can be related to geomorphic features of the floodplain as well as to biological features, processes and responses (Table 4; adapted from Minshall, 1988; Poff and Ward, 1990; Salo, 1990). At the ecosystem scale aspects of variability in the flood regime may be reflected in processes such as fluxes of nutrients, organic matter and energy (Howard-Williams 1985; Hill *et al.*, 1992; Gibson *et al.*, 1992; Boulton and Lake, 1992; Grimm, in press), and in responses such as the evolution of life history strategies in endemic taxa (Table 5; Junk, 1984; Boulton and Lake, 1988; Schlosser, 1990; Robinson *et al.*, 1992). Variations in flow history will be reflected in community and population dynamics through competition, recruitment and mortality (Table 6; Kushlan, 1976; Holcik and Bastl 1977; Beumer, 1980; Boulton and Lloyd, 1992). Variation in features of a given flood pulse will operate principally at the level of the individual organism, evoking physiological and behavioural responses like spawning and migration (Table 7, Welcomme, 1979; Lowe-McConnell, 1987).

IMPLICATIONS OF INTERVENTION

The spectrum of hydrological variation found in a given river is likely to be a major determinant of the physical habitat templet of that river, and of its evolutionary and ecological characteristics. Human intervention may alter aspects of this templet in a number of ways. Catchment clearance and flow regulation alter flood duration, amplitude and pulse shape (Grubaugh and Anderson, 1988; Walker and Thoms, 1993) while flow regulation affects minimum flows (Thomson, 1992) and pulse frequencies (Carlson and Muth, 1989; Walker and Thoms, 1993). Such changes may produce permanent shifts in ecosystem or community structure and function (Cadwallader, 1986; Regier *et al.*, 1989; Walker *et al.*, 1992).

The complexity of flow variation in large rivers suggests the need for caution when predicting the outcomes of intervention. Although flow regulation may reduce variability at a broad scale (cf. Grossman *et al.*, 1990; Bayley and Li, 1992), it may, at certain time-scales, actually increase some components of variability (Thomson, 1992). Further, intervention may change interactions between temporal and spatial variation;

for example, changes in amplitude variability may alter the pattern of floodplain inundation and affect habitat heterogeneity (Copp, 1991).

Given this complexity, and the rudimentary state of our knowledge of the role of hydrological variability in large lotic systems, alteration in hydrological patterns—either directly through regulation or indirectly through catchment development—should be avoided. Unregulated systems are increasingly rare, and their conservation should be a high priority. Where intervention is unavoidable, a full analysis of the components of the unaltered flow regime, their biological significance, the changes in each component anticipated under regulation or intervention and prediction of the biological effects should be required. "The cost of correcting mistakes in management of the exploitation process is negligible compared to that of correcting or compensating for the effects of permanent changes to the environment ..." (Bayley and Li, 1992, p. 271).

Where regulation or catchment modification have occurred, the restoration of as much as possible of the original spectrum of hydrological variability on a basin-wide scale (Arthington *et al.*, 1991; Bayley, 1991; Naiman *et al.*, 1993) should take precedence over designing flow strategies for particular species groups or segments of the system (cf. Lubinski *et al.*, 1991; Cambray, 1991). The former strategy is more consistent with the growing emphasis on protection of ecosystem processes (Regier *et al.*, 1989; Bayley and Li, 1992). However recovery of the river ecosystem to a pre-intervention state is unlikely because of the lasting effects of intervention in flow history.

ACKNOWLEDGEMENTS

JP and FS have been supported in this work by Australian Postgraduate Research Awards, and AB by an ARC postdoctoral fellowship.

REFERENCES

Allan, R. (1988). Meteorology and Hydrology. pp. 31-50 In Reid, J. and J. Gillen (Eds.) 'The Coongie Lakes Study'. South Australian Department of Environment and Planning, Adelaide.

Amoros, C. and A.L. Roux (1988). 'Interaction between water bodies within the floodplains of large rivers: function and development of connectivity'. pp. 125-130 In Schreiber, K.F. (Ed.), *Connectivity in Landscape Ecology.* Proceedings of 2nd International Seminar of the International Association for Landscape Ecology. Munstersche Geographische Arbeiten, Munster.

Amoros, C., A.L. Roux, J.L. Reygrobellet, J.-P. Bravard and G. Patou (1987). 'A method for applied ecological studies of fluvial hydrosystems'. *Regulated Rivers: Research and Management* **1**: 17-36

Arthington, A.H., S.E. Bunn, B.J. Pusey, D.R. Bluhdorn, J.M. King, J.A. Day, R. Tharme and J.H. O'Keeffe (1991). 'Development of an holistic approach for assessing environmental flow requirements of riverine ecosystems', pp. 69-76 In Pigram, J.J. and B.P. Hooper (Eds.), *Water Allocation for the Environment.* Centre for Water Policy Research, University of New England, Armidale.

Bayley, P.B. (1989). 'Aquatic environments in the Amazon Basin with an analysis of carbon sources, fish production and yield'. *Canadian Special Publications of Fisheries and Aquatic Sciences* **106**: 399-408

Bayley, P.B. (1991). 'The flood pulse advantage and the restoration of river-floodplain systems'. *Regulated Rivers: Research and Management* **6**: 75-86

Bayley, P.B. and H.W. Li (1992). 'Riverine Fishes', pp. 251-281 In Calow, P. and G.E. Petts (Eds.), *The Rivers Handbook,* Vol. 1. Blackwell Scientific Publishers, Oxford.

Beckinsale, R.P. (1969). 'River regimes', pp. 455-471 In Chorley, R. (ed.), *Water, Earth and Man.* Methuen, London.

Benech, V., J.-R. Durand and J. Quensiere (1983). 'Fish communities of Lake Chad and associated rivers and floodplains', pp. 293-356 In Carmouze, J.-P. (Ed.), *Lake Chad.* Dr.W. Junk, The Hague.

Beumer, J.P. (1980). 'Hydrology and fish diversity of a North Queensland tropical stream'. *Australian Journal of Ecology* **5**: 159-186

Boulton, A.J. and P.S. Lake (1988). 'Australian temporary streams—some ecological characteristics'. *Verh. Internat. Verein. Limnol.* **23**: 1380-1383

Boulton, A.J. and L.N. Lloyd (1992). 'Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia'. *Regulated Rivers: Research and Management* **7**: 137-151

Boulton, A.J. and P.S. Lake (1992). 'Benthic organic matter and detritivorous macroinvertebrates in two intermittent streams in southeastern Australia'. *Hydrobiologia* **241**: 107-118.

Brinson, M.M., H.D. Bradshaw and R.N. Holmes (1983). 'Significance of floodplain sediments in nutrient exchange between a stream and its floodplain' pp. 199-221 In Fontaine, T.D. and S.M. Bartell (Eds.), *Dynamics of Lotic Ecosystems.* Ann Arbor, Michigan.

Cadwallader, P.L. (1986). Flow regulation in the Murray River system and its effect on the native fish fauna. pp. 115-133 In Campbell, I.C. (Ed.), *The Management of Rivers for Instream Uses.* Water Studies Centre, Chisholm Institute of Technology, ACT.

Cambray, J.A. (1991). 'The effects of fish spawning and management implications of impoundment water releases in an intermittent South African river'. *Regulated Rivers: Research and Management* **6**: 39-52

Carlson, C.A. and R.T. Muth (1989). 'The Colorado River: lifeline of the American Southwest'. *Canadian Special Publications of Fisheries and Aquatic Sciences* **106**: 220-239

Colwell, R.K. (1974). 'Predictability, constancy and contingency of periodic phenomena'. *Ecology* **55**: 1148-1153

Connell, J.H. (1978). 'Diversity in tropical rainforests and coral reefs'. *Science* **199**: 1302-1310

Copp, G.H. (1991). 'Typology of aquatic habitats in the great Ouse, a small regulated lowland river'. *Regulated Rivers: Research and Management* **6**: 125-134

Erskine, W.D. and R.F. Warner (1988). ' Geomorphic effects of alternating flood - and drought-dominated regimes on New South Wales coastal rivers', pp. 223-244 In Warner, R.F. (Ed.), *Fluvial Geomorphology in Australia*. Academic Press, Sydney.

Falkenmark, M. (1989). 'Comparative hydrology – a new concept', pp. 10-42 In Falkenmark, M. and T. Chapman (Eds.), *Comparative Hydrology*. UNESCO, Paris.

Farquharson, F.A.K., J.R. Meigh and J.V. Sutcliffe (1992). 'Regional flood-frequency analysis in arid and semi-arid areas'. *Journal of Hydrology* **138**: 487-501

Fausch, K.D. and R.G. Bramblett (1991). 'Disturbance and fish communities in intermittent tributaries of a Western Great Plains river'. *Copeia* **1991**: 659-674

Finlayson, B.L. and T.A. McMahon (1988). Australia v the World: A comparative analysis of streamflow characteristics. pp. 17-40 In Warner, R. (Ed.), *Fluvial Geomorphology of Australia*. Academic Press, Sydney.

Fisher, S.G. (1990). 'Recovery processes in lotic ecosystems: limits of successional theory'. *Environmental Management* **14**: 725-736

Fisher, S.G., L.C. Gray, N.B. Grimm and D.E. Busch (1982). 'Temporal succession in a desert stream ecosystem following flash flooding'. *Ecological Monographs* **52**: 93-110

Fisher, S.G. and N.B. Grimm (1988). 'Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem'. *Verhandlungen der Internationale Vereinigung fur Theoretische und Angewandt Limnologie* **23**: 1183-1189

Friedel, M.H., G.Pickup and D.J. Nelson (in press). 'The interpretation of vegetation change in a spatially and temporally diverse arid Australian landscape'. *Journal of Arid Environments*.

Frissell, C.A., W.J. Liss, C.E. Warren and M.D. Hurley (1986). 'A hierarchical framework for stream habitat classification: viewing streams in a watershed context'. *Environmental Management* **10**: 199-214

Gibson, K.S., P.A. Chambers and E.E. Prepas (1992). 'The role of discharge rate and riverbed composition in determining porewater phosphorus concentrations in an unregulated river in Alberta, Canada', pp. 267-268 In Robarts, R.D. and M.L. Bothwell (Eds.), *Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management.* Environment Canada, Saskatoon.

Graf, W.L. (1988). 'Definition of the floodplains along arid region rivers', pp. 231-242 In Baker, V.R., R.C. Kochel and P.C. Patton (Eds.), *Flood Geomorphology.* Wiley, New York.

Gregory, S.V., F.J. Swanson, W.A. McKee and K.W. Cummins (1991). 'An ecosystem perspective of riparian zones'. *Bioscience* **41**: 540-551

Grimm, N.B. (in press). 'Biogeochemistry of nitrogen in Sonoran Desert streams'. *Journal of the Arizona-Nevada Academy of Science.*

Grossman, G.D., J.F. Dowd and M. Crawford (1990). 'Assemblage stability in stream fishes: a review'. *Environmental Management* **14**: 661-671

Grubaugh, J.W. and R.V. Anderson (1988). 'Spatial and temporal availability of floodplain habitat: long-term changes at Pool 19, Mississippi River'. *American Midland Naturalist* **119**: 402-411

Gustard, A. (1992). 'Analysis of river regimes', pp. 29-47 In Calow, P. and G.E. Petts (Eds.), *The Rivers Handbook*, Vol.1. Blackwell Scientific Publishers, Oxford.

Hill, B.H., T.J. Gardner and O.F. Ekisola (1992). 'Predictability of streamflow and particulate organic matter concentration as indicators of stability in prairie streams'. *Hydrobiologia* **242**: 7-18

Holcik, J. and I. Bastl (1977). 'Predicting fish yield in the Czechoslovakian section of the Danube River based on the hydrological regime'. *Int. Revue ges. Hydrobiol.* **62**: 523-532

Holland, M.M. (1988). 'SCOPE/MAB technical consultations on landscape boundaries: report of Scope/MAB workshop on ecotones'. *Biology International Special Issue* **17**: 47-106

Horwitz, R.J. (1978). 'Temporal variability patterns and the distributional patterns of stream fishes'. *Ecological Monographs* **48**: 307-321

Howard-Williams, C. (1985). 'Cycling and retention of nitrogen and phosphorus in wetlands: a theoretical and applied perspective'. *Freshwater Biology* **15**: 391-431

Junk, W.J. (1984). 'Ecology of the Varzea floodplain of the Amazonian white-water rivers'. pp. 215 In Sioli, H. (Ed.), *The Amazon*. Junk, Dordrecht, Netherlands.

Junk, W.J., P.B. Bayley and R.E. Sparks (1989). 'The Flood Pulse Concept in river-floodplain systems'. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 110-127

Junk, W.J. and R.L. Welcomme (1990). Floodplains. pp. 491-524 In Patten, B.C.(Ed.) Wetlands and Shallow Continental Water Bodies, Vol.1. SPB Academic Publishing, The Hague.

Kodric-Brown, A. (1981). 'Variable breeding systems in pupfishes (Genus *Cyprinodon*): adaptation to changing environments', pp. 205-235 In Naiman, R.J. and D.L. Soltz. (Eds.), *Fishes in North American Deserts*. Wiley, New York.

Kotwicki, V. (1986). *Floods of Lake Eyre*. South Australian Engineering and Water Supply Department, Adelaide.

Kresan, P.L. (1988). 'The Tucson, Arizona flood of October 1983', pp. 465-489 In Baker, V.R., R.C. Kochel and P.C. Patton.(Eds.) Flood Geomorphology. Wiley, New York.

Kushlan, J.A. (1976). 'Environmental stability and fish community diversity'. *Ecology* **57**: 821-825

Livdahl, T.P. (1979). 'Environmental uncertainty and selection for life-cycle delays in opportunistic species'. *American Naturalist* **113**: 835-842

Lowe-McConnell, R.H. (1987). *Ecological Studies in Tropical Fish Communities.* Cambridge University Press, Cambridge.

Lubinski, K.S., G. Carmody, D. Wilcox and B. Drazkowski (1991). 'Development of water level regulation strategies for fish and wildlife, Upper Mississippi River system'. *Regulated Rivers: Research and Management* **6**: 117-124

McArthur, J.V. (1988). 'Aquatic and terrestrial linkages: floodplain functions', pp. 107-116 In Hook, D. and R. Lea (Eds.), *Forested Wetlands of the Southern United States.* USDA Forest Service, .

McMahon, T.A. (1979). 'Hydrological characteristics of arid zones', pp. 105-123 In *The Hydrology of Areas of Low Precipitation.* IAHS-AISH, Canberra.

McMahon, T.A. and B.L. Finlayson (1991). Australian surface and groundwater hydrology - regional characteristics and implications. pp. 21-41 In Pigram, J.J. and B.P. Hooper (Eds.), *Water Allocation for the Environment.* Centre for Water Policy Research, University of New England, Armidale.

Minshall, G.W. (1988). 'Stream ecosystem theory: a global perspective'. *Journal of the North American Benthological Society* **7**: 263-288

Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell and R.L. Vannote (1985). 'Developments in stream ecosystem theory'. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1045-1055

Molles, M.S.J., C.N. Dahm and M.T. Crocker (1992). 'Climatic variability and streams and rivers in semi-arid regions', pp. 197-202 In Robarts, R.D. and M.L. Bothwell (Eds.) *Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management.* Environment Canada, Saskatoon.

Naiman, R.J., H. Decamps, J. Pastor and C.A. Johnston (1988). 'The potential importance of boundaries to fluvial ecosystems'. *Journal of the North American Benthological Society* **7**: 289-306

Naiman, R.J., H. Decamps and M. Pollock (1993). 'The role of riparian corridors in maintaining regional biodiversity'. *Ecological Applications* **3**: 209-212

Neckles, H.A., H.R. Murkin and J.A. Cooper (1990). 'Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats'. *Freshwater Biology* **23**: 311-322

Newbold, J.D., J.W. Elwood, R.V. O'Neill and W. Van Winkle (1981). 'Measuring nutrient spiralling in streams'. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 860-863

Nicholls, N. (1989). 'How old is ENSO?' *Climate Change* **14**: 111-115

Pearson, T.N., H.W. Li and G.A. Lamberti (1992). 'Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages'. *Transactions of the American Fisheries Society* **121**: 427-436

Pickett, S.T.A. and P.S. White (1985). 'Patch dynamics: a synthesis', pp. 371-384 In *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, New York.

Pickup, G. (1991). 'Event frequency and landscape stability on the floodplain systems of arid Central Australia'. *Quaternary Science Reviews* **10**: 463-473.

Poff, N.L. (1992). 'Why disturbances can be predictable: a perspective on the definition of disturbance in streams'. *Journal of the North American Benthological Society* **11**: 86-92

Poff, N.L. and J.V. Ward (1989). 'Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns'. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1805-1818

Poff, N.L. and J.V. Ward (1990). 'Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity'. *Environmental Management* **14**: 629-645

Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme and M.J. Winterbourn (1988). 'Patch dynamics in lotic systems: the stream as a mosaic'. *Journal of the North American Benthological Society* **7**: 503-524

Quiros, R. and S. Cuch (1989). 'The fisheries and limnology of the Lower Plata Basin'. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 429-443

Regier, H.A., R.L. Welcomme, R.J. Steedman and H.F. Henderson (1989). 'Rehabilitation of degraded river ecosystems'. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 86-97

Reice, S.R., R.C. Wissmar and R.J. Naiman (1990). 'Disturbance regimes, resilience and recovery of animal communities and habitats in lotic ecosystems'. *Environmental Management* **14**: 647-659

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace and R. Wissmar (1988). 'The role of disturbance in stream ecology'. *Journal of the North American Benthological Society* **7**: 433-455

Robinson, C.T., L.M. Reed and G.W. Minshall (1992). 'Influence of flow regime on life history, production, and genetic structure of *Baetis tricaudatus* (Ephemeroptera) and *Hesperoperla pacifica* (Plecoptera)'. *Journal of the North American Benthological Society* **11**: 278-289

Rodier, J.A. (1985). 'Aspects of Arid Zone Hydrology', pp. 205-247 In Rodda, J.C.(Ed.) *Facets of Hydrology*, Vol.2. Wiley, Chichester.

Rykiel, E.J. (1985). 'Towards a definition of ecological disturbance'. *Australian Journal of Ecology* **10**: 361-365

Salo, J. (1990). 'External processes influencing origin and maintenance of water-land ecotones', pp. 37-64 In Naiman, R.J. and H. Decamps.(Eds.), *The Ecology and Management of Aquatic-Terrestrial Ecotones.* Parthenon, Paris.

Schick, A.P. (1988). 'Hydrologic aspects of floods in extreme arid environments', pp. 189-203 In Baker, V.R., R.C. Kochel and P.C. Patton (Eds.), *Flood Geomorphology.* Wiley, New York.

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

Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford and C.P. Hawkins (1990). Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* **14**: 711-724

Sedell, J.R., J.E. Richey and F.J. Swanson (1989). 'The River Continuum Concept: a basis for the expected ecosystem behaviour of very large rivers?' *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 49-55

Smock, L.A., J.E. Gladden, J.L. Riekenberg, L.C. Smith and C.R. Black (1992). 'Lotic macroinvertebrate production in three dimensions: channel surface, hyporheic, and floodplain environments'. *Ecology* **73**: 876-886

Sousa, W.P. (1984). 'The role of disturbance in natural communities'. *Annual Review of Ecology and Systematics* **15**: 353-391

Southwood, T.R.E. (1977). 'Habitat, the templet for ecological strategies'. *Journal of Animal Ecology* **46**: 337-365

Southwood, T.R.E. (1988). 'Tactics, strategies and templets'. *Oikos* **52**: 3-18

Sparks, R.E., P.B. Bayley, S.L. Kohler and L.L. Osborne (1990). 'Disturbance and Recovery of Large Floodplain Rivers'. *Environmental Management* **14**: 699-709

Stanley, E.H. and S.G. Fisher (1992). 'Intermittency, disturbance and stability in stream ecosystems'. pp. 271-280 In Robarts, R.D. and M.L. Bothwell (Eds), *Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management.* Environment Canada, Saskatoon.

Thomson, C. (1992). *The impact of river regulation on the natural flows of the Murray-Darling Basin.* Murray-Darling Basin Commission, Canberra.

UNESCO (1971). *Discharge of Selected Rivers of the World*, Vol.2. UNESCO, Paris.

Vannote, R.L., C.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing (1980). 'The River Continuum Concept'. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137

Vogl, R.J. (1980). 'The ecological factors that produce perturbation-dependent ecosystems', pp. 63-94 In Cairns, J. (Ed.), *The Recovery Process in Damaged Ecosystems.* Ann Arbor Science, Ann Arbor, Michigan.

Walker, K.F. and M.C. Thoms (1993). 'A case history of the environmental effects of flow regulation on a semi-arid lowland river: the River Murray, South Australia'. *Regulated Rivers: Research and Management* **7**: 103-119

Walker, K.F., M.C. Thoms and F. Sheldon (1992). 'Effects of weirs on the littoral environment of the River Murray, South Australia', pp. 271-292 In Boon, P.J., P. Calow and G.E. Petts (Eds.), *River Conservation and Management.* Wiley, New York.

Ward, J.V. (1989). The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society **8**: 2-8

Ward, J.V. and J.A. Stanford (1983). 'The Intermediate Disturbance Hypothesis: an explanation for biotic diversity patterns in lotic ecosystems', pp. 347-356 In Fontaine, T.D. and S.M. Bartell.(Eds.), *Dynamics of Lotic Ecosystems.* Ann Arbor Science, Ann Arbor, Michigan.

Ward, J.V. and J.A. Stanford (1989). 'Riverine ecosystems: the influence of man on catchment dynamics and fish ecology'. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 56-64

Welcomme, R.L. (1979). *Fisheries Ecology of Floodplain Rivers.* Longman, London.

Welcomme, R.L. (1988). 'Concluding remarks I: On the nature of large tropical rivers, floodplains and future research directions'. *Journal of the North American Benthological Society* **7**: 525-526

Welcomme, R.L. (1989). 'Review of the present state of knowledge of fish stocks and fisheries of African rivers'. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 515-532

Welcomme, R.L. and D. Hagborg (1977). 'Towards a model of a floodplain fish population and its fishery'. *Environmental Biology of Fishes* **2**: 7-24

Wiens, J.A. (1985). 'Vertebrate responses to environmental patchiness in arid and semiarid ecosystems', pp. 169-193 In Pickett, S.T.A. and P.S. White (Eds), *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, New York.

Winterbourn, M.J. (1982). 'The River Continuum Concept—reply to Barmuta and Lake'. *New Zealand Journal of Marine and Freshwater Research* **16**: 229-231

Winterbourn, M.J., J.S. Rounick and B. Cowie (1981). 'Are New Zealand stream ecosystems really different?' *New Zealand Journal of Marine and Freshwater Research* **15**: 321-328

Zwolinski, Z. (1992). 'Sedimentology and geomorphology of overbank flows on meandering river floodplains'. *Geomorphology* **4**: 367-379

Table I.

	Site	Years	Area (km^2)	Mean Discharge (m^3s^{-1})
Chari River	Fort Lamy	1937-1962	600000	15007.26
Columbia River	The Dalles	1880-1899	614000	74141.85
Cooper Creek	Cullyamurra	1973-1992	236700	1700.86
River Danube	Orsova	1850-1869	578300	61127.75
Diamantina River	Birdsville	1967-1986	115000	1216.63
Darling River	Wilcannia	1924-1943	569800	1163.05
Krishna River	Vijayawada	1902-1920	251355	20674.55
Mekong River	Mukdahan	1925-1944	391000	100727.8
Mississippi River	Alton III	1928-1947	444200	32239.75
River Murray	Lock 6	1902-1921	1073000	9030.52
Niger River	Dire	1925-1944	340000	13928.6
Parana River	Guaira	1921-1940	806000	101807
Syr-Darya River	Tyumen-Aryk	1949-1964	219000	8389.62
Winnipeg River	Slave Falls	1927-1946	124000	9167.05
Don River	Razdorskaya	1891-1910	378000	9751.6
Darling River*	Wilcannia	1960-1979	569800	2281.6
River Murray*	Lock 6	1970-1989	1073000	6959.4

*regulated

Table II.
Components of variability and predictability used in the ordination analysis (CV = Coefficient of Variation). A "pulse" is a rise and fall in monthly discharge. The three components of predictability were computed according to Colwell (1974)

Components of Variability	Components of Predictability
CV of all annual CVs	Index of Contingency
CV of all monthly CVs	Index of Constancy
CV of monthly peak discharge	Index of Predictability
CV of monthly minimum discharge	
CV of amplitude of falling limb of pulse	
CV of amplitude of rising limb of pulse	
CV of months between low flows[1]	
CV of number of floods per year	
CV of mean annual discharge	
CV of mean discharge over three years	
CV of mean discharge over five years	
CV of timing of flows each year[2]	
% of months of zero flow	
Mean of CVs of monthly discharges	
Mean of CVs of annual discharges	

[1]Pulse duration
[2]CVof the number of floods in each month. A high value signifies regular flooding.

Table III.
The eight phases of a hypothetical flood-pulse.

1	Dry	
2	Hyporheic Rising	Subsurface flow rising within the riverbed
3	Channel Rising	Surface flow rising within the 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 the channel
8	Hyporheic Receding	Subsurface flow receding within the riverbed

Table IV.
A framework relating hydrological and geomporphic features at various scales to biological processes and responses. "Scale" is a rough guide, dependent on the life-span and spatial range of the target organism(s) or system(s).

Feature			Process	Response	Scale	
Geomorphic	Hydrological	Biological	Biological	Biological	Spatial (m^2)	Temporal (y)
Macroform	Components of river flow regime	Ecosystem	Fluxes of nutrients, energy	Evolutionary: life-history strategies	$>10^5$	$>10^2$
Mesoform (Events in local flow history)		Community, population	Competition, recruitment, mortality	Ecological: changes in community structure	10^3 - 10^8	1 - 10^2
Microform	Instantaneous features of flood pulse	individual	Life-history strategies	Physiological, Behavioural: diapause, migration, reproduction.	$< 10^4$	<1

Table V.

Responses to variation in the flow regime

Variation	Life-history implications
High timing variability	Bet-hedging
High duration variability	Brief life-cycles
High amplitude variability	Mobility, periodicity
Long periods of zero flow	Broad physiological tolerances
High spatial variability	High endemicity, mobility
Low predictability	Opportunism, generalism
Significant surface drying	Mobility, diapause

Table VI.

Responses to variation in flow history

Variation	Community and population responses
Protracted dry at surface	Populations and diversity decline, populations age, resting stages decline
Protracted zero flow	Relative increase in lentic species, populations and diversity decline, few cohorts
Repeated low flows	Enhanced competition, relative increase in predators, many small cohorts
Recent extreme flood	One dominant year-class, high population densities, high diversity
Repeated high flow	Decline in opportunistic species, decline in recruitment , reduced diversity

Table VII.
Responses to variation in the flood pulse

Variation	Behavioural and physiological responses
Extreme flood peak	Strong migration and breeding
Steep rising limb	Flood refuge seeking, strong downstream displacement
Steep falling limb	Avoidance of floodplain, breeding reduced
Extreme drawdown	Refuge seeking, physiological stress, reduction of feeding
Localized flooding	Weak breeding, weak migration, physiological stress
Large area flooded	Strong emergence, migration, feeding and breeding
Cessation of flow	Cessation of migration and displacement, physiological stress
Surface drying	Development of resting stages, retreat to hyporheic zone

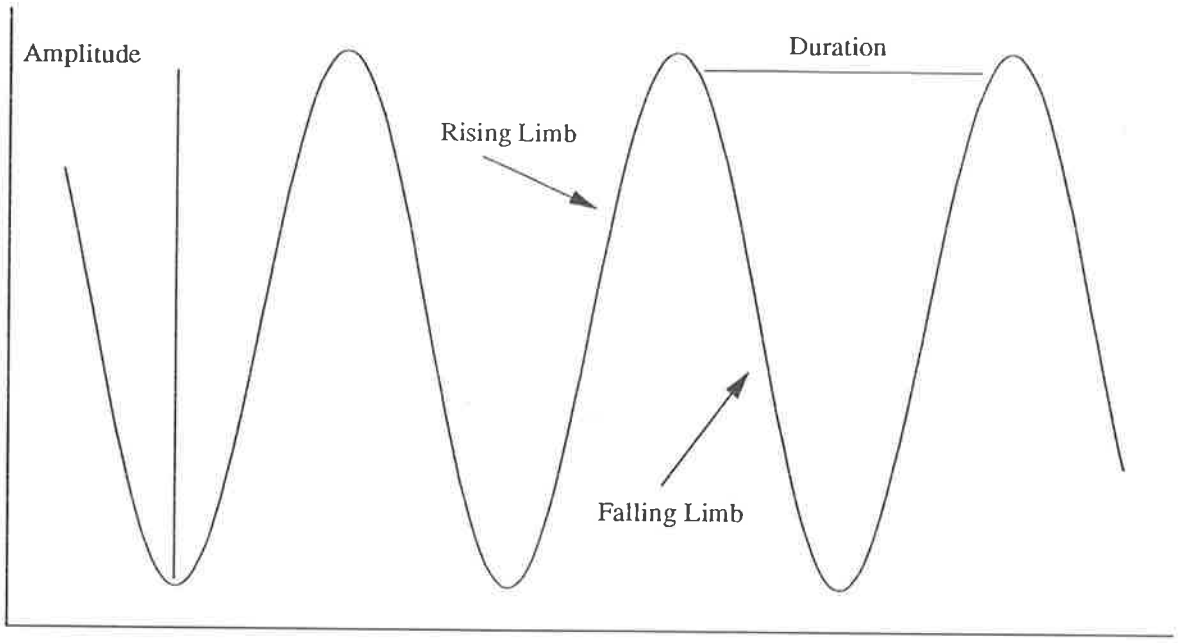
Figure Legends

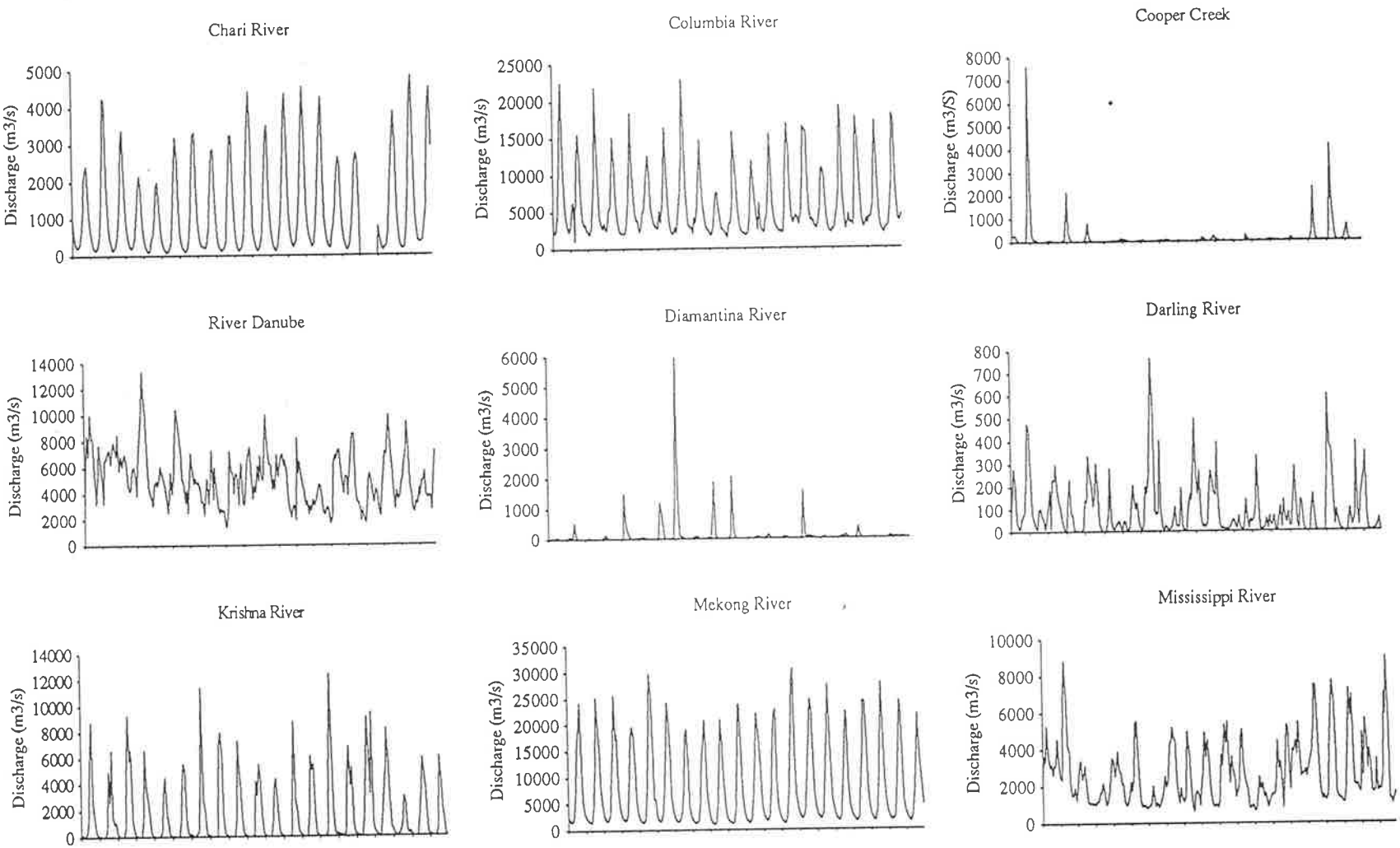
Figure I.
Idealised hydrograph depicting a sequence of flood pulses at a given point on a river.

Figure II.
Twenty-year hydrographs of mean monthly discharge for 15 rivers, including pre- and post-regulation hydrographs of the Australian River Murray and Darling River.

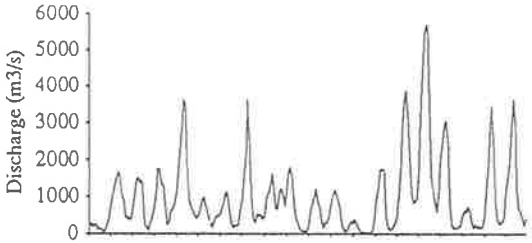
Figure III.
Profiles for each river of the coefficients variation and Colwell's indexes of predictability, constancy and contingency.

Figure IV.
PCA plot for the 15 rivers. Rivers are denoted "CH", Chari River; "CL". Columbia River; "CO", Cooper Creek; "DN", River Danube; "DM", Diamantina River; "DL", Darling River; "KR", Krishna River; "MK", Mekong River; "MS", Mississippi River; "MY", River Murray; "NG", Niger River; "PR", Parana River; "SD", Syr-Darya River; "WN", Winnipeg River; "DO", Don River; "DR", Darling River (Regulated); "MR", Murray River (Regulated).

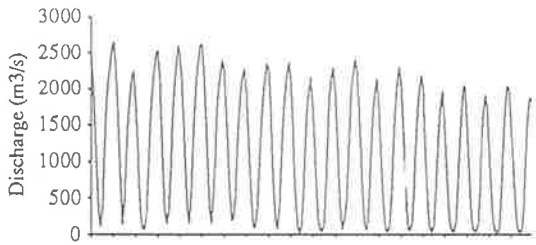

Amplitude
Duration
Rising Limb
Falling Limb


Chari River
Discharge (m3/s)
5000
4000
3000
2000
1000
0
Columbia River
Discharge (m3/s)
25000
20000
15000
10000
5000
0
Cooper Creek
Discharge (m3/S)
8000
7000
6000
5000
4000
3000
2000
1000
0
River Danube
Discharge (m3/s)
14000
12000
10000
8000
6000
4000
2000
0
Diamantina River
Discharge (m3/s)
6000
5000
4000
3000
2000
1000
0
Darling River
Discharge (m3/s)
800
700
600
500
400
300
200
100
0
Krishna River
Discharge (m3/s)
14000
12000
10000
8000
6000
4000
2000
0
Mekong River
Discharge (m3/s)
35000
30000
25000
20000
15000
10000
5000
0
Mississippi River
Discharge (m3/s)
10000
8000
6000
4000
2000
0

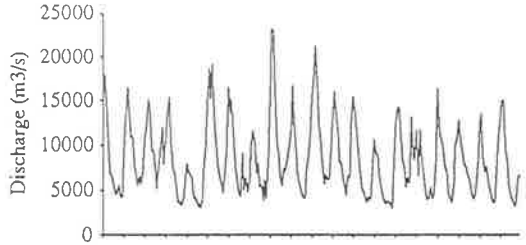
River Murray



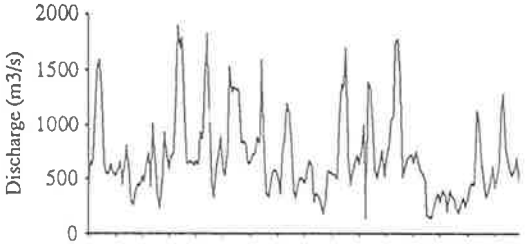
Niger River



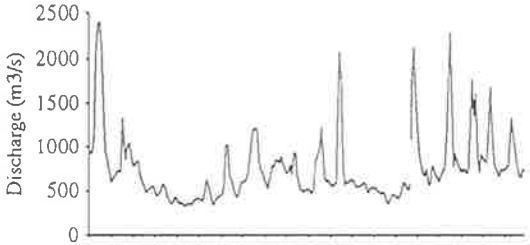
Parana River



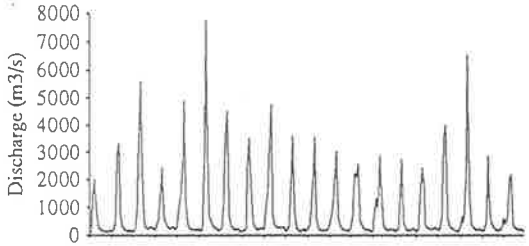
Syr-Darya River



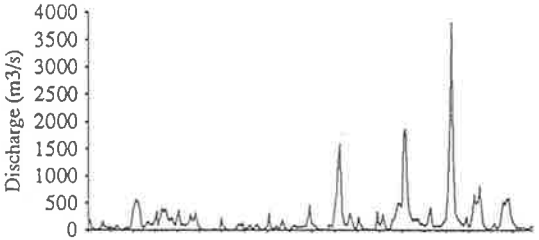
Winnipeg River



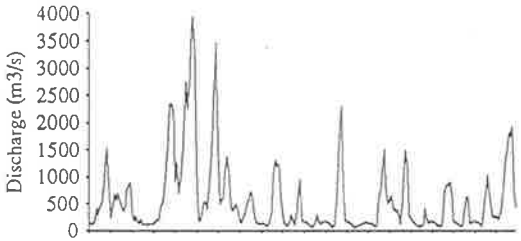
Don River

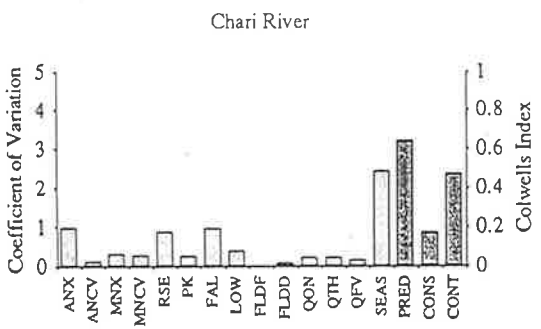


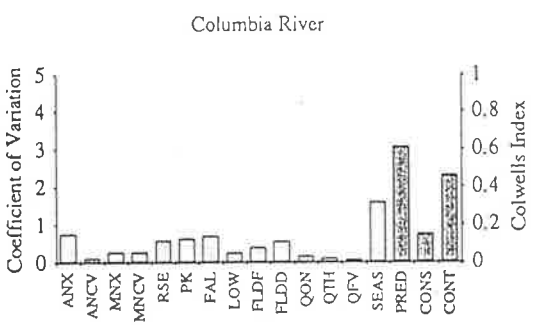
Darling River (Regulated)

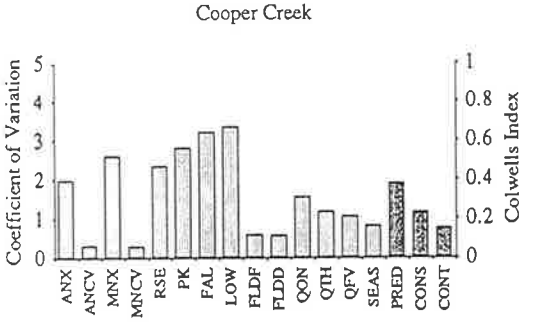


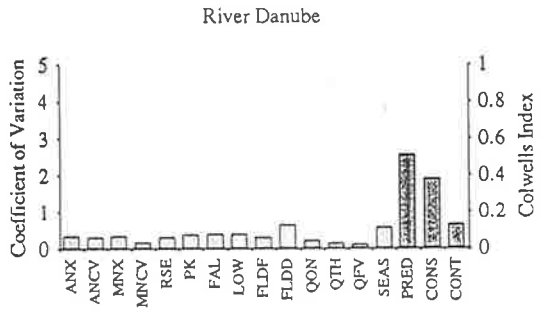
River Murray (Regulated)

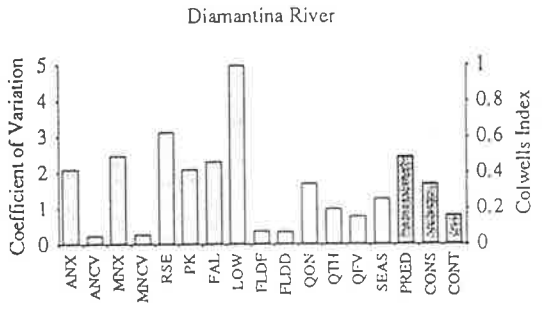


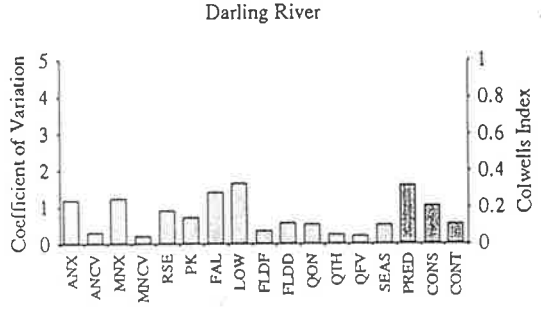

Chari River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

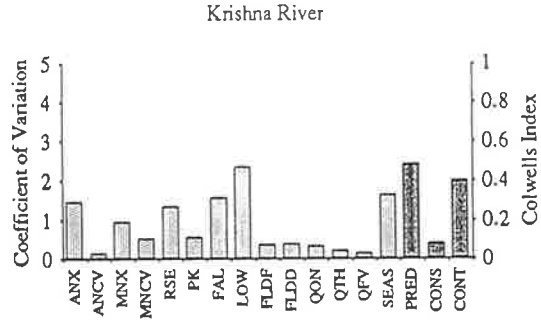

Columbia River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

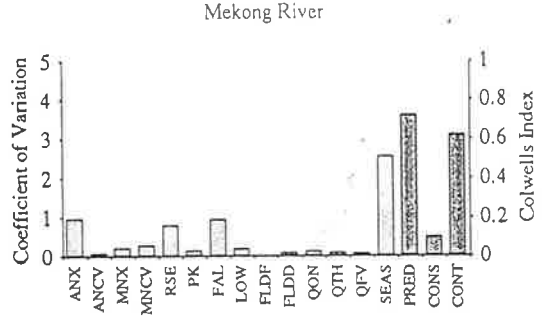

Cooper Creek
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

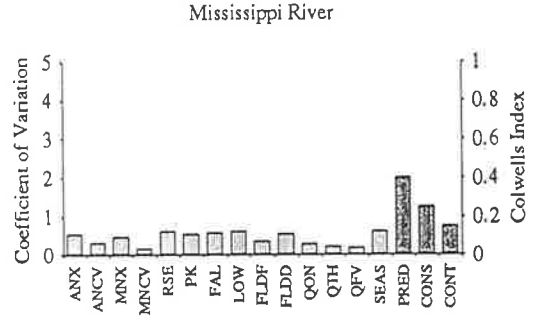

River Danube
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT


Diamantina River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

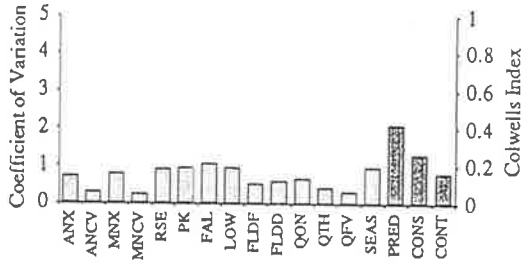

Darling River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT


Krishna River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

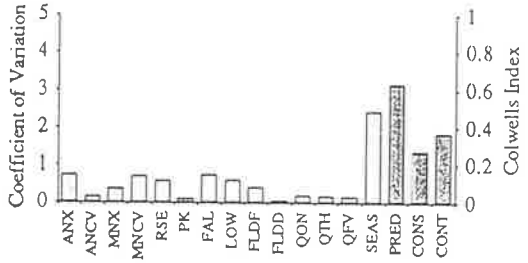

Mekong River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT


Mississippi River
Coefficient of Variation
Colwells Index
ANX ANCV MNX MNCV RSE PK FAL LOW FLDF FLDD QON QTH QFV SEAS PRED CONS CONT

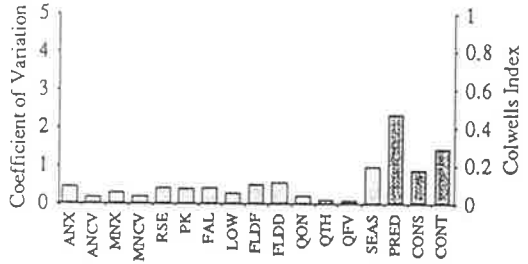
River Murray



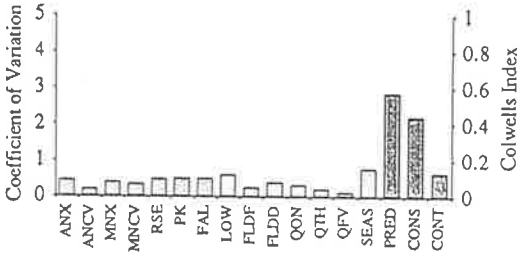
Niger River



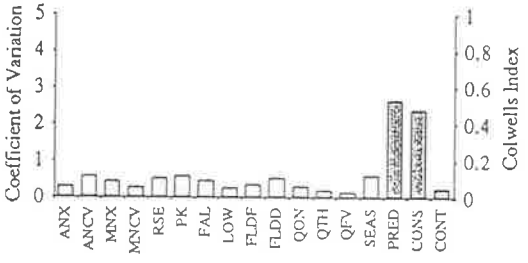
Parana River



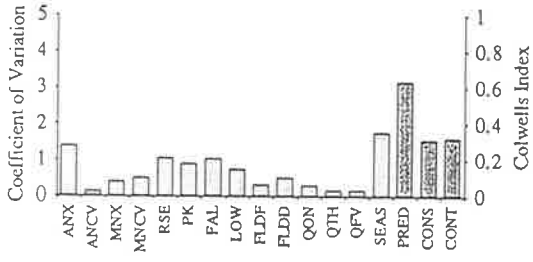
Syr-Darya River



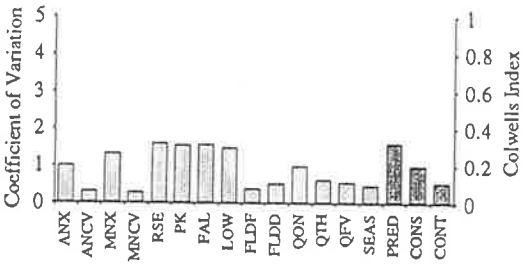
Winnipeg River



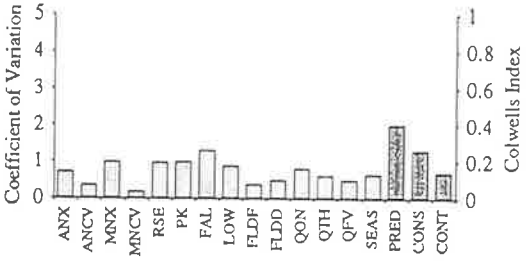
Don River

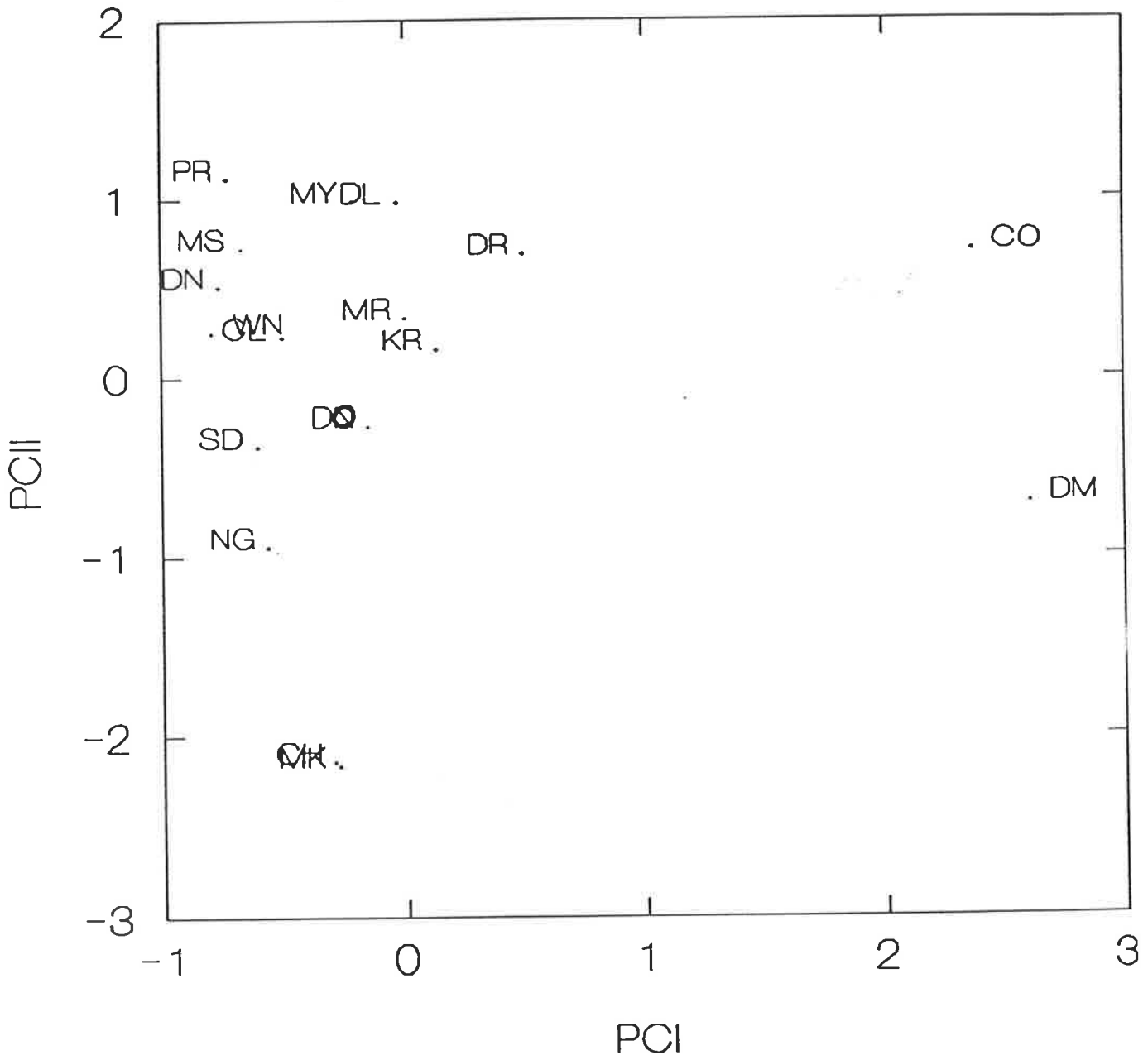


Darling River (Regulated)



River Murray (Regulated)




2
1
0
-1
-2
-3
-1
0
1
2
3
PCII
PCI
PR.
MYDL.
MS.
DR.
CO.
DN.
MR.
KR.
SD.
DM.
NG.