



Flow related variation in diets of Murray-Darling fish

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Report No. 2/2002



1 Introduction

Fish communities in the Murray Darling Basin have been significantly impacted by human activities in the 200 years since European settlement. The severity of the impact has been realised through the extinction of species, the contraction of ranges and reduced abundances leading to isolated and/or unsustainable populations. There has been a dramatic decline in most of the 42 native fish species historically recorded in the basin (Cadwallader 1986).

The current status of Murray-Darling fish species is of real concern. Native fish populations are estimated at only 10% of pre-European settlement levels (Murray-Darling Ministerial Council 2002) and fish diversity has diminished to only 33 native species (Cottingham *et al.* 2001a). Eight of these species are classed as nationally threatened (critically endangered, endangered, vulnerable or lower risk) under the International Union for the Conservation of Nature Red List of Threatened Species (IUCN 2000), indicating concern over their future. A recent review recommended that trout cod *Maccullochella macquariensis* (endangered to critically endangered), silver perch *Bidyanus bidyanus*, Murray jollytail *Galaxias rostratus* (vulnerable to endangered), and southern purple-spotted gudgeon *Mogurnda adspersa* (lower risk to endangered) be upgraded and a further seven species listed as threatened (Morris *et al.* 2001).

Commercial fisheries species that were once widespread are now absent in many parts of the basin and listed as threatened by IUCN, including silver perch, trout cod, catfish *Tandanus tandanus*, and Murray cod *Maccullochella peeli*. For instance, there is now only one natural population of the once widespread trout cod in the Murray-Darling Basin (Douglas *et al.* 1994). Further, in the recent NSW River Survey, only eight silver perch were recorded in four rivers, three of which are regularly stocked with fingerlings (Harris and Gehrke 1997). In the same survey no Murray cod or catfish were caught in the Murray region (Gehrke and Harris 2001). Unless significant improvement of Murray-Darling river systems is achieved, the alarming rate of decline of native fish species will continue (Morris *et al.* 2001).

To compound the problem, the system has been invaded by 11 alien species that have now formed self-sustaining populations (Harris 1995). These species can impact native fish species through competition for resources, predation, introduction of diseases and indirect environmental effects (Fletcher 1986). In particular, the common carp *Cyprinus carpio* has

significantly extended its range since introduction of the Boolarra strain in the 1960s and is now having widespread destructive effects on native fish and habitat (Koehn *et al.* 2000).

The decline in native fish populations has been attributed to a variety of factors including, flow modification (Gehrke *et al.* 1995), loss of habitat (Crook and Robertson 1999), alien species, barriers to migration (Morris *et al.* 2001) and over-exploitation (Cadwallader and Lawrence 1990). All of these factors have contributed, but it is the widespread modification of flow within the basin that has had the most significant impacts on fish native populations (Morris *et al.* 2001).

The lives of fish are controlled by flow (Humphries *et al.* 2002) with the presence of suitable habitat, ability to complete their life history and the availability of food all affected by flow conditions (Arthington 1992; Humphries *et al.* 1999). The relationships between flow and habitat (e.g. Stalnaker *et al.* 1996; Crook and Robertson 1999; Lamouroux *et al.* 1999) and flow and life history (e.g. Geddes and Puckridge 1989; Humphries *et al.* 1999; Humphries *et al.* 2002) have been investigated, and despite a growing body of information on the diets of fish species (Kennard *et al.* 2001), little is known of the relationship between flow and fish diet.

The bottom-up template of lowland river models (e.g. river continuum concept, flood pulse concept and riverine productivity model) emphasises the importance of food abundance and availability to the survival and health of fish communities (Vannote *et al.* 1980; Junk *et al.* 1989; Thorp and Delong 1994; Thorp and Delong 2002). Investigations of flow-food resource relationships are, therefore, necessary to indicate the flow requirements to ensure an adequate food supply to support healthy native fish populations. This information will assist river managers to design and implement effective environmental flow strategy.

The majority of native fish in the Murray-Darling Basin are carnivorous feeding predominantly on aquatic insects (Kennard *et al.* 2001). Microcrustacean, molluscs, large crustaceans, algae and fish are other common dietary items. Terrestrial materials represent an important source of food, particularly for surface feeders (Pusey and Kennard 1995). Murray-Darling fish species are largely opportunistic (Koehn and O'Connor 1990), switching between these food sources (benthic, pelagic and terrestrial) in response to temporal, spatial and environmental influences and by ontogenetic changes. Diets are also constrained by flow related impacts on prey availability and abundance.

The temporal and spatial variation in productivity and food availability in river systems is reflected in the diets of fish species (Kennard *et al.* 2001). Dietary composition varies on large spatial scales (e.g. regional and between rivers) but variation may also be evident on localised levels (e.g. open water and littoral zone within river). Seasonal environmental variation (predominantly temperature) also appears to affect food availability. The warm summer flows experienced in the basin are conducive to increased microcrustacean (Nielsen *et al.* 2002) and macroinvertebrate diversity and abundance (Nielsen *et al.* 1999), leading to greater food availability relative to winter conditions. The availability of allochthonous material may be seasonally dependent, and this would influence its contribution to fish diet (Pusey and Kennard 1995).

Ontogenetic variation influences the food requirements of Murray-Darling fish species, with juvenile and adult large-bodied species having different dietary compositions (Kennard *et al.* 2001). As they develop from juvenile to adults, morphological changes (e.g. increased gape size) allow fish to consume larger prey items. Juvenile fish feed predominantly on microcrustacean and aquatic insects, whilst macrocrustaceans and fish make a large contribution to the diet of adults.

Despite the lack of quantitative data on the effects of changes in flow on fish diets, if fish are dietary generalists, it would appear reasonable to predict that flow would significantly affect fish diets because it has an impact on prey communities.

Microcrustaceans have been found to be heavily impacted by flow regime with highest abundances occurring during periods of low flow (Pace *et al.* 1992). Microcrustacean biomass is believed to be negatively correlated with flow (Thorp and Delong 1994) so as flow increases it is anticipated that microcrustacean biomass will decline and its importance as a food source will diminish. However, the decline may not be as pronounced with recent evidence suggesting that, despite rises in flow in the main channel (Dettmers *et al.* 2001), backwaters are created, which can still support high abundances of microcrustaceans (Spaink *et al.* 1998; Tans *et al.* 1998; Viroux 1999; Dettmers *et al.* 2001). Over bank flooding of lowland rivers, produces a lateral expansion of the temporary aquatic habitat (Goulding 1980; Lowe-McConnell 1985; Junk *et al.* 1989; Ward 1989) supporting a massive boom in microcrustacean biomass (Nielsen *et al.* 2002) and sustain fish, particularly juveniles (Geddes and Puckridge 1989; Humphries *et al.* 1999)

Macroinvertebrate communities are also strongly influenced by flow (Young 2001). In low flow conditions, benthic and snag dwelling macroinvertebrates are found in high concentrations. Rising flow levels lead to an enhancement of invertebrate habitat, through immersion of snags and increases in litter, ensuring that aquatic insects continue to be an important food resource. During flood conditions, the increased primary and secondary production (Goulding 1980; Lowe-McConnell 1985; Robertson *et al.* 1999), leads to a greater abundance and diversity of aquatic insects on the floodplain (Boulton 1999).

Fluctuating flow levels influence the contribution of allochthonous inputs to the diets of fish. As flow levels increase, the contribution of allochthonous inputs increases with litter and terrestrial organisms on benches and other previously dry areas, becoming available. During flood conditions, these inputs are greatest and are likely to contribute considerably to diet. On average, allochthonous inputs represent 10% of the diet of Australia fish species, but the contribution is highly variable (Pusey and Kennard 1995).

Objectives

1. To determine the spatial and temporal variation in the diets of common fish,
2. To examine the relationship between flow regime and the food resources of fish communities,
3. To evaluate the food requirements of common fish species and determine the role of particular food types in structuring native fish communities, and
4. To provide specific environmental flow recommendations to enhance the food availability for native fish species.
5. The project will provide managers with a significant knowledge to help in the design and implementation of environmental flows.

This project used two techniques (direct gut analysis and stable isotope analysis) to determine the diets of native species at three sites under base flow, rising flow, bank full flow and during or immediately after a flood. Stable isotopes such as $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and, to a lesser extent, $\delta^{34}\text{S}$ have increasingly been used to analyse aquatic food web structure (e.g. Peterson *et al.* 1985; Sullivan and Moncrieff 1990; Bunn and Boon 1993) because they give an estimate that is integrated over the last few months of the fish's life, which offers unique insights into the diets of aquatic animals.

only 10% of discharge is annually diverted, during the duration of our sampling the Broken River was extremely regulated with predominately base flow conditions present.

The riparian zone of the Broken River is riverine grassy woodland, dominated by River Red gum *Eucalyptus camaldulensis*, which contribute high numbers of in-channel fallen trees and snags. Silver wattle *Acacia dealbata* and sedges and grasses form an understorey while willows *Salix*. spp. occur occasionally. The study area has been cleared for agriculture and the riparian zone can be restricted to single tree width.

Characteristic in-channel macrophytes include common reed *Phragmites australis* occurring in patches at the water line and on river banks, and the occasional occurrence of emergent water ribbons *Triglochin* sp. and ribbon weed *Vallisneria* sp in slow-flowing patches near the channel margin.

There have been no formal studies of the geomorphology the Broken River, however, limited published information and anecdotal reports suggests that the geomorphology has been affected by previous 'river improvements'. Snag removal, decreasing channel roughness and the construction of levees are thought to have contributed to bank erosion and reduced in-stream habitat. The river bed varies between mud, clay and silt with anthropogenically sourced sand.

The fish community within the Broken River is considered diverse, despite only 10 of the 16 historically recorded native fish still present (Cottingham *et al.* 2001b). Importantly, the Broken River contains seven threatened species with reports of the critically endangered trout cod, endangered Macquarie perch *Macquaria australasica* and silver perch (Humphries and Lake 2000). Further, there are healthy populations of the Murray cod and golden perch *Macquaria ambigua*. Seven alien species have been recorded including carp, goldfish *Carassius auratus*, redbfin *Perca fluviatilis* and gambusia *Gambusia holbrooki*.

River Murray at Barmah-Millewa forest

The River Murray is 2530 km long flowing from the Australian Alps 40 km south of Mount Kosciusko in New South Wales to the sea at Goolwa in South Australia (Mackay and Eastburn 1990). About 1000 km downstream of its origin the River Murray flows through the Barmah-Millewa Forest, a relatively intact 65 000 ha floodplain forest containing Australia's

largest red gum forest (Crabb 1997; Kingsford 2000). Our second 5 km site was located within the forest (35°49'S, 145°05'E).

The flow through Barmah forest is constrained by the Barmah Choke, the product of a slight uplift 25 000 years ago, which limits capacity to 10 600 ML per day. The flow regime at Barmah is defined by the flow at Yarrawonga Weir and flow is held constant or near channel capacity for much of the year. Highest flows are recorded in summer, but high flows also occur in late winter or spring as a result of floodwaters entering the Murray from the Ovens River. During high flows, water temporarily banks up behind the Barmah Choke flooding low-lying sections of the forest.

The red gums dominating the riparian zone are tall, to 39 metres, with narrow crowns. Old trees are uncommon, the result of silvicultural practices of the past 100 years, but there is a wide range of young size classes. Silver wattle is the only other woody species present. The understorey is herbaceous, with a mixture of perennial and annual forbs and grasses. The river bed has numerous sand bars and benches of sand, silt and mud. Many of the benches support beds of macrophytes such as Cumbungi *Typha orientalis* and common reed although active riverbank erosion has removed many of these benches.

The river margin is fringed by common reed, the density, width and height of which is controlled by accessibility to grazing stock, which is in turn controlled by the height and steepness of the banks. Cumbungi is the major emergent macrophyte on the benches and suffers less impact from grazing than common reed, but does not grow on the banks. Clumps of rush *Juncus ingens* and umbrella sedge *Cyperus exaltatus* are less common components of the vegetation on the benches. No submerged aquatic species were found in the main channel.

McKinnon (1997) conducted an extensive fish survey of River Murray within the Barmah forest during various flow conditions. In total, 11 native and eight alien species were recorded (we have considered carp gudgeons as a species complex). Smelt and carp gudgeon were the most abundant native species, accounting for 11% and 6%, respectively. Of the larger species, golden perch was most common followed by Murray cod, with low numbers of trout cod and silver perch also recorded. The fish community was, however, dominated by alien species with carp representing 44% of all fish abundance followed by redfin (18%), goldfish (11%) and gambusia (8%).

Flow variation appeared to influence fish communities within this river section. During low flow periods only seven species (three native and four alien) were observed but as flow increased to flood levels the diversity of fish, particularly native species, dramatically expanded.

In a recent study of the River Murray within the Barmah-Millewa forest, nine species were recorded, with natives including smelt and carp gudgeons and larger species Murray cod and golden perch (Gawne *et al.* in press). Three alien species were observed (carp, gambusia and oriental weatherloach *Misgurnus anguillicaudatus*).

Ovens River at Peechelba East

The Ovens River is 227 km long within a basin of 7778 km² in northern Victoria and represents one of the last unregulated river systems in the Murray-Darling Basin (Cottingham *et al.* 2001a). It joins the Murray River in the north where it discharges into Lake Mulwala. Due to its unregulated nature, the Ovens River is strongly seasonal and one of the few rivers, which maintain a natural winter-spring flooding regime in its lower sites. Its annual discharge of 1620 GL contributes 14% of the average total flow from the entire Murray-Darling Basin while comprising only 0.75% of the total catchment area of the basin. A significant proportion of the water comes from snowmelt. Water use within the Ovens Basin is minimal at only 26 GL year⁻¹.

Our work focused on a 3 km section at Peechelba East (36°09'S, 146°14.5'E), 26 km downstream from Wangaratta. The river meanders within a floodplain up to 3 km wide and is highly sinuous within this section. Due to the nature of the floodplain material, the river banks and bed are mostly silt, clay and sand. The main channel is 3-5 m deep with near vertical banks and numerous anabranches. Meander migration and cut-offs have created many billabongs across the floodplain, which fill directly from the main channel or by over-bank flow during floods.

Significant disturbance to many streams in the Ovens Basin has come through agricultural clearing and mining for alluvial gold. Consequently, the river has a long history of river management works aimed at stabilising stream channels and preventing flooding, some of which have been successful at improving channel stability. Others, such as excessive de-snagging and channel cuts, have increased erosion, promoted channel instability, potentially contributed to increased flooding and have significantly reduced instream habitat values.

Large amounts of large woody debris remain in-channel and this section of river is recognised as one of the best examples of a lowland river remaining in Victoria with significant instream habitat.

Riparian overstorey consists of river red gum and shrub species silver wattle, river bottlebrush *Callistemon paludosus*. There are no major infestations of weed species such as willow and blackberry *Rubus* sp., although the introduced canary grass *Phalaris* spp. is widespread. Instream and emergent vegetation is limited in the main river channel with knotweed *Persecaria decipiens* developing on benches and occasional sparse stands of sedge *Cyperus* spp. Backwaters however, contain a wide diversity of submerged and emergent vegetation. Anecdotal evidence suggests that ribbonweed was once present in the main channel of the Ovens River.

The Ovens River supports 15 native fish species but five are either nationally threatened or rare and there are concerns about the future of a further five species (Cottingham *et al.* 2001a). Despite the decline in many native fish populations, the Murray cod population is considered to be the healthiest remaining in Victoria. Stocking programs exist for Murray cod, golden perch and, recently trout cod. There are eight alien fish species within the Ovens River, many of which are widespread including the Brown trout *Salmo trutta*, Rainbow trout *Oncorhynchus mykiss*, carp, goldfish and redfin.

Flow data

Hydrological data for the three sites was obtained from gauging stations operated by Thiess Environmental Services. This data was represented as the flow event during each sampling trip (Table 1).

Table 1. Summary of flow events sampled at each site during the study period.

Sampling period	Flow event		
	Broken River	River Murray	Ovens River
May 2001	Base	Base	Base
August 2001	Base	Base	Rising
September 2001	Base	Rising	Flood
October 2001	Rising	-	-
December 2001	Base	Bank full	Base
February 2002	-	Base	Base
May 2002	Base	Bank full	Base
August 2002	Base	Bank	Rising

Between May 2001 and August 2002, each site was sampled on seven occasions. During each trip, physicochemical parameters, zooplankton, macroinvertebrate and fish communities were sampled using the methods detailed in the following sections.

Physicochemical parameters

A HORIBA Ltd U-10 multi-probe (Australian Scientific Ltd.) was used to record physicochemical parameters including dissolved oxygen, pH, temperature, electrical conductivity and turbidity at upstream and downstream points in each site.

Microcrustacean community

Data on the Microcrustacean communities at each site was provided by Daryl Nielsen. The communities in each river site were collected from four backwaters and two open water sites. Quantitative samples were collected by filtering water through a 50 µm mesh net using a Jabsco self-priming pump filtered through a 50 µm mesh net (e.g. Nielsen *et al.* 2000; Nielsen *et al.* 2002). A set volume of water was collected for each sample allowing an estimate of the number of animals per litre to be calculated. At each site a sample was collected from the open water (20 litres) by moving the pump throughout the water column and a second sample was collected from the bottom of the backwater (10 litres) by moving the pump along the substrate. At each end of the site, one open water overt microcrustacean community sample was taken by pumping 20 litre of water from the top one metre of water column.

Samples were preserved in 100% ethanol for later enumeration. Where possible identification was to the generic level of taxonomic resolution. All microcrustacean abundance data were converted to density (individuals/litre).

Macroinvertebrate community

The macroinvertebrate community on large woody debris at each site was sampled using the snag bag developed by Grouns *et al.* (1999). The snag bag enabled the collection of macroinvertebrates from a known area of snag, and hence allowed for a quantitative comparison between macroinvertebrate communities. During each field trip to each of the three sites, snag bag samples were taken from three randomly selected snags and preserved in 70% ethanol for later identification. The length and circumference of sampled snag segment was measured and the total area sampled was calculated. Macroinvertebrates were identified

to the lowest possible taxon and counted. All macroinvertebrate abundance data were converted to density (individuals/m²).

Fish community

The fish community at each site was sampled using a combination of passive (small and large mesh fyke nets) and active (2 m and 5 m seine net and Smith-Root backpack and boat electro-fisher) techniques. The varied sampling regime enabled fish to be collected from a range of habitats including open river, within aquatic vegetation and snag areas. All fish were identified to species, measured (standard length) and counted. The data was converted to presence/absence at each site.

Fish dietary analysis

Gut content analysis was conducted on a random selection of actively sampled small-bodied fish collected during each sampling trip and preserved in 70% ethanol immediately after capture. In addition, gut samples from large-bodied species at each study site were obtained from angling groups. The gut contents of a total of 240 individuals from 10 species were examined.

The digestive tract (stomach and intestines) of these fish were removed and examined in a petri dish under a low power dissecting microscope. Every attempt was made to identify prey items to the lowest possible taxonomic level, but rapid digestion, in many cases only family level identification was possible. The gut contents of fish were analysed according to the frequency of occurrence of prey items and the points method. The points method provided an indication of the relative volume of the different prey items in the gut (Hynes 1950). It involves assigning the total contents of a gut a fullness value and then giving each item a value appropriate to its relative volume in the gut.

Dietary information was assigned to broad functional categories (e.g. Kennard *et al.* 2001), which allowed more rapid and meaningful analysis (*see* appendix 1). Mean percentage abundance and points contribution of dietary items were calculated for each species. Due to the low abundance of fish species, capture ability and irregular flow patterns, analysis of the impact of particular flow events was only possible for carp gudgeon and smelt.

Multivariate analysis was used to examine differences in fish diets among sites, seasons, and flow events. It was also used to examine overlap between diets of Murray-Darling fish species.

Dietary item abundance and points data were $\log(x+1)$ transformed and standardised prior to Bray-Curtis sample-by-sample dissimilarity matrices being developed. Non-metric multidimensional scaling (MDS), based on group-average linking, was used to graphically represent the extent of similarity between data (close together points represent samples that have similar dietary composition and points that are far apart have different compositions: Clarke and Gorley 2001).

The similarity/dissimilarity relationships identified by the MDS were then statistically evaluated using analysis of similarities (ANOSIM: Clarke 1993). The Global R-statistic and significant level returned by ANOSIM, describes the relationship of within and between site variations. If the Global R is distributed around zero (sign. level $> 5\%$), there is no difference between sites (similarities within sites equal to between sites). However, if values are approaching 1 (in fact, >0.15 , sign. level $< 5\%$) then sites are significantly dissimilar (e.g. replicates within sites are more similar than between sites: Clarke and Warwick 1994). All multivariate analysis was conducted using the Primer 5 statistical package (Clarke and Gorley 2001).

Stable isotope analysis

Isotope samples were obtained from major food sources during each trip to each site. Leaves of dominant terrestrial plants, aerial shoots of aquatic macrophytes and clumps of filamentous algae were collected. Vegetation samples were thoroughly cleaned using distilled water (to eliminate contamination of isotope signals) and frozen. Macroinvertebrate samples were obtained using dip nets, drift nets and fyke nets. They were sorted to family and left to purge in small aerated vials. Several hours later, all macroinvertebrate samples were removed from vials, cleaned using distilled water, returned to vials and frozen (whilst continuing to purge). The shell or carapace of snails, mussels and larger decapods were removed to attain clean tissue samples. Fish were sampled (electrofishing and fyke netting) and tissue and fin clips samples were obtained. These samples were cleaned with distilled water and frozen.

All frozen isotope samples thawed out and dried in an oven at 60°C for 24 hours. The dried samples were ground into a fine powder with a mortar and pestle. They were then sent to the

CSIRO Plant Industry Analysis Lab in Black Mountain, Australian Capital Territory where carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were measured from all samples.

3 Results

Physicochemical parameters

There were no major trends in water quality as flow level increased (Table 2). Instead, parameters appeared to fluctuate independently of flow. In base flow, EC and dissolved oxygen levels were highest. As flow increased, most parameters decline except turbidity, which increased slightly. Interestingly, temperature was highest in bank full flow, but this is perhaps biased by the timing of bank full flows (during summer). The lowest pH, Dissolved oxygen and turbidity levels were experienced during flood conditions

Table 2. Fluctuations in physicochemical parameters (mean \pm SE) during flow events (sites pooled).

Physicochemical parameter	Flow Event			
	Base	Rising	Bank full	Flood
pH	7.4 \pm 0.1	7.3 \pm 0.1	7.9 \pm 0.9	6.7 \pm 0.2
Electrical Conductivity ($\mu\text{S cm}^{-1}$)	229.6 \pm 61.0	111.0 \pm 30.9	157.0 \pm 89.1	208.2 \pm 168.4
Temperature ($^{\circ}\text{C}$)	13.0 \pm 0.6	11.1 \pm 1.2	22.0 \pm 0.0	12.8 \pm 0.1
Dissolved Oxygen (mg L^{-1})	10.4 \pm 0.3	10.3 \pm 0.8	8.8 \pm 0.0	7.1 \pm 3.1
Turbidity (NTU)	65.8 \pm 7.0	72.1 \pm 7.9	61.5 \pm 3.7	50.5 \pm 2.7

Microcrustacean community

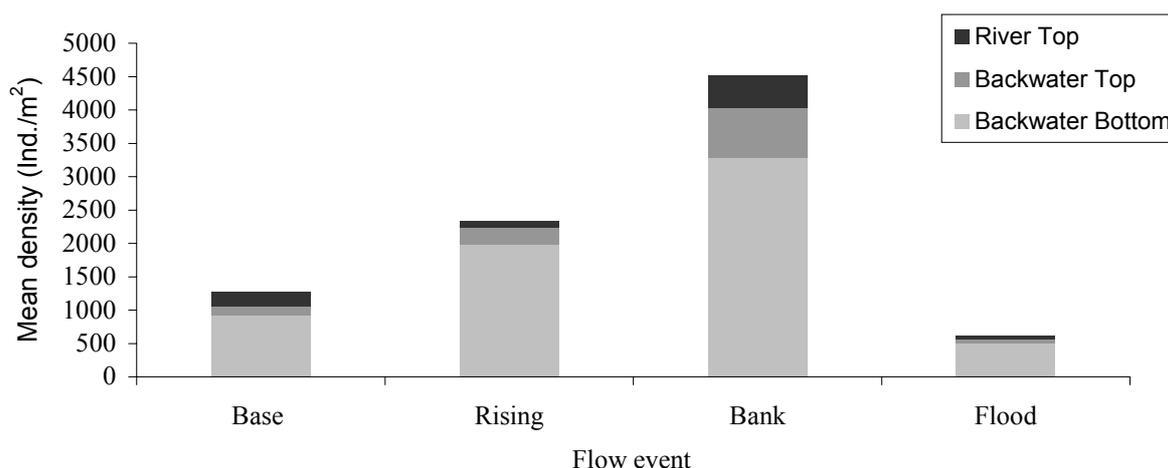


Figure 2. Flow related variation in microcrustacean density in backwater and open river areas (data courtesy of Daryl Nielsen).

The density of microcrustacean communities in open river, backwater top and bottom varied considerably between flow events (Fig. 2). The mean microcrustacean density at the top of

the water column in backwaters was 144.1 individuals/litre during base flow. Density increased during rising flow (238.8 individuals/litre) and bank full conditions (746.0 individuals/litre). After this peak, mean density dramatically decline with only 64.4 individuals/litre present during flood conditions. A similar pattern was observed in microcrustacean communities at the bottom of backwaters, although densities were considerably higher. Densities ranged from 918.2 individuals/litre (base flow) to 3282.0 individuals/litre (bank full) and then dropped to only 505.3 individuals/litre during flood flows.

The microcrustacean density during base flow conditions in the open river was 215.1 individuals/litre. Unlike backwater areas, the density declined during rising flow (101.2 individuals/litre). However, density increased during bank full conditions (493.5 individuals/litre) and then dropped during flood (48.5 individuals/litre) as in backwaters.

Macroinvertebrate community

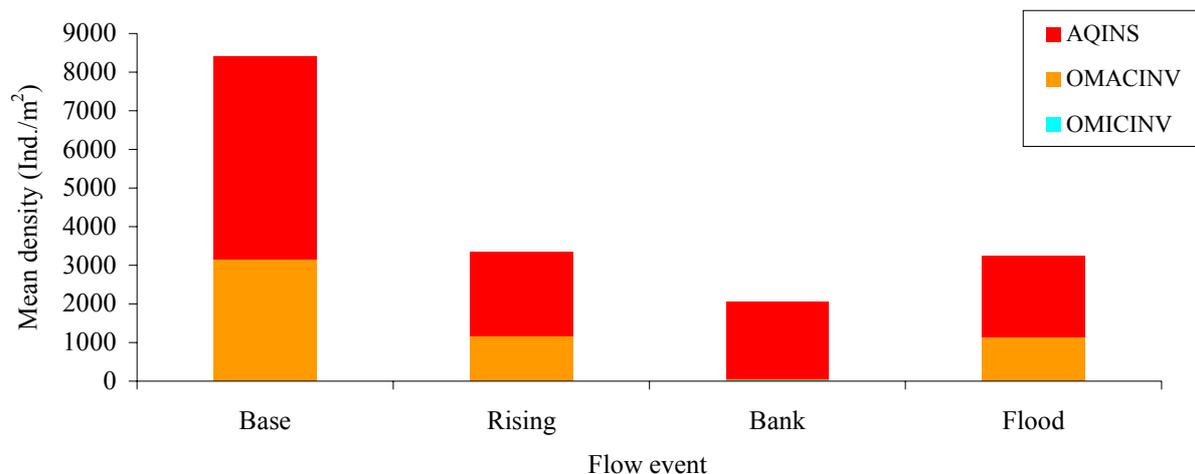


Figure 3. Flow related variation in macroinvertebrate community density on large woody debris.

The mean density of macroinvertebrates living on large woody debris appeared to be affected by flow although the community composition remained similar throughout flow events (Fig. 3). In base flow conditions the highest mean density was observed (8411 individuals/m²) of which 63% were aquatic insects, and 37% other macroinvertebrates (e.g. Amphipods, Isopods, Oligochates, Nematodes, etc). As flow increased, macroinvertebrate density dramatically declined to 3356 individuals/m² (65% aquatic insects, and 35% other macroinvertebrates). Mean density continued to decline during bank full flow conditions (1913 individuals/m²: 97% aquatic insects, and 3% other macroinvertebrates) but moderately

increased during flood levels (3228 individuals/m²: 65% aquatic insects, and 35% other macroinvertebrates). Community composition ranged from 63-65% aquatic insects and 35-37% other macroinvertebrates during all flow events, except bank full conditions when aquatic insects were dominant (97%).

Fish community

The Ovens River had the greatest fish diversity with 12 species observed compared to 11 in the River Murray and 10 in the Broken River (Table 3). Six species were present at all three sites namely native species, carp gudgeon, smelt and golden perch and the alien common carp, redfin and gambusia. Carp gudgeon and smelt were the most abundant species at all three sites.

Table 3. Presence/absence summary of fish species caught at each study site.

Species	River Site		
	Broken	Murray	Ovens
Native			
Australian smelt <i>Retropinna semoni</i>	●	●	●
Carp gudgeon <i>Hypseleotris</i> spp.	●	●	●
Flathead gudgeon <i>Philypnodon grandiceps</i>		●	●
Golden perch <i>Macquaria ambigua</i>	●	●	●
Murray cod <i>Maccullochella peelii</i>	●		●
Murray hardyhead <i>Craterocephalus fluviatilis</i>		●	
Murray River rainbowfish <i>Melanotaenia fluviatilis</i>	●		
River blackfish <i>Gadopsis marmoratus</i>	●		●
Silver perch <i>Bidyanus bidyanus</i>		●	
Southern pygmy perch <i>Nannoperca australis</i>			●
Alien			
Common carp <i>Cyprinus carpio</i>	●	●	●
Gambusia <i>Gambusia holbrooki</i>	●	●	●
Goldfish <i>Carassius auratus</i>	●	●	●
Oriental weatherloach <i>Misgurnus anguillicaudatus</i>		●	●
Redfin <i>Perca fluviatilis</i>	●	●	●
Total native species	6	6	7
Total alien species	4	5	5
Total species	10	11	12

Native species accounted for 60% of fish species within the Broken River. Only one of these species, the Murray River rainbowfish, was not recorded at the other sites. The Broken River had the lowest number of alien species with only four recorded including carp, gambusia, redfin and goldfish.

The seven native species present within the Ovens River included carp gudgeon, smelt and flathead gudgeon, and large-bodied species, golden perch and Murray cod. The other native species, southern pygmy perch, was unique to the Ovens site. The alien fish community consisted of both large (carp, redfin and goldfish) and small-bodied species (oriental weatherloach and gambusia).

The same alien species (five species) present in the Ovens River were found at the River Murray site. The other six species were native including the Murray hardyhead, which was only recorded at this site.

Fish dietary analysis

Spatial and temporal variation in diets

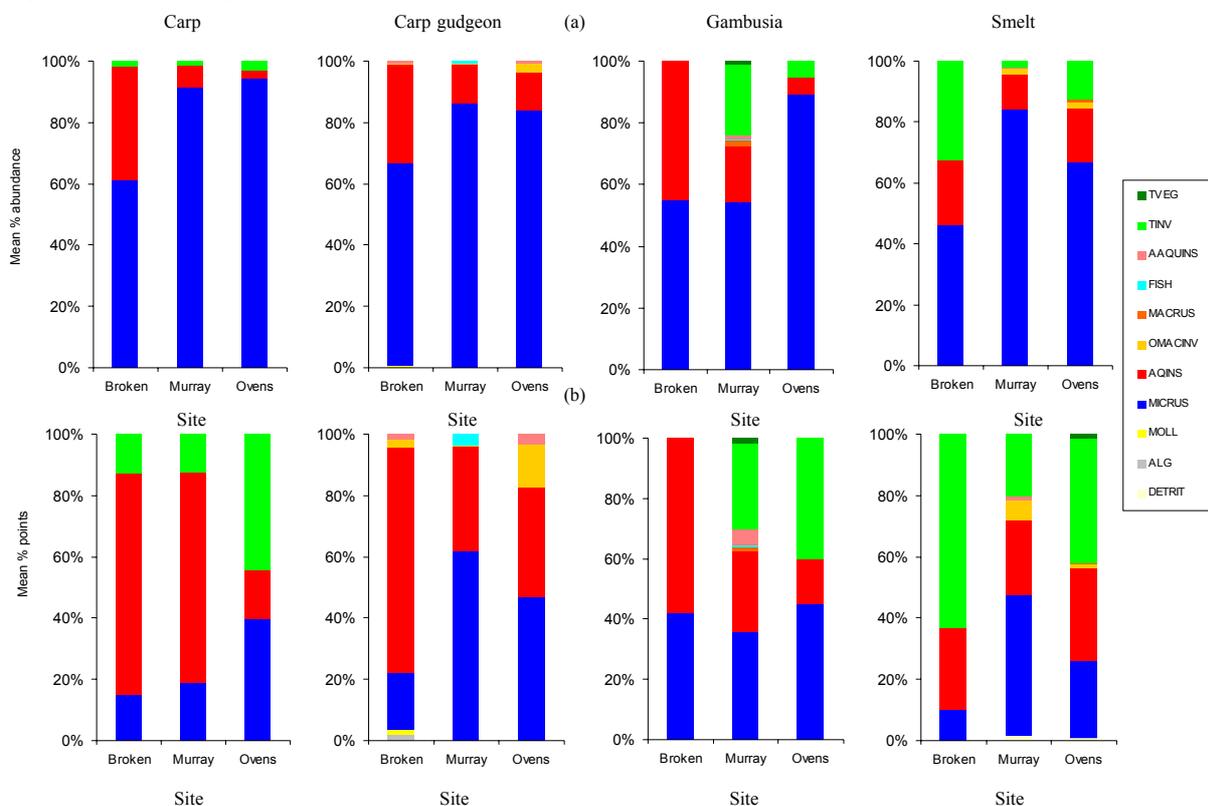


Figure 4. Spatial variation (river scale) in dietary composition of Murray-Darling fish species by (a) abundance, and (b) points.

Microcrustaceans were the dominant food source by abundance and aquatic insects by points in the diet of fish at the three sites (Fig. 4). Terrestrial insects also appeared in the diet of juvenile carp, gambusia and smelt. The contribution of each food source fluctuated between sites for all species but a significant variation was only observed in the diet of smelt (abundance $Global R = 0.115$, $P = 0.3\%$)(Fig. 5; Fig 6). In particular, the microcrustacean dominated diet of smelt (84% by abundance) at the Murray site varied significantly from the

diet observed in the Broken River (microcrustaceans (46%), terrestrial insects (33%) and aquatic insects (21%)).

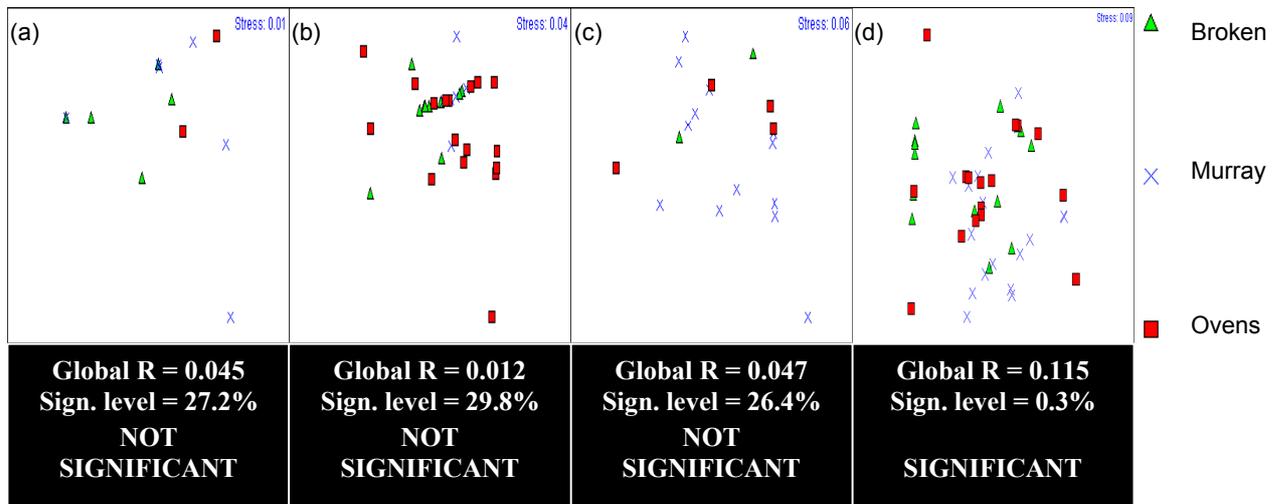


Figure 5. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of spatial variation in prey abundance contribution to diet of (a) juvenile carp, (b) smelt, (c) gambusia, and (d) smelt.

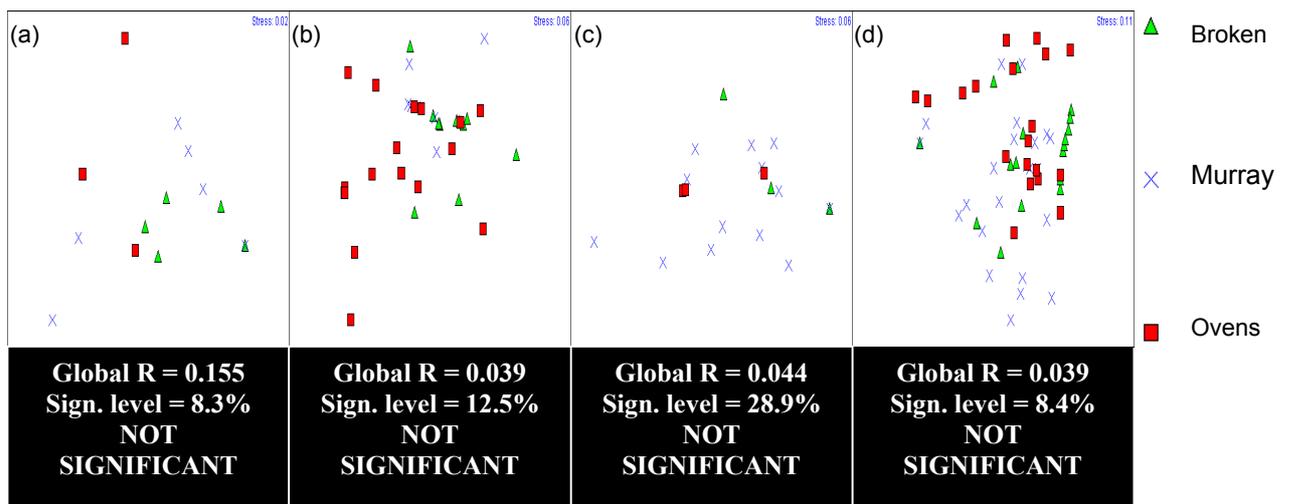


Figure 6. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of spatial variation in prey points contribution to diet of (a) juvenile carp, (b) smelt, (c) gambusia, and (d) smelt.

There was significant seasonality in the dietary composition of smelt (abundance $Global R = 0.172$, $P = 0.1\%$, points $Global R = 0.058$, $P = 2.5\%$) but not carp gudgeon ($Global R = 0.027$, $P = 21.7\%$)(Fig. 7; Fig 8; Fig. 9). During summer months, smelt fed predominately on terrestrial insects (46% by abundance; 66% by points) and aquatic insects (44% by abundance; 31% by points). However, during the cooler seasons (autumn, winter and spring) microcrustaceans become the dominant food source (62-82% by abundance; 27-44% by points) and the contribution of terrestrial insects (3-13% by abundance; 32-36% by points) and aquatic insects (23-32% by abundance; 7-23% by points) declined.

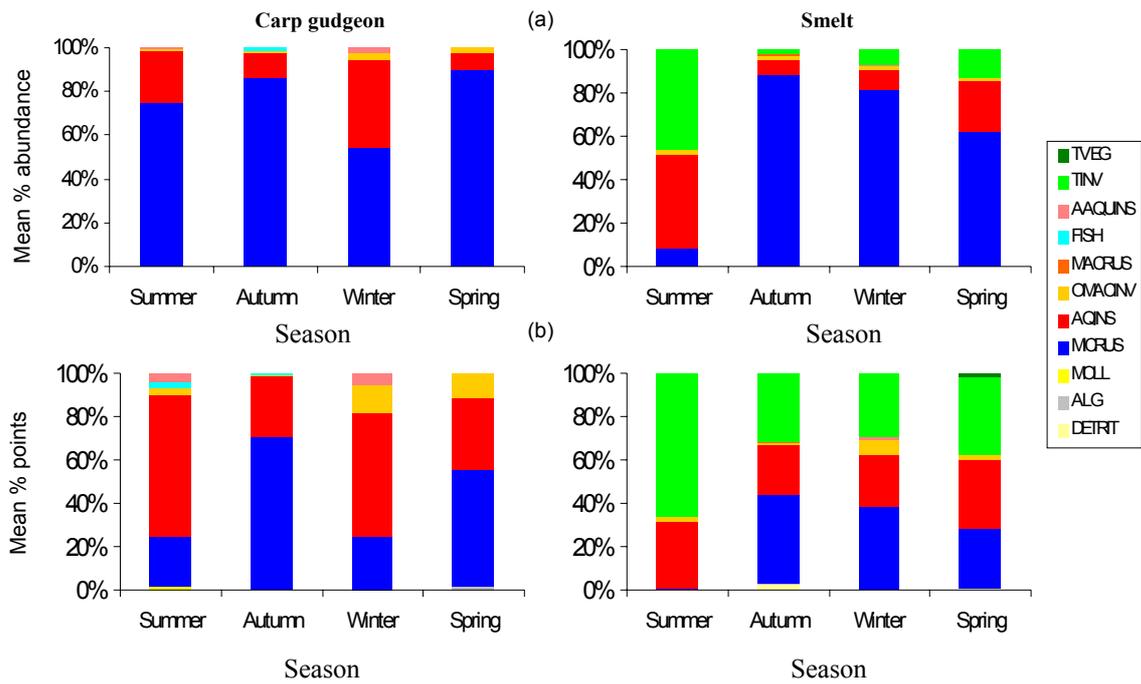


Figure 7. Temporal variation (seasonal) in dietary composition of carp gudgeon and smelt by (a) abundance, and (b) points.

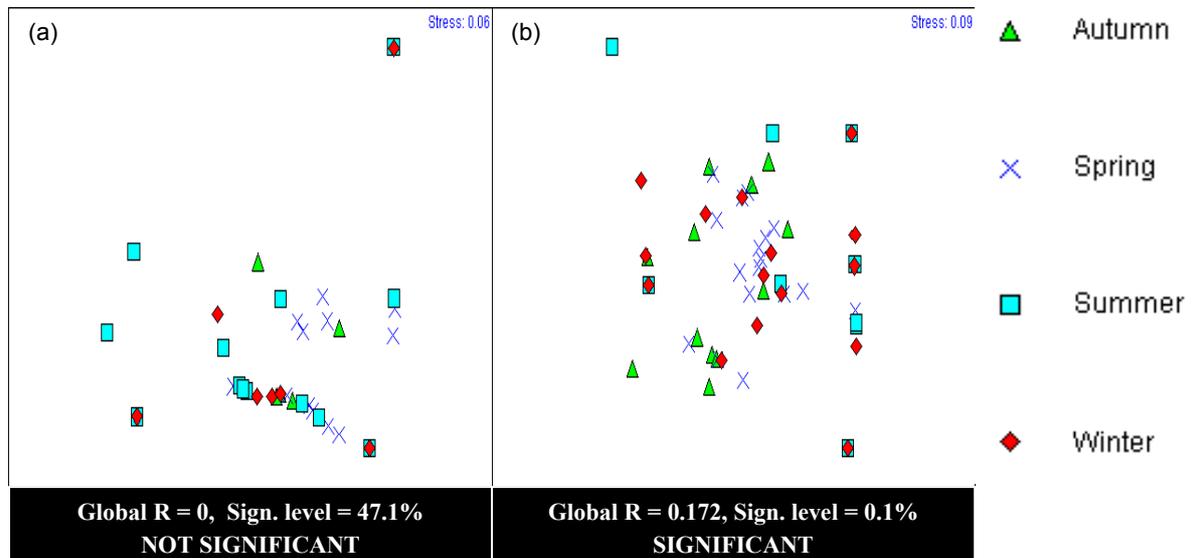


Figure 8. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of temporal variation in prey abundance contribution to diet of (a) carp gudgeon, and (b) smelt.

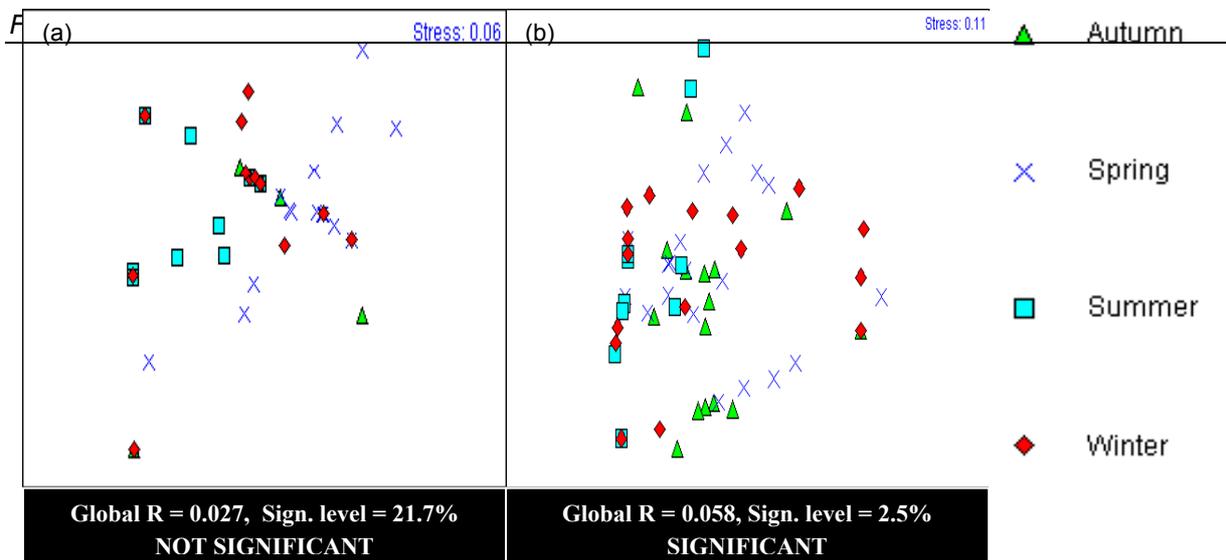


Figure 9. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of temporal variation in prey points contribution to diet of (a) carp gudgeon, and (b) smelt.

Relationship between flow and food resources

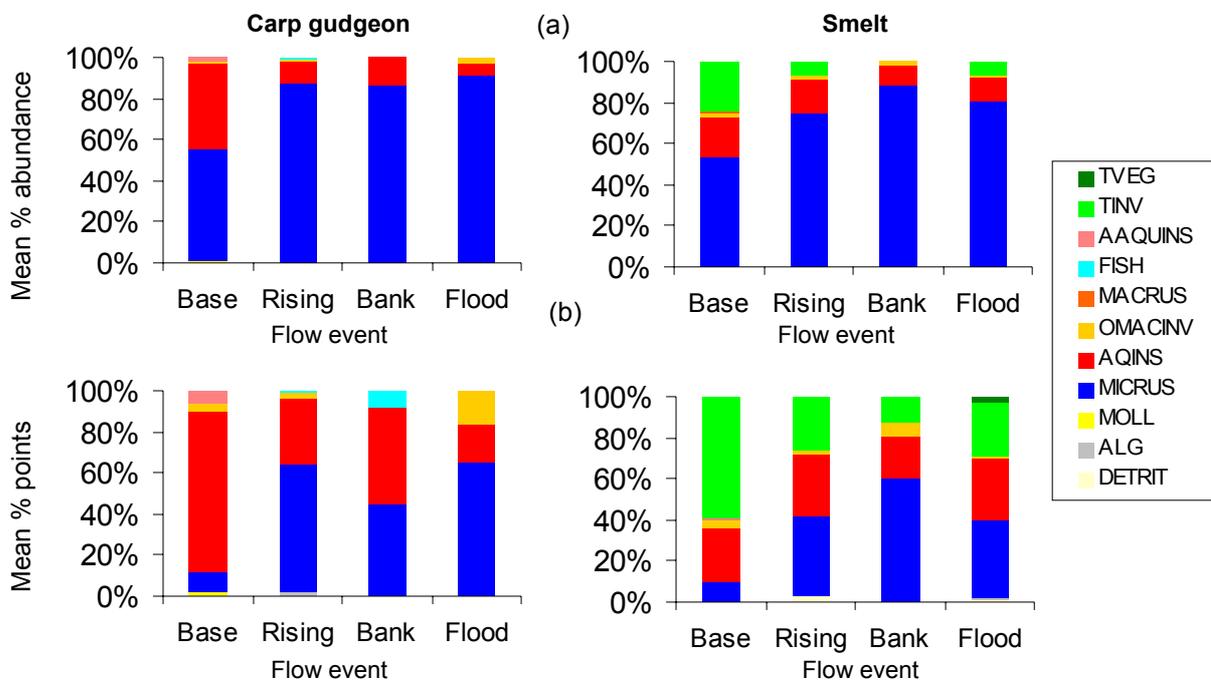


Figure 10. Flow related variation in dietary composition of smelt and carp gudgeon by (a) abundance, and (b) points.

The points contribution of prey items in the diet of carp gudgeon ($Global R = 0.081$, $P = 4.9\%$) and smelt ($Global R = 0.194$, $P = 0.2\%$) varied significantly during fluctuations in flow level (Fig. 10; Fig 12). In base conditions, carp gudgeon consumed mainly aquatic insects (79%). During rising flow levels, the dominant prey item in the carp gudgeon was microcrustaceans (62%) and aquatic insects only accounted for 32% of diet.

There was a slight decline in microcrustaceans (44%) and increase in aquatic insects (48%) during bank full flows. During flood conditions, microcrustacean levels increased again

(65%). These flood conditions were statistically different to base flow conditions (points $Global R = 0.173, P = 2.1\%$).

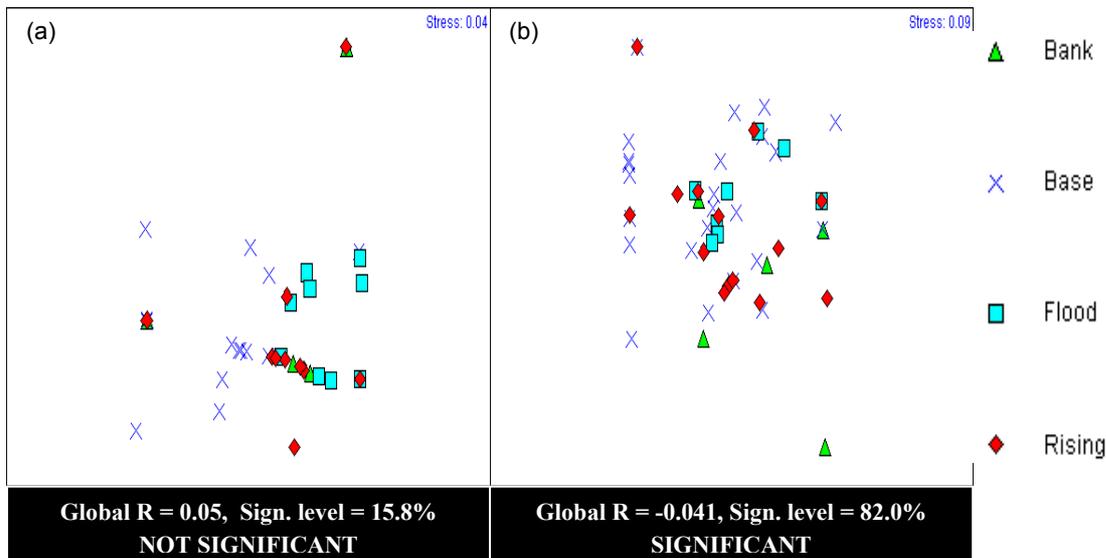


Figure 11. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of flow related variation in prey abundance contribution to diet of (a) carp gudgeon, and (b) smelt.

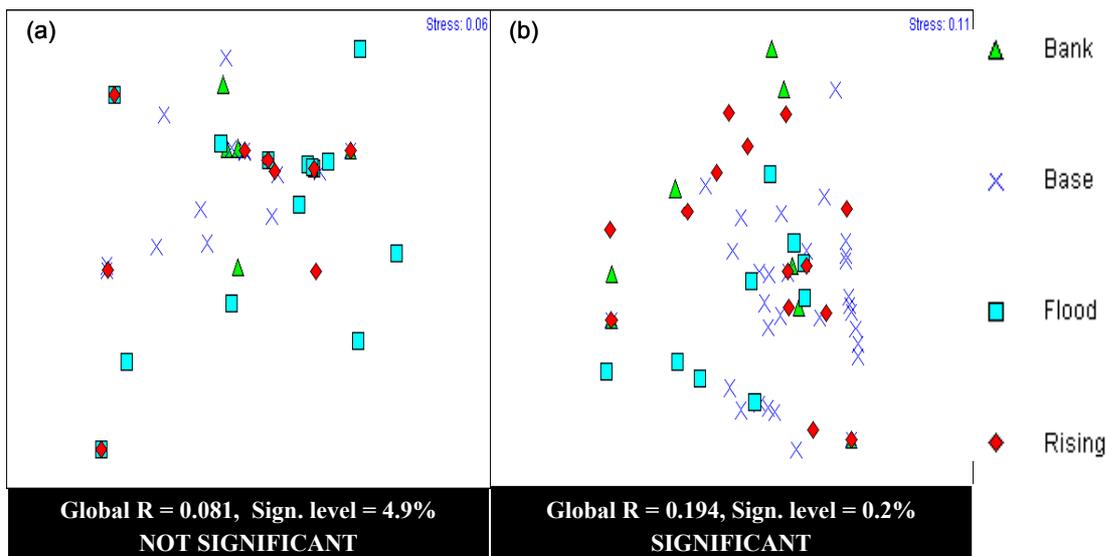


Figure 12. Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of flow related variation in prey points contribution to diet of (a) carp gudgeon, and (b) smelt.

Smelt fed predominately on terrestrial insects (59%) during base flow but switched to a more balanced diet as flow increased (microcrustaceans, 39%, terrestrial insects, 26% and aquatic insects 20%). In bank full conditions, microcrustaceans accounted for 60% of smelt diet with terrestrial insects declining to 13%. Smelt reverted to a more balanced diet during flood levels with terrestrial insects (27%), microcrustaceans (38%) and aquatic insects (38%). Aquatic insects accounted for 27-30% of smelt diet during all four flow events. Pairwise

testing indicated that base diet varied significant from rising diet (points $Global R = 0.372$, $P = 0.2\%$) and bank full diet (points $Global R = 0.224$, $P = 0.8\%$).

Food requirements of common fish species

Microcrustaceans accounted for over 60% of the total prey abundance in the diet of juvenile carp and redfin, carp gudgeon, gambusia, hardyhead, and smelt (Fig. 13). The points contribution of microcrustaceans in the diet of these species, however, was less than 40% in the diets of these species. Aquatic insects, although accounting for only 20% of the abundance, had the greatest points contribution in juvenile carp and redfin, carp gudgeon, gambusia, hardyhead. ANOSIM analysis of small-bodied or juvenile fish revealed significant variation between the diets of the species by abundance ($Global R = 0.07$, $P = 0.8\%$) and points ($Global R = 0.256$, $P = 0.1\%$)(Fig. 14).

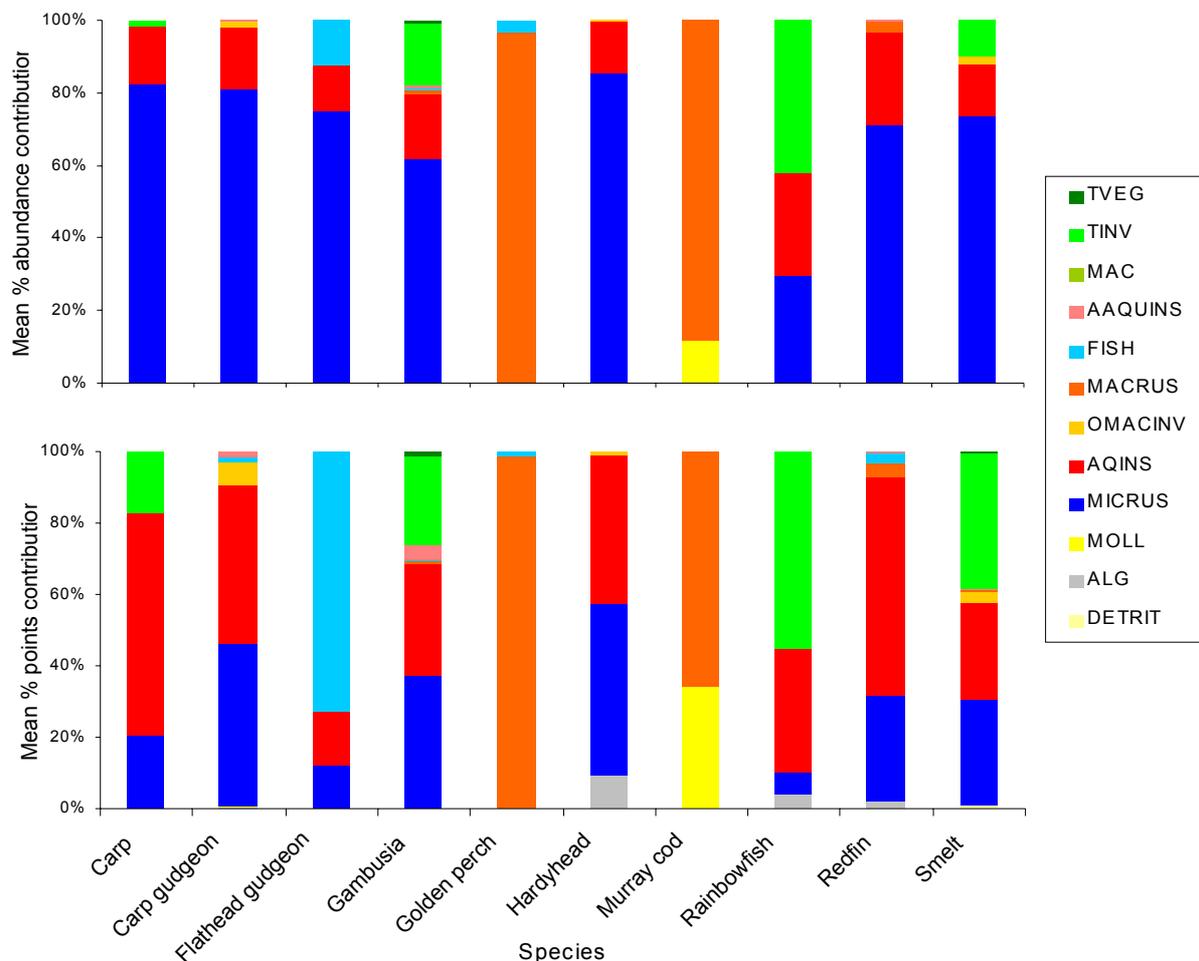


Figure 13. Mean dietary composition for Murray-Darling fish species by (a) abundance, and (b) points.

There were, however, significant similarities in the dietary composition of juvenile carp and several fish species including gambusia (abundance $Global R = -0.033$, $P = 90.3\%$; points $Global R = -0.015$, $P = 57.3\%$), hardyhead by abundance ($Global R = -0.053$, $P = 71.0\%$), and smelt by abundance (abundance $Global R = -0.028$, $P = 64.5\%$). Hardyhead and gambusia (abundance $Global R = -0.025$, $P = 63\%$), and hardyhead and carp gudgeon (abundance $Global R = -0.028$, $P = 64.5\%$; points $Global R = 0$, $P = 49.0\%$) also showed similarities in diet.

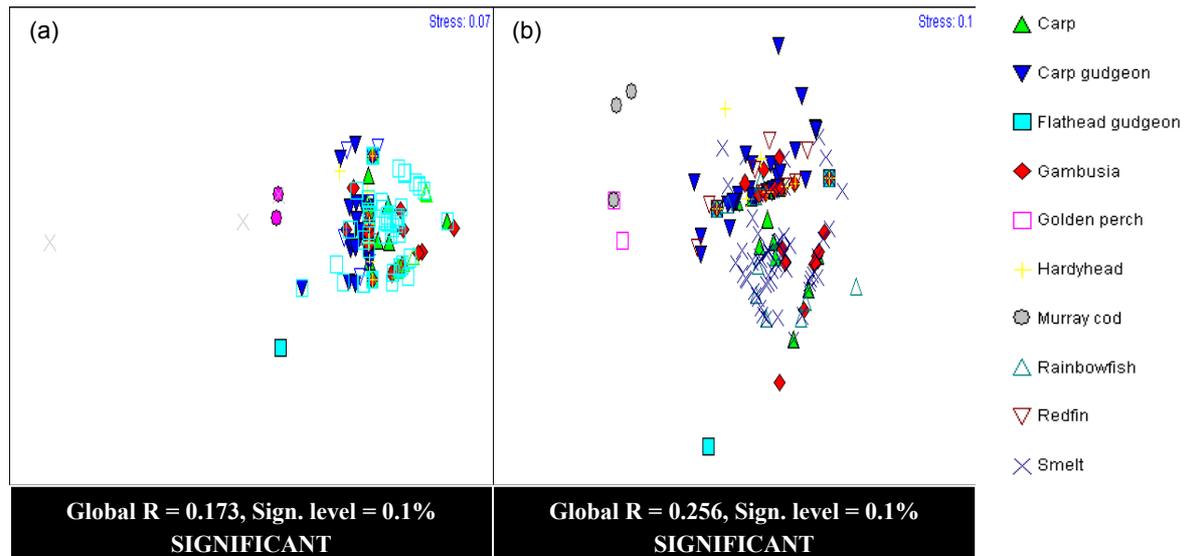


Figure 14. Results of the multidimensional scaling (MDS) and analysis of similarity (ANOSIM) by (a) abundance, and (b) points.

Macrocrustaceans were the main prey item in the diets of Murray cod (88% abundance, 65% points) and golden perch (97% abundance, 99% points). Molluscs also contributed to the diet of Murray cod, while golden perch also fed on fish. There was significant overlap in the diet of these two species (abundance $Global R = -0.073$, $P = 74.5\%$; points $Global R = -0.053$, $P = 57.6\%$)(Fig. 14).

Stable isotope analysis

Primary producers within the Broken River site had $\delta^{13}C$ values ranging between -25 and -29.2 range and 4 and 10.3 for $\delta^{15}N$ (Fig. 16). The fish species appear to be more enriched than the sampled primary producers, indicating an important primary producer was not sampled. Carp (-22.1 to -28), redfin (-23.7 to -26.2) and smelt (-24.6 to -27.3) had highly variable $\delta^{13}C$ values.

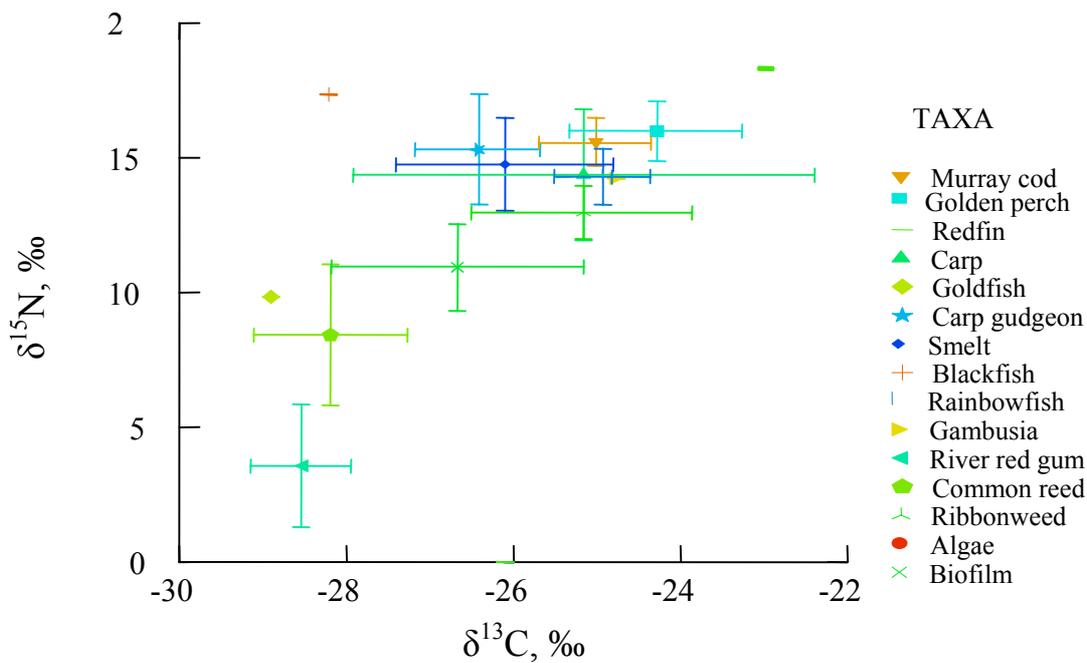


Figure 15. Dual stable isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SE) for primary producers and consumers within the Broken River site.

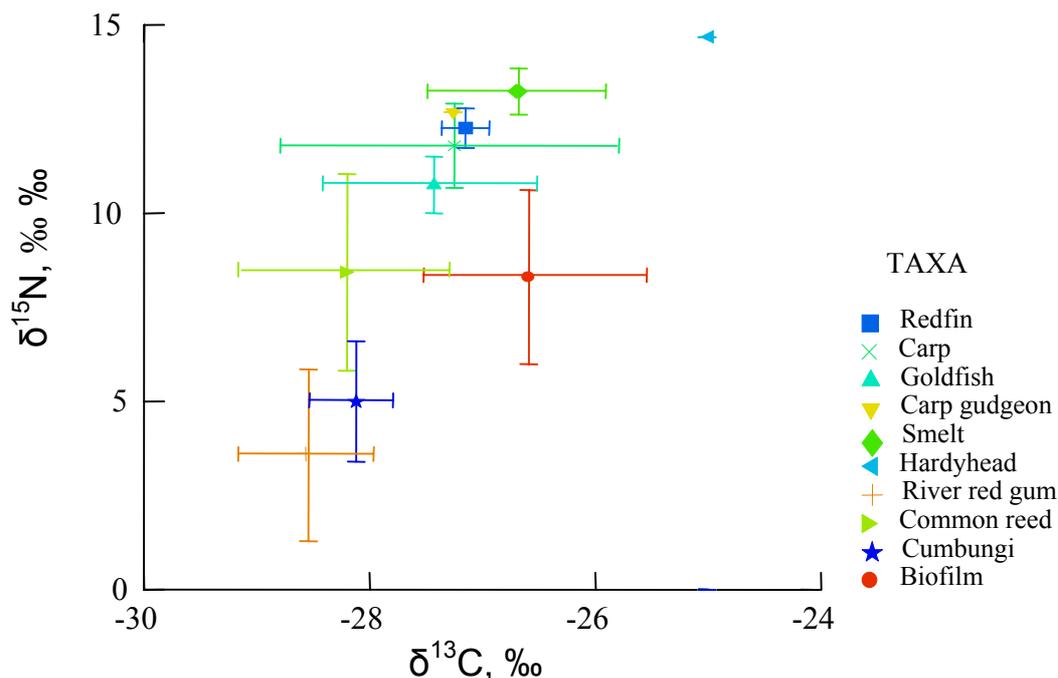


Figure 16. Dual stable isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SE) for primary producers and consumers within the River Murray site.

Primary producers within the River Murray site had $\delta^{13}\text{C}$ values ranging between -26.5 and -28.1 range and 4 and 8.3 for $\delta^{15}\text{N}$ values (Fig. 16). Both biofilm (8.3) and common reed (5) had high $\delta^{15}\text{N}$ value indicating contamination of isotope sample with other food sources. The 6 fish species had $\delta^{13}\text{C}$ values between higher plants (common reed and cumbungi) and biofilm indicating the consumption of prey items that have fed on a variety of organic

materials. In particular, carp (-25.8 to -28.7) and goldfish (-26.3 to -28.1) were obtaining carbon from a wide range of organic sources.

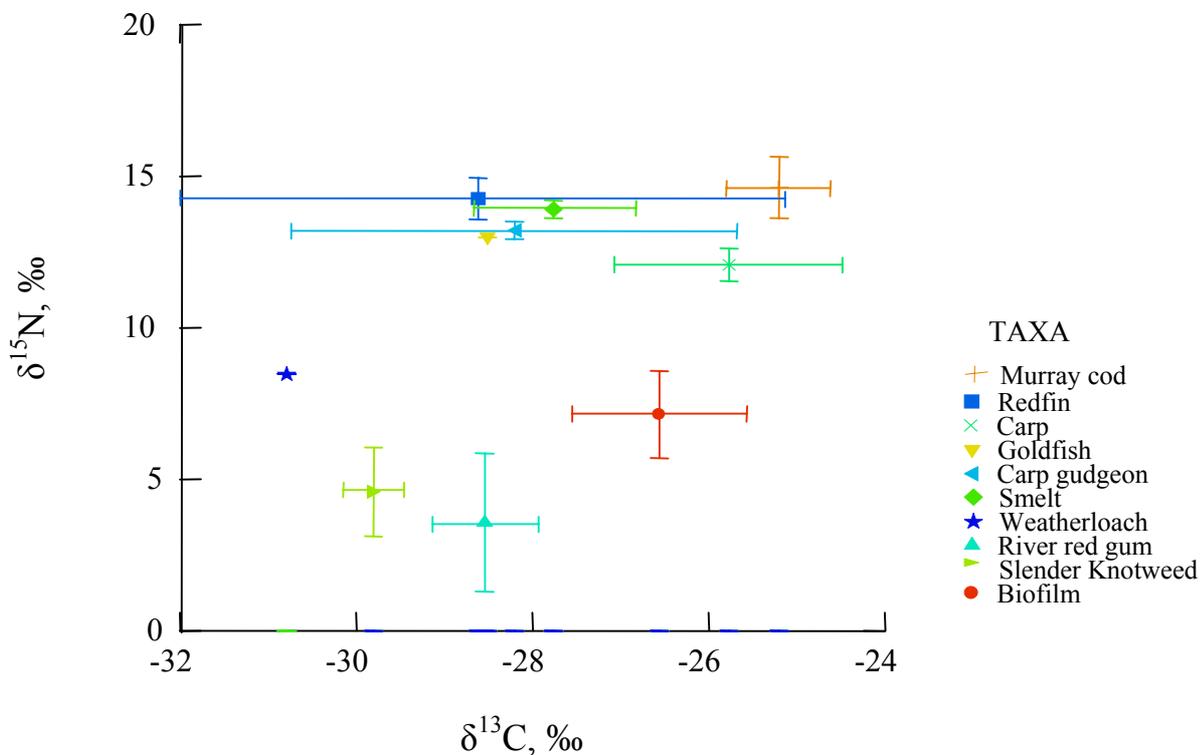


Figure 17. Dual stable isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SE) for primary producers and consumers within the Ovens River site.

Ovens River primary producers had $\delta^{13}\text{C}$ values ranging between -25.7 and -30.2 range and 4.3 and 7.5 for $\delta^{15}\text{N}$ (Fig. 17). The spread of $\delta^{13}\text{C}$ values for consumers was broader than that of these primary producers. For instance, carp and Murray cod had lower $\delta^{13}\text{C}$ values than that of the less enriched primary producer (biofilm). Both redfin (-25.4 to -32) and carp gudgeon (-25.8 to -30.8) exhibited extreme variation in their $\delta^{13}\text{C}$ values.

4 Discussion

Dietary requirements of Murray-Darling fish species

Aquatic insects and microcrustaceans were the dominant food sources in the diet of small-bodied and juvenile Murray-Darling fish species. Terrestrial insects were also important dietary resources with algae and fish making minor contributions to their diets. Larger species fed predominantly on macrocrustaceans, but also molluscs and fish although fish did not contribute to the diet of Murray cod. These prey items have been identified as major dietary resources in previous work (e.g. Kennard *et al.* 2001).

The opportunistic feeding nature of fish species leads to a variable contribution of these food sources. The abundance of prey items was erratic in the guts of fish species. Further, stable isotope analysis revealed most fish species fed on prey items that obtained carbon from a wide range sources. However, the factors responsible for variations in the contribution are poorly understood. This study was designed to investigate these variations in the dietary requirements of Murray-Darling fish species. Particular attention was focused on flow related variations in diet in an attempt to provide information that would assist the development of effective environmental flow allocation.

This study identified overlap in the diets of juvenile carp and hardyhead and smelt. Further, the diet of gambusia was significantly similar to that of hardyhead. These dietary overlaps suggest that there is potential resource competition between these native and alien fish species. However, these findings are contrary to that of Kennard *et al.* (2001) who gave these species different trophic designations. Juvenile carp were classed as microphagic omnivores, where as hardyhead (microphagic detritivore and zooplanktivore) and smelt (microphagic carnivore) belonged to different groups. Further, gambusia (aquatic and terrestrial invertivore) had a considerably difference feeding pattern to hardyhead.

The small sample sizes used in our study (due to unavailability of fish) ensure that conclusions about competition are speculative and while there may be dietary competition between native and alien species, but further analysis on a larger number of individuals is necessary.

Spatial and temporal variations in fish diet

Despite limited supporting evidence (e.g. Pusey and Kennard 1995; Kennard *et al.* 2001), the diet of Murray-Darling fish species are believed to exhibit considerable temporal and spatial variation. The findings of this present study were able to provide more understanding of the spatial and temporal influence on fish diet.

The diet of smelt exhibited significant seasonality resulting from the major contribution of terrestrial insects during summer months. However, there was little variation in carp gudgeon diet between seasons. Kennard *et al.* (2001) observed that smelt had a greater preference for terrestrial insects compared to carp gudgeon due to the feeding mode of each species. Smelt are visual surface feeders with large eyes and are hence able to access allochthonous food sources falling on the water's surface (Pusey and Kennard 1995). On the other hand, carp

gudgeon prefer heavily vegetated areas in the littoral zone and are unlikely to have access to terrestrial materials.

The seasonality of smelt diet is, therefore, linked to the strong seasonal nature of the input of allochthonous materials into lowland rivers. The greater contribution of terrestrial materials in the diet of smelt was not reflected by stable isotope analysis. Smelt should be more depleted in ^{13}C if terrestrial insects are making a greater contribution to diet compared to carp gudgeon. However, smelt were ^{13}C -enriched compared to carp gudgeon, indicating that their terrestrial sources of carbon were no greater.

Previous research identified the potential for spatial variation in diets of Australian fish species (e.g Arthington 1992; Pusey and Kennard 1995; Kennard *et al.* 2001). For instance, Kennard *et al.* (2001) observed dietary variations of fish species from southern and northern regions of Australia. This variation was attributed to regional differences in food availability and productivity. It is reasonable to expect variations in food availability and productivity on smaller spatial scales. However, our findings (by mean points contribution) failed to reveal any significant variations in diet of four Murray-Darling species between rivers (smaller spatial scale). This may suggest homogeneity in productivity and food availability between the three study sites.

Isotope analysis of the three sites indicated variation in the sources of carbon in diets of consumers between sites but also within sites. Within the River Murray site, the 6 fish species had ^{13}C values between higher plants and biofilm indicating consumption of prey items that have been consuming a variety of organic material. This is consistent with production data from the River Murray site (Gawne *et al.* in press), which showed equal contributions of macrophytes, riparian vegetation and algae to total production. Several primary producers had high $\delta^{13}\text{N}$ value indicating complexity of carbon sources. For instance, the high $\delta^{13}\text{N}$ value of biofilm suggests that microcrustaceans were present in biofilm. Further, common reed was $\delta^{13}\text{N}$ -enriched indicating the considerable microbial activity.

Fish species also had highly variable $\delta^{13}\text{C}$ values at the Broken River and Ovens River sites. At these sites the spread of $\delta^{13}\text{C}$ values was broader than that of the primary producers. This indicates that there was an important primary producer that was not sampled. At the Ovens River, there were both $\delta^{13}\text{C}$ depleted and enriched producers that were not sampled. Identification and sampling of these producers will help to determine if diverse organic matter

inputs or spatial variation in organic matter availability within the reach are responsible for the broad $\delta^{13}\text{C}$ values observed in fish species. At the Broken site, the food web was heavily dependent of algae and, therefore, uncontaminated algae are most probably the source of the unknown enriched carbon driving the system. The reliance on algae at the Broken site may be a product of constant flows reducing riparian inputs. This narrow range of primary producers is in contrast to the Ovens and Murray sites where food webs have a broader base.

The similarity in diet between sites identified by direct gut analysis was partially rejected by stable isotope analysis. It is, therefore, probable that the sample size, particularly that of juvenile carp and gamba, used in gut content analysis was too small to detect a significant. More detailed analysis, involving a greater number of individuals, is necessary to delineate the variation in diet on smaller spatial scales.

Impacts of flow on lowland river systems

Flow is a dominant influence in lowland rivers systems (Walker and Thoms 1993) with essential ecological functioning controlled by flow variability (Puckridge *et al.* 1998). Flow conditions have a major impact on the lives of fish species (Humphries *et al.* 2002) potentially altering the abundance and availability of food resources including macroinvertebrates (Nielsen *et al.* 1999; Quinn *et al.* 2000) and microcrustaceans (Dettmers *et al.* 2001; Nielsen *et al.* 2002). However, the role that flow plays in the selection of these prey items by fish, and therefore the diet of fish, is poorly understood.

The diets of smelt and carp gudgeon altered significantly in varying flow conditions. Carp gudgeon switched from an aquatic insect dominated diet in base flow to a diet consisting predominantly of microcrustaceans in flood conditions. In base flow conditions, smelt fed on terrestrial insects and small amounts of aquatic insects and microcrustaceans. As flow increased, the contribution of terrestrial declined so that in bank full conditions, microcrustaceans and aquatic insects were dominant. During floods smelt had a balanced diet of terrestrial insects, aquatic insects and microcrustaceans.

The variations in both species diet mirrored the flow-induced fluctuations in prey density. As flow increased, microcrustacean density markedly increased to bank full conditions and then slightly declined. Conversely, snag-dwelling macroinvertebrate density was high in base flow conditions but declined with flow until stabilising during flood conditions.

The findings support the inference that flow has a major impact on prey availability and abundance of food resources. The diet of carp gudgeon and smelt reflected the fluctuation in prey imposed by flow. Given the opportunistic nature of fish it is not surprising that they switch to the most abundant food sources as flow conditions change. It is also unlikely that they have a preference for individual flow events but favour fluctuating conditions. Therefore, a fluctuating flow regime (e.g. natural conditions) may provide adequate food resources for Murray-Darling fish species. However, without productivity and food resource information from our study sites (sites with varying flow regimes) this is a tentative conclusion. Understanding the whole system productivity (and that of components) and food resource abundance and availability at each site will help to confirm this conclusion (*see conclusions*).

Interestingly, microcrustacean and snag dwelling macroinvertebrate densities were relatively low during flood conditions. These food sources still made large contributions to carp gudgeon and smelt in these conditions but diet was supplemented other food sources. For instance, benthic (oligocheates, polychates) and open water macroinvertebrates (amphipods, isopods) were common in carp gudgeon. Terrestrial insects made a larger contribution to smelt diet during flood compared to rising and bank full flows. This is due largely to the increased accessibility of the previously unavailable allochthonous material on the floodplain. However, only one flood event occurred during the project duration and further sampling of this flow condition is required.

Management recommendations

Native fish populations within the Murray-Darling Basin are at alarmingly low levels. Without intervention, Murray-Darling fish populations will decline to only 5% of pre-European levels in the next 40-50 years (Murray-Darling Ministerial Council 2002). This will lead to the extinction of species and have cascading effects on river ecology. To rectify the problem, Murray-Darling river systems need to be rehabilitated. One such rehabilitation tool is the provision of environmental flows. However, the development of environmental flow allocation needs to be based on sound scientific knowledge. The present project aimed to provide knowledge of the impact of flow on the diets of native fish species.

The findings indicated that flow has a major impact on the abundance and availability of food resources. The diets of fish species reflect the fluctuations in food resource-flow relationship. Fluctuating flow conditions appear to provide the adequate food supplies to native fish

species. These findings further support the reinstatement of natural flow regimes in Murray-Darling rivers.

Further work

This study helped to increase our understanding of the relationship between flow conditions and food resources. However, the project was hampered by the low abundance of fish species, capture ability and irregular flow patterns. This meant that flow-food resource analysis was only possible for a limited number of species. As a result, there still are significant gaps in our knowledge of this area. In particular, understanding of the following areas is necessary:

- Flow-food resource relationships of a wider range of species and greater number of individuals,
- Influence of fluctuating flow conditions on food resources (e.g. prolonged rise, rapid rise, rise then fall, etc),
- Density of food resources necessary to support fish species,
- Resource competition between fish species during various flow conditions,

Knowledge of these areas will increase our understanding of flow-food resource relationships and will help to ensure that environmental flow development is based on sound knowledge.

Conclusions

This study demonstrated that there is significant variation in the diets of several small-bodied Murray-Darling fish species. The diets of fish varied in the face of flow related constraints. Further, seasonality in diet composition was identified reflecting the seasonal availability of food resources. Despite previous research indicating spatial variation in diet, the findings of the gut content analysis did not reveal any variation on a river level spatial scale. However, variations in food web structure between sites were identified through isotope analysis. The sources of variation in fish diet identified in the study will have implications for the management of river systems and development of environmental flows. The study also identified dietary overlap and potential food resource competition between Murray-Darling fish species.

There were several areas in which further research is required before meaningful conclusions can be reached. To this end, this research project will be enhanced by its incorporation into a detailed investigation of the impacts of flow on productivity and trophic linkages in arid

lowland rivers conducted by the Murray-Darling Freshwater Research Centre. This large-scale project will help to investigate knowledge gaps in our understanding of lowland river ecology (including gaps identified by this study).

5 Acknowledgments

This project would not have been possible without the funding from the Natural Heritage Trust (NHT) Fishrehab program administrated by the Department of Agriculture, Fisheries, Forestry – Australia (AFFA). The Cooperative Research Centre ran the project for Freshwater Research Centre (CRCFE).

The authors would like to thank all members of the Lowland River Project trophic linkage team who helped during field and laboratory work (Daryl Nielsen, John Hawking, Garth Watson, Helen Gigney). A special thanks to Daryl Nielsen, who provided microcrustacean data for the sites. Other staff from the Murray-Darling Freshwater Research Centre who provided assistance were Rob Cook, Trish Bowen and Rex Conallin. Thanks go out the Felecity Smith for her analysis of snag bag samples (and congratulations on her new arrival).

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7 Appendix 1

Table 4. Functional diet categories and used in analysis (from Kennard *et al.* (2001)).

Diet category	Code	Description
Unidentified	UNID	Unidentified, other, miscellaneous
Terrestrial invertebrates	TINV	Hymenoptera, Formicidae, arachnids, annelids, isopods, gastropods
Aerial and surface aquatic invertebrates	AAQUINS	Primarily Diptera, occasionally Odonata
Terrestrial vertebrates	TVERT	Mammals, birds, reptiles & amphibians
Terrestrial vegetation	TVEG	Wood, bank, leaves, fruit, seeds & pollen
Detritus	DETRIT	Organic detritus, mud or sand
Aquatic vegetation	MAC	Macrophytes & charophytes
Algae	ALG	Algae & phytoplankton
Aquatic insects	AQINS	Larval + adult stages of all aquatic insects (benthos + water columns)
Molluscs	MOLL	Bivalves + gastropods
Macrocrustaceans	MACRUS	Decapod crustaceans
Microcrustaceans	MICRUS	Copepods, Cladocera, Ostracoda & Chonchostraca
Other macroinvertebrates	OMACINV	Amphipods, Isopods, Oligochates, polychates, nematodes, aquatic annelids, Nematomorpha & Hirudinae
Other microinvertebrates	OMICINV	Hydracarine, Rotifers, Hydra
Fish	FISH	Scales & eggs

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