A seven year study was conducted in three hydrologically-distinct sections within the highly regulated, lowland Campaspe River to investigate the influence of hydrology on temporal and spatial patterns in fish composition, abundance and recruitment. One section had six months, one section two months and one section no months of increased flow due to storage releases. The fish fauna of the less regulated, nearby Broken Rive served as a reference to which that of the Campaspe River was compared for the last three years of the study to allow insight into the relative effects of hydrology, barriers to movement and other environmental characteristics. The study included one high-flow year, a moderate-flow year and five low-flow years. A total of 16 fish species – 10 native and six alien – were caught in the Campaspe River, although of the native species, only three are considered to have self-sustaining populations. The remaining species are either itinerants or a result of stocking. Alien species comprised approximately 64% of the total biomass of all fish caught. Overall composition of the fish fauna did not differ significantly by year, but did by section of river. Species richness and the abundance of most of the dominant species also differed significantly by river section, but there was little inter-annual variation in the abundance of any species, except for European perch and for common carp; the latter showing an increase in abundance following a high-flow event during the Spring of 2000 as a result of recruitment. Overall faunal composition was not influenced by hydrology. However, multiple regression indicated that species richness, abundance of the dominant species and abundance of the young-of-year golden perch, European perch and common carp all were influenced significantly by hydrological variables. The nature of the relationships was dependent on river section and hydrological season (‘winter’ or ‘spring/summer’). Of note was the result that the total abundance of fish and that of YOY common carp were significantly positively related to the number of spells above the threshold for movement upstream through the lower two weirs in the Campaspe River. Only one significant relationship between hydrological and fish-related variables was found for the upper river section, whereas seven and five were found for the lower and middle sections, respectively. Comparisons with fish collected in the Broken River over three years suggest that the fauna of the Broken River is in a more natural state than that of the Campaspe River. Since the two rivers do not differ substantially in water quality, and since both contain significant weirs, which act as barriers to movement of fish, flow regulation is most likely to be the major reason for the poor state of the fauna in the Campaspe River.
Flow-related patterns in abundance and composition of the fish fauna of a degraded Australian lowland river

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Running head: Regulated river fish fauna

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SUMMARY

1. A seven year study was conducted in three hydrologically-distinct sections within the highly regulated, lowland Campaspe River to investigate the influence of hydrology on temporal and spatial patterns in fish composition, abundance and recruitment. One section had six months, one section two months and one section no months of increased flow due to storage releases. The fish fauna of the less regulated, nearby Broken River served as a reference to which that of the Campaspe River was compared for the last three years of the study to allow insight into the relative effects of hydrology, barriers to movement and other environmental characteristics. The study included one high-flow year, a moderate-flow year and five low-flow years.

2. A total of 16 fish species - 10 native and six alien - were caught in the Campaspe River, although of the native species, only three are considered to have self-sustaining populations. The remaining species are either itinerants or a result of stocking. Alien species comprised approximately 64% of the total biomass of all fish caught.

3. Overall composition of the fish fauna did not differ significantly by year, but did by section of river. Species richness and the abundance of most of the dominant species also differed significantly by river section, but there was little inter-annual variation in the abundance of any species, except for European perch and for common carp;
the latter showing an increase in abundance following a high-flow event during the
spring of 2000 as a result of recruitment.

4. Overall faunal composition was not influenced by hydrology. However, multiple
regression indicated that species richness, abundance of the dominant species and
abundance of young-of-year of golden perch, European perch and common carp all
were influenced significantly by hydrological variables. The nature of the
relationships was dependent on river section and hydrological season (‘winter’ or
‘spring/summer’). Of note was the result that the total abundance of fish and that of
YOY common carp were significantly positively related to the number of spells
above the threshold for movement upstream through the lower two weirs in the
Campaspe River. Only one significant relationship between hydrological and fish-
related variables was found for the upper river section, whereas seven and five were
found for the lower and middle sections, respectively.

5. Comparisons with fish collected in the Broken River over three years suggest that the
fauna of the Broken River is in a more natural state than that of the Campaspe River.
Since the two rivers do not differ substantially in water quality, and since both
contain significant weirs, which act as barriers to movement of fish, flow regulation
is most likely to be the major reason for the poor state of the fauna in the Campaspe
River.

Introduction
Flow is the overriding force in rivers. Flow defines river geomorphology and sediment transport, determines the type, amount and accessibility of habitat for riverine animals and plants, it drives food webs through transportation of carbon and it has a major influence on animal and plant behaviour and life histories (see Vannote et al., 1980; Junk et al., 1989; Calow & Petts, 1992; Thorp & Delong, 1994; Matthews, 1998; Frissell et al., 1986; Fausch et al., 2002). The flow regime of a river can be described by five major components: magnitude, duration, timing, frequency and rate of change. These components operate at a number of temporal and spatial scales, and riverine biota have evolved in their context, and must either take advantage of the predictable aspects of the components, such as annual, widespread flooding of forests in tropical South America, or deal as best they can with the less predictable aspects, e.g. summer spates or supra-seasonal droughts (Walker et al., 1995; Poff et al., 1997; Richter et al., 2003; Lake, 2003). High flows, and especially spates, seem to play a major role in influencing the variability in fish assemblages, at least in the short term (Schiemer et al., 2001; Oberdorff, Hugueny & Vigneron, 2001; Koel & Sparks, 2002; Li & Gelwick, 2005).

River regulation is widespread throughout the world and it typically alters one or more of the components of a flow regime, depending on whether the regulation exists for irrigation, hydroelectricity generation, river transport or other purposes (Ward & Stanford, 1979; Petts, 1984; Calow & Petts, 1992). Riverine fishes are some of the more conspicuous victims of river regulation, with flow alteration and the structures which effect it, being implicated in disrupting life histories, degrading habitat, impeding movement, affecting food webs and so on (see Ward & Stanford, 1979; Petts, 1984; Welcomme, 1985; Walker, 1986, 1992; Matthews, 1998). The result of this is, as a
general rule, to alter the composition of fish assemblages; with intolerant species declining in abundance or becoming locally extinct and opportunistic native and alien species often coming to dominate (e.g. Gehrke et al., 1995; Aarts, Van den Brink & Nienhuis, 2004; Lamaroux & Cattaneo, 2006). Barriers to movement exacerbate the effects of flow alteration by preventing movement into and out of affected areas and preventing recolonisation (Matthews, 1998; Lucas & Baras, 2001).

Whilst many studies exist which highlight the likely effects of river regulation on fish (see above reviews), most have been of relatively short duration, which limits their ability to draw meaningful conclusions. Moreover, few are able to make definite links between hydrology and characteristics of fish assemblages and populations, such as composition, abundance/biomass, recruitment and movement, because appropriate spatial and/or interannual comparisons are unable to be made (see Cattaneo et al., 2002; Daufresne et al., 2003 for notable exceptions). For example, although the study by Gehrke et al. (1995) suggests that the more altered the flow of a river is, the fewer natives species and the greater the dominance by alien species, the results are based on two sampling occasions (despite a good geographic spread) and so questions remain about temporal variation. It is only by conducting multi-year studies, under a range of hydrological conditions, such as floods, droughts and ‘average’ flows, that we are likely to be able to establish how hydrology influences fish faunal characteristics (Lloyd et al., 2003; Lytle & Poff, 2003). By so doing, this will provide the type of knowledge needed for effective management of regulated rivers.

Australian lowland rivers and their fish faunas, like many throughout the world, are in a parlous state (Murray-Darling Basin Commission, 2004). The highly regulated
Campaspe River, in northern Victoria, is one example of a severely degraded river system, with a fish fauna dominated by alien species and few native species having self-sustaining populations (Humphries & Lake, 2000; Humphries et al., 2002). The Campaspe River provides an opportunity to study the effects of flow alteration on a fish fauna because, below the major regulating structure (Lake Eppalock) there are three river sections, each with its own distinct hydrology, all within about 175 river km from its junction with the Murray River at Echuca. Lake Eppalock stores winter and early spring runoff, releasing it at a later date, primarily for irrigation purposes. Unless a major rainfall event occurs, the ‘upper’ section of the Campaspe River typically experiences highly regulated, enhanced flows for six months over later spring-early autumn, whereas the ‘middle’ section only receives enhanced flow for about two months during autumn and the ‘lower’ section receives only minor ‘maintenance’ flows for most of the year.

We present here the results of a seven-year study of the Campaspe River below Lake Eppalock, in which we compare the fish faunas in the three hydrologically-distinct river sections. We were thus able to investigate the role of river section (with contrasting hydrologies) and year (the period of the study included one high-flow, one moderate-flow and five low-flow years), focusing on components of the fauna which we considered would give us insight into the role of hydrology in structuring fish assemblages and populations (species composition, abundance/biomass and recruitment) and correlated these with hydrological variables. To strengthen our study further, we included, in the final three years of the study, a comparison of the fish fauna of the Campaspe River with that of the much less regulated nearby Broken River. This has allowed us to speculate on how much of an effect barriers to movement, since both rivers contained significant
weirs, and other environmental variables had on characteristics of the fish faunas from each river.

The current paper thus aims to (i) determine how the composition, species richness, abundance and biomass of the fish fauna of the Campaspe River varied among the three hydrologically distinct sections of river and among the seven years of the study, with the prediction that the greater the degree of flow alteration, the fewer species and the greater the dominance of alien species; (ii) relate characteristics of the fish fauna (specifically, composition, species richness, abundance of dominant species and juvenile recruitment) to hydrological variables (high, low, average and threshold flows for fish passage upstream of weirs) of the Campaspe River among the three river sections and for two seasons (‘winter’ and ‘spring/summer’), with the prediction that the fish-related variables will respond more to high and threshold flows because of greater ability for fish to move between river sections during these times and (iii) compare the composition, species richness, abundance and biomass of fish in the Campaspe River with that of the less regulated and nearby Broken River, with the prediction that there will be more native species, and that they will comprise a larger proportion of the fish fauna, in the Broken than in the Campaspe River. We emphasise spatial and temporal differences and also speculate on the proximate and ultimate roles of flow in shaping the Campaspe River fish fauna.
Methods

Study area and hydrology

The Campaspe River is located in the southern Murray-Darling Basin and is a tributary of the Murray River (Fig. 1). Since the early 1960s, c. 50% of the mean annual discharge of about 2 x 10^8 m^3 has been stored in Lake Eppalock for later release downstream (Fig. 2a). The river downstream of Lake Eppalock can be divided into three sections, based on hydrology and the presence of weirs: the ‘upper’ section from Lake Eppalock to Campaspe Weir (c. 9 m high); the ‘middle’ section from Campaspe Weir to Campaspe Siphon (c. 2 m high) and the ‘lower’ section from Campaspe Siphon to the confluence with the Murray River (Fig. 1). There is also a small, c. 1 m high, gauging weir in the Campaspe River, near Echuca. The entire river downstream of Lake Eppalock experiences reduced duration of high winter flows due to the capture of water (Fig. 2a). In addition, the upper and middle sections of the river experience approximately six and two months, respectively, of enhanced summer flows because of irrigation releases. Most of this irrigation flow is extracted from the river at the Campaspe Siphon and so the lower section has only marginally enhanced flows at this time. Prior to our study, Lake Eppalock filled and spilled approximately every two years during which time high flows would pass down the entire length of the river (Fig 2b). This only occurred once, early in the present study. Before the construction of Lake Eppalock and the weirs (pre-regulation), the Campaspe River would have ceased to flow during the dry summer period in most years. This no longer occurs.

Long (up to 1 km), deep (up to 8 m) and still or very slow flowing natural pools are common in the upper section of the Campaspe River and are separated by relatively
shallow (0.3-1.5 m), still to moderate velocity (0-0.5 m s⁻¹) run habitats. The middle and lower sections of the river have no large natural pools and consist mostly of run habitat, characterised by alternating shallow (<1 m) and deep (1-3 m) regions. The river immediately downstream of Lake Eppalock is typically 30-40 m wide, with high banks and few anastomosing channels or oxbow lakes. Further downstream, the river becomes less constrained (40-50 m wide mostly), in places it has multiple channels and is more likely to move out on to the floodplain. The dominant instream structure is coarse woody debris (or ‘snags’) mainly from riparian river redgums, *Eucalyptus camaldulensis* (Dehnhardt) and stands of aquatic macrophytes, mostly common reed, *Phragmites australis* (Cav). Records indicate that the Campaspe River once supported approximately 20 species, however, recent evidence suggests that the fish fauna is now highly degraded, and dominated by the alien species common carp, *Cyprinus carpio* L, and European perch, *Perca fluviatilis* L (Humphries & Lake 2000, Humphries et al., 2002).

Between 1993 and 2002, approximately 182,000 golden perch juveniles (0.8-1.6 g) were released into the Campaspe River below Lake Eppalock: 20,000–45,000 were stocked each year except in 1996 and 1997. Official records indicate that stocking of Murray cod juveniles in the Campaspe River below Lake Eppalock only took place in 2001 (5,000 upper, 10,000 lower section), 2002 (19,000 juveniles and 25 one-year olds, middle section) and 2003 (10,000 upper and middle sections).

The Broken River is a tributary of the Goulburn River, which itself is a tributary of the Murray River (Fig. 1). It was chosen as a reference river with which to compare the fish fauna of the Campaspe River, because it is less regulated than the Campaspe River, with a smaller fraction of its mean annual discharge of $2 \times 10^8$ m$^3$ diverted for
offstream use and responds more naturally to rainfall events in the catchment than does the Campaspe River (Smith & Humphries, 1997). The impoundments, Lakes Nillahcootie (built 1967) and Mokoan (built 1971), are the primary regulating bodies in the Broken River. Two weirs (Casey and Gowangardie Weirs, both c. 3 m high) downstream of the major impoundments, whilst creating pools upstream and inhibiting fish movement, have a relatively small effect on the hydrology of the river. The Broken River was similarly divided into three sections: Benalla Weir to Casey Weir, the ‘upper’ section; Casey Weir to Gowangardie Weir, the ‘middle’ section and Gowangardie Weir to the confluence with the Goulburn River at Shepparton, the ‘lower’ section (Fig. 1).

The Broken River channel width is marginally smaller than the Campaspe (typically 25-35 m) and has no large natural pools comparable to those in the upper Campaspe River, however, the run habitat is similar to the Campaspe, comprising alternating shallow (<1 m) and deep (1-3 m) areas with still to moderate velocities (0-0.5 m s⁻¹). Instream structure similarly comprises snags, derived from riparian river redgums, and aquatic macrophytes, dominated by common reed.

Historically, the Campaspe and Broken Rivers would have had a similar suite of fish species (Humphries & Lake, 2000). The native fish fauna of the Broken River has no doubt also suffered as a result of a variety of anthropogenic disturbances, however, nowadays there are still approximately 12 native species extant in the Broken River, with several large and small native species present in significant numbers (Humphries & Lake, 2000). Stocking of golden perch (0.8-1.5 g) also occurred in this river during the current study at the rate of, typically, 20,000 juveniles annually (Victorian Department of
Primary Industries, unpublished data). In 1993 there were no records of golden perch being stocked, and in 2002, 9,000 juveniles and 25 one-year-old fish were stocked.

Collection and processing of fish

Fish were collected from two reaches, randomly chosen from a range of possible reaches, on each occasion, from within each section of the Campaspe River bimonthly between October 1995 and June 2000. Because of changes in funding, between August 2000 and February 2003 the sampling frequency decreased to four times per year: February, June, October and December. During the latter period, sampling also included two randomly chosen reaches within each section of the Broken River. The Campaspe and Broken Rivers were sampled within the same week on each occasion and following identical protocols. Thus our sampling consisted of a total of eight replicates per section per year, including four from each reach. This frequency of sampling is twice and sometimes four times that of most comparable studies (e.g. Gehrke et al., 1995) and it encompasses the warm and cool, wet and dry and non-breeding and breeding times of the year.

Sampling over the first year of the study using large and small fyke nets, bait traps, seines, dip nets and back-pack and boat electrofishers indicated that a combination of large and small fyke nets was able to be used in a consistent manner, and was able to be deployed in all river conditions and captured juveniles and adults of the large-bodied species and most of the smaller-bodied species in similar proportions to a combination of all the other methods trialled. Fyke nets were not efficient in catching Australian smelt or gambusia, which were better collected using light traps and/or other active methods.
(see Humphries et al., 2002 and Humphries & Richardson, unpublished data). Therefore, fish were collected using a combination of seven large fyke nets (35 mm mesh, 0.5 m diameter mouth, 3 m long, 5 m central wing) and three small fyke nets (4 mm mesh, 0.5 m mouth [with 30 mm mesh at front to prevent large fauna from entering], 1.3 m long, 3 m central wing). Nets were set facing downstream at an angle to the bank, randomly along a 100-350 m reach, approximately 3 h before dusk and retrieved within approximately 4 h after dawn the next day.

Opportunistic electrofishing sampling by backpack (Smith-Root model 15-C POW and model 12-A) and boat (Smith-Root model 5.0 GPP) was undertaken between October 1995 and June 2000. However, because this method could not be carried out consistently due to frequent difficulties gaining access to the river, the results from this sampling is only included in a description of the presence of species in the river as a whole, over time (Fig. 4) and was not included in any other analyses.

Fish were anaesthetised, identified to species, weighed to 1 g (if fish were less than 1 g, they were pooled and the total weight of that species for a net was determined) and measured to 1 mm. All fish, except common carp (which, by law must be destroyed), were then allowed to recover in clean water, before being returned to the river. It is recognised that some small species will not be sampled as efficiently by fyke nets as other gear (see below in Discussion), but the consistency of sampling for all reaches and sampling occasions using fyke nets allows for meaningful comparisons throughout the entire study.

Environmental and hydrological data
Duplicate measurements of temperature, dissolved oxygen, turbidity, conductivity and pH were taken at each reach on each sampling occasion using a Horiba® Water Checker U-10.

Hydrological data were obtained from Goulburn-Murray Water through gauging stations operated by Thiess Environmental Services. Gauging stations are located at Lake Eppalock, Campaspe Weir and Campaspe Siphon on the Campaspe River (thus providing flow records for each of the three sections of the river) and at Benalla and Casey Weir on the Broken River (only providing flow records for the upper section and the combined middle and lower sections) (Fig. 1).

*Analysis of fish data*

The occurrence of species of fish in the Campaspe River over time was described by the presence or absence of species derived from samples collected using backpack and boat electrofishing and large and small fyke netting. All other analyses were carried out on fyke net data only (seven large and three small fyke nets per reach), since these were employed consistently throughout the entire study.

Relative contribution of species to the fish fauna was used as an overall descriptor of the fauna and was derived from fish abundance and biomass data for each section of the Campaspe River, calculated from the summed values of fish collected in two reaches within that section (from 14 large and six small fyke nets per section per sampling trip) for the entire study period (October 1995-February 2003). Relative contribution of species to the Broken River fish fauna, between August 2000 and February 2003, were
calculated in the same way and were compared with data from the Campaspe River obtained during the same period.

An overall description of the fish fauna of the Campaspe River over time and space was performed using non-metric multidimensional scaling (NMDS) analysis on fish abundance data collected using fyke nets. Rare species were excluded from the NMDS; rare species were those that occurred in samples only once. Data were $\log_{10}(x+1)$ transformed and a Bray-Curtis dissimilarity matrix calculated. Fifty random starts were used. To determine whether fish assemblages differed significantly with ‘Year’ and ‘Section’ two-way analysis of similarity (ANOSIM) was carried out. A ‘year’ was defined as being a spawning year: beginning in August of one year and ending in June of the following. NMDS and ANOSIM were carried out using the PRIMER V5 package (Clark & Warwick, 2001).

To determine if species richness and abundance differed significantly over the seven year study period and among river sections in the Campaspe River, four of the bimonthly sampling occasions per year were used as replicates (June, October, December and February), since these were sampled for the entire study period. Two-way ANOVAs were carried out examining the effects of ‘Year’ and ‘Section’ on species richness, mean abundance of total fish, common carp, golden perch, European perch and flathead gudgeon. These four species were the only species collected in sufficient abundance to allow such a comparison. Richness data met the assumptions of ANOVA and so raw values were used, whereas abundance data were $\log_{10}(x+1)$ transformed to satisfy the assumptions of ANOVA.
Recruitment

Recruitment was investigated by determining the number of young-of-year (YOY) fish collected in any one year. A ‘recruitment season’ was assumed to begin approximately two months after the commencement of spawning (although, in the case of golden perch, this was not possible, because no larvae were ever collected), when fish would have become juveniles and it is assumed that they would have already suffered the bulk of mortality, and to finish before spawning commenced in the following season. Thus, the ‘recruitment season’ for common carp and European perch was designated from October-June and for golden perch, from December-June. YOY carp were designated as fish up to 125 mm (Brumley, 1996; Villizzi & Walker, 1999), YOY European perch as fish up to 100 mm (Shafi & Maitland, 1971) and YOY golden perch as fish up to 200 mm (Anderson et al., 1992).

Relationships between hydrological and fish variables

The Echuca gauging weir is only about 1 m in height, but its ‘drowning-out’ is a function of discharge of both the Campaspe River and that of the Murray River, since the waterlevel backs up the Campaspe, when the Murray River runs high. Analysis of hydrological data, consultation with Goulburn-Murray Water hydrologists and personal observations suggest that a discharge of approximately 23.15 m$^3$.s$^{-1}$ or above in the Campaspe River would make upstream fish passage possible. The Campaspe Siphon is constructed of a single, concrete apron, rounded in section and set between relatively steep banks. It is estimated that this structure, despite being higher than the Echuca weir, is similarly ‘drowned-out’ at approximately 23.15 m$^3$.s$^{-1}$, and personal observations
suggest that the discharge at which upstream fish passage is possible would be at this level or marginally lower. Thus, 23.15 m$^3$.s$^{-1}$ is taken as the threshold level above which upstream fish passage from the lower section to the middle section of the Campaspe Rivers is possible. It is estimated from field observations and confirmed by hydrologists from Goulburn-Murray Water, that upstream fish passage through the 9 m Campaspe Weir would be possible at around 185.18 m$^3$.s$^{-1}$, which is close to minor flood level (c. 243.06 m$^3$.s$^{-1}$; B. Viney, pers. comm.). It is at this discharge that there is sufficient flow over and around the weir to provide a range of velocities likely to allow fish passage. Thus, 185.18 m$^3$.s$^{-1}$ is taken as the threshold level above which upstream fish passage from the middle section to the upper section of the Campaspe Rivers is possible. It is presumed, for the purposes of this study, that downstream passage over all weirs is possible at all times.

To relate the hydrology of the Campaspe River with characteristics of the fish fauna (composition, species richness, abundance and recruitment), a number of hydrological variables were calculated (Table 1). Analysis was conducted using the River Analysis Package 2.0.1 (Marsh, Stewardson & Kennard, 2003). Two periods of the year were chosen for separate analysis, representing the ‘winter’ or non-growing season (April-July) and the ‘spring/summer’ or growing season (August-March), in a similar manner to Cattaneo et al. (2002). The hydrology of each river section – upper, middle and lower - was treated separately. Hydrological variables were chosen to take into account high (maximum flow, number and duration of 10$^{th}$ percentile flows), low (minimum flow, number and duration of 90$^{th}$ percentile flows), median and variability of flows, as well as number and duration of spells above threshold levels of 23.15 m$^3$.s$^{-1}$
Aspects of the fish fauna of the Campaspe River were related to hydrological variables in two ways. Firstly, a BIOENV analysis was performed on the NMDS carried out earlier; BIOENV compares environmental data, in this case the hydrological variables described above, with the dissimilarity matrix derived from the fish data by maximising a rank correlation between their respective (dis)similarity matrices (PRIMER V5 package, Clark and Warwick, 2001). This was done for the ‘winter’ and ‘spring/summer’ periods separately. Secondly, a series of stepwise multiple regressions was carried out to determine the effects of the hydrological variables (as described above, Table 1) on species richness, $\log_{10}(x+1)$ transformed total abundance of all fish and the total abundance of the dominant species (common carp, European perch, golden perch, flathead gudgeon) and $\log_{10}(x+1)$ transformed total abundance of recruits, i.e. YOY common carp, European perch and golden perch. The seven years were used as replicates. Each river section and hydrological season (winter and spring/summer) was analysed separately.

All analyses, except NMDS, ANOSIM and BIOENV were performed using Excel 2002 and SPSS Version 14.

**Results**

*Environmental and hydrological variables*
For virtually the entire seven and a half year period of the study, the Campaspe River experienced the failure of normal winter rains (Fig. 3a). Only at the commencement of the study, in the winter of 1996, and to a lesser degree in the winter of 2000, was there substantial runoff into the river, causing significant rises in flow, not attributable to irrigation releases. Irrigation releases took place in each year of the study, generally between October and May in the upper section of the river and for a shorter period in the middle section. Releases from Lake Eppalock generated enhanced flow along the lower section over the summer in the order of 0.35-0.46 m³.s⁻¹, compared with the 3.5-4.6 m³.s⁻¹ during this time in the upper section.

The Campaspe River in the lower and middle sections experienced zero flows on several occasions: in the winter of 1996 and spring/summer of 1997 in the lower section and in spring/summer and winter in 1998 and winter of 1998 in the middle section (Appendix). The upper section never experienced zero flows. The Campaspe River reached the 23.15 m³.s⁻¹ threshold three times in the spring/summer of 1996 for a total duration of 34-35 d in each river section and once or twice in the winter of the same year, for a total of 13 d. This threshold was also reached in the spring/summer of 2000, 2-3 times, but this time only for a duration of 3-4 d. The threshold of 185.18 m³.s⁻¹ was reached only in the spring/summer of 1996 twice for a total of 3 d in the middle and upper sections.

Water temperature each year fell to a minimum of 7-8 °C usually in June and a maximum of 20-24 °C usually in January (Fig. 3b). The upper section of the Campaspe River experienced water temperatures 1-2 °C cooler than the lower and middle sections during most summer months, whereas this difference decreased or occasionally was
reversed during the winter months. There was a trend in the lower section of the river for
slightly higher temperatures in summer and slightly lower temperatures in winter
compared with the middle section of the river.

  Conductivity ranged from approximately 300 to 2000 µS.cm⁻¹ in the lower
section, from 300 to 1300 µS.cm⁻¹ in the middle section and from 300 to 1100 µs.cm⁻¹ in
the upper section of the Campaspe River between 1995 and 2003 (Fig. 3c). There was
typically an increase in conductivity from the upper section to the lower section of the
river. Most notable, however, was the lower conductivity of the water in the upper
section, relative to the other two sections.

  Turbidity generally fluctuated between 10 and 50 NTUs during the study period,
although there were spikes of considerably higher turbidity at times (Fig. 3d). In some
cases these spikes were attributable to rainfall events (e.g. in 2000), but at other times
there was no obvious cause. Turbidity in general increased with distance downstream
from Lake Eppalock. Dissolved oxygen varied predictably with temperature, rarely
dropping below 5 mg.L⁻¹ and rarely exceeding 10 mg.L⁻¹ (Fig. 3e). Presumably, for this
reason, dissolved oxygen tended to be lower in summer in the lower section than in the
upper section and vice versa in winter. pH was generally between 7 and 8 in all sections
of the Campaspe River during the study and there were no consistent differences among
river sections (Fig. 3f).

Composition of the Campaspe River fish fauna

A total of 16 species, 10 native and six alien, were recorded from the Campaspe River
between October 1995 and February 2003 (Fig. 4). Four native species, flathead gudgeon
(Philypnodon grandiceps), Australian smelt (Retropinna semoni), carp gudgeons (Hypseleotris spp.; species have been combined because of taxonomic uncertainties [Bertozi et al., 1999]) and golden perch (Macquaria ambigua), and three alien species, common carp (Cyprinus carpio), European perch (Perca fluviatilis) and mosquitofish (Gambusia holbrooki), were collected consistently throughout the entire study period. The native Murray cod (Macullochella peeli peeli) and the alien goldfish (Carassius auratus) were collected less consistently, but on at least half of the sampling trips. Several native species were recorded only rarely.

A total of 1972 fish were collected over the study period, with approximately 40% of them flathead gudgeons, 19% European perch, 18% common carp and 12% golden perch (Table 2). Overall, native fish comprised a little more than half of all fish recorded. By contrast, only about 1/3 of the total biomass of 370 kg of fish recorded was made up of native species. Almost half of the total biomass was common carp, approximately 33% was golden perch and 14% was European perch.

More than twice the number of fish were recorded from the lower and middle sections of the Campaspe than from the upper section (Table 2). This was a result of the relatively high abundance of golden perch, common carp and European perch in the lower section and a result of the contribution of flathead gudgeon, primarily, and golden perch, secondarily, in the middle section. Flathead gudgeon dominated the abundance of fish recorded from the middle and upper sections, whereas flathead gudgeon, common carp and European perch contributed approximately equally to the abundance of fish from the lower section. Golden perch made up just over 10% in all three sections of the river. Native species contributed the least in the lower section, making up only 39% of
the abundance of fish recorded and the most in the middle section, making up approximately 75% of the total. Species richness declined from the lower section to the upper section of the Campaspe River, with only two native species recorded from the upper section. Murray cod and carp gudgeons were absent from the upper Campaspe section.

The biomass of fish was greatest in the lower section of the Campaspe River, totaling approximately 162 kg, with the totals in the other two sections each approximately 100 kg (Table 2). Common carp contributed the most biomass to the fauna in each river section (44-48%), with golden perch second (29-37%). The only other species to contribute more than 10% was European perch. Native species comprised 33-39% of the total biomass of fish from each reach. Common carp and European perch together comprised approximately 60% in each reach.

Non-metric multidimensional scaling analysis and ANOSIM of the fish abundance data for the seven years and three river sections indicated that there were different assemblages among sections (global R = 0.231, P < 0.01), but not among years (global R = -0.185, P > 0.05) (Fig. 5). Posthoc comparisons showed that there was no difference in the assemblages between the lower and middle sections (R = 0.086, P > 0.05), but there were differences between the lower and upper sections (R = 0.285, P < 0.05) and the middle and upper sections (R = 0.357, P < 0.01).

Species richness and abundance of dominant species

Species richness and the abundance of total fish and flathead gudgeons varied significantly with section of river, whereas abundance of common carp and European
perch varied with section and year (Table 3, Fig. 6). In the case of species richness and all species, the mean square was greatest for ‘section’. Interaction terms for all variables were non-significant and abundance of golden perch did not vary significantly with either factor. There were more species in the lower and middle sections than in the upper section (Tukey’s test, $P < 0.001$ and $P < 0.01$, respectively), but there were similar numbers of species collected in the lower and middle sections. For total fish, common carp and European perch, Tukey’s test indicated that there were significantly more fish in the lower section than in the upper section of the Campaspe River ($P < 0.01$). There were also more total fish and flathead gudgeons in the middle section than in the upper section of the river ($P < 0.05$ and $P < 0.01$, respectively) and more common carp and European perch in the lower section than in the middle section ($P < 0.05$ and $P < 0.01$, respectively). There was evidence for a gradual, but consistent decline in abundance of European perch from 1996 until 2002, whereas the abundance of common carp declined from 1996 to 1999, increased in 2000 and subsequently declined again to February 2003 (Fig. 6).

**Recruitment**

Common carp, European perch and golden perch were the only species which were caught consistently and in sufficient numbers to adequately examine patterns in population structure ($0+$ versus $\geq 1+$) and recruitment. There were almost no YOY carp collected in the upper section of the Campaspe River throughout the entire study, only a small number in the middle section and highly variable, but sometimes large numbers in the lower section (Fig. 7a). YOY carp were highly abundant and dominated the carp
population in the 2000/01 season and made up approximately 50% of the fish collected in the 1996/97 season.

In a similar pattern to carp, there were virtually no YOY European perch in the upper section and very few in the middle section of the Campaspe River throughout the study period (Fig. 7b). Only in the first year of the study were YOY collected in the middle section, and these made up approximately 1/3 of all fish collected in that season. By contrast, YOY European perch were collected in most years in the lower section of the river. Furthermore, apart from the 2000/01 and 2001/02 seasons, the abundance of YOY European perch in the lower section was relatively consistent among years.

There were small numbers of YOY golden perch collected in most years in each of the three sections of the Campaspe River during the study period (Fig. 7c). Only in 1996/97 in the lower section were YOY golden perch reasonably abundant and made up a substantial proportion of all fish collected.

*Relationships between hydrological and fish variables*

The BIOENV analysis relating fish assemblage composition with hydrological variables, using all seven years’ data, but for each section separately, indicated that there were no significant relationships either for the ‘winter’ or the ‘spring/summer’ seasons (Spearman’s r = 0.127 and r = 0.108, respectively). However, when multiple regressions were carried out relating species richness, the abundance of individual species and the abundance of YOY common carp, European perch and golden perch with the hydrological variables, several significant relationships were found (Table 4). The fish variables that were positively related to high flow variables were golden perch, European
perch (lower section, winter), and common carp and species richness (middle, spring/summer). The fish variables that were positively associated with low flow variables were total fish and YOY common carp (lower section, in winter), YOY golden perch (upper, winter) and European perch (middle, spring/summer). Total fish (lower, winter) and flathead gudgeon (middle, winter) were significantly associated with variability in flows, the former positively, and the latter negatively. YOY golden perch (lower, winter) and total fish (lower, spring/summer) were positively related to the threshold flow for the lower two weirs (23.15 m$^3$.s$^{-1}$), whereas for YOY common carp, the relationship was less clear; abundance of this group was positively related to the number of spells over the 23.15 m$^3$.s$^{-1}$ and negatively related to the duration of these spells and maximum flow in the lower section in spring/summer.

**Comparison of the Campaspe and Broken River environments: 2000-2003**

The Campaspe and Broken Rivers experienced drought conditions for most of the period between October 2000 and February 2003 (Figs. 3a & 8a). The only time when significant rainfall and runoff occurred was during the spring of 2000, when mean monthly discharge in the Broken River peaked at approximately 28.94 m$^3$.s$^{-1}$ and in the Campaspe River at approximately 11.57 m$^3$.s$^{-1}$.

Mean monthly water temperatures were generally similar for the Campaspe and Broken Rivers, although the latter reached marginally higher levels in mid-summer and mid-winter than the former (Figs. 3b & 8b). Conductivity was always lower in the Broken River than the Campaspe River (Figs. 3c & 8c). There was a gradual rise in conductivity over the three-year study period in the Broken River, however, levels never
reached 400 μS.cm⁻¹, whereas they were rarely below 400 μS.cm⁻¹ in the Campaspe River, even in the upper section. Turbidity, on the other hand, was often higher in the Broken River than the Campaspe River (Figs. 3d & 8d): the three-year mean turbidity in the lower and upper Broken River was 51.0±5.1 and 34.3±1.8 NTU, respectively, whereas in the lower and upper Campaspe River it was 39.1±4.0 NTU and 23.1±4.6 NTU, respectively. Turbidity levels, like conductivity, showed an overall rise during the study period. Dissolved oxygen concentrations were comparable in the Broken and Campaspe Rivers during the three-year comparison, dropping to approximately 5 mg.L⁻¹ in mid-summer and reaching approximately 10 mg.L⁻¹ in mid-winter (Figs. 3e & 8e). As with pH levels in the Campaspe River, those in the Broken River were never lower than 7 and rarely greater than 8 (Figs. 3f & 8f).

Comparison of the Campaspe and Broken River fish faunas: 2000-2003

A total of three native and four alien species were recorded from the Campaspe River and a total of five native and four alien species were recorded from the Broken River between August 2000 and February 2003 (Table 5). All together, 657 fish, comprising 56.6% natives, were recorded from the Campaspe River and a total of 398 fish, comprising 85.7% natives, were recorded from the Broken River during this time. The dominant species by number in the Campaspe River was the flathead gudgeon, with common carp a close second. The Broken River fish fauna was dominated by golden perch, with common carp and carp gudgeon species ranked approximately equal second. Flathead gudgeon was never collected from the Broken River, and Murray cod, river blackfish and crimson-spotted rainbowfish were never collected from the Campaspe River.
Almost twice the biomass of fish was collected in the Broken River than the Campaspe River during the three years of study (Table 5). By weight, the Campaspe River fish fauna comprised 28.5% native species, whereas the Broken River comprised 49.6% native species. Carp comprised approximately half of the biomass, with golden perch ranked second, in each river. Whilst European perch ranked third in biomass in the Campaspe, Murray cod ranked third in the Broken River.

The contribution of native species to the abundance of all fish was highest in the middle section, intermediate in the upper section and lowest in the lower section of the Campaspe River (Table 5). This pattern can be explained almost entirely by the relatively large number of carp collected from the lower section and the relatively large abundance of golden perch collected from the upper section of this river. The contribution of native species to the lower section of the Broken River was also the lowest of all sections, but was intermediate in the middle and highest in the upper section. Native species always comprised more than 75% of the fish fauna in sections of this river. The increasing percentage of native species from the lower to upper section of the Broken River was a result of greater abundances of golden perch and carp gudgeons.

Percentage biomass of native fish in the Campaspe River did not show the same trends as abundance; in this case the greatest percentage biomass of natives was recorded in the lower section (Table 5). The overall pattern was dominated by common carp and, to a lesser degree, golden perch, because of their large size. A greater biomass of carp was collected in the upper section of the Campaspe River than in the other two sections combined. The percentage of native fish contributing to the biomass of fish in the Broken River followed a similar trend, albeit lower, than that of abundance: lowest in the
lower section and highest in the upper section. Again, carp and golden perch contributed the most to patterns in relative biomass.

Discussion

The Campaspe River fish fauna and its condition

The 10 native species recorded in the Campaspe River between October 1995 and February 2003 is almost certainly not a true reflection of the resident native fish fauna in this river. Only four of the 10 species were recorded consistently and in abundance over the 7 ½ year study. Of these four, flathead gudgeon, Australian smelt and the carp gudgeon complex are small, short-lived species known to spawn and recruit every year (Humphries et al., 2002). The remaining species, golden perch, is a large, long-lived species, but is stocked most years in the Campaspe River in large numbers (Department of Primary Industries, Victoria, unpublished data). Furthermore, there was no evidence that this species spawned during the entire study period (Humphries et al., 2002; Humphries, unpublished data). The fact that there was no effect of section on the abundance of golden perch, whereas there was for all other non-stocked dominant species, suggests, perhaps, that regular stocking is maintaining this species throughout the river as a whole. Considering that approximately 18-20 of the 34 Murray-Darling Basin native fish species probably once inhabited this river (Humphries & Lake, 2000), the extant native fish fauna of the Campaspe River is thus extremely poor. Historically, this river was known for its abundant Macquarie perch and Murray cod populations
(Anonymous, 1973; Langtry in Cadwallader, 1977), but it is now virtually unheard-of for
the former, and uncommon for the latter, to be caught by anglers.

A total of six alien species was recorded during the study, and those collected
consistently are also the most common alien species encountered in south-eastern
Australia (Cadwallader, 1978; Arthington & Mitchell, 1986; Koehn, 2002, 2004;
Kennard, Arthington, Pusey & Harch, 2005). Common carp and European perch
comprised approximately 64% of the biomass and 36% of the abundance of fish collected
overall; a figure comparable to studies elsewhere in Australia where these species occur
(Gehrke et al., 1995).

Our results indicated that there were substantial differences in the fish fauna of
each of the hydrologically-distinct sections of the Campaspe River and broadly confirm
our predictions related to the degree of flow alteration and richness and dominance of
native and alien species. Thus, species richness of natives was greatest in the lower
section, lowest in the upper section and intermediate in the middle section. These
differences were a result of the presence of carp gudgeons, Murray cod, Australian smelt,
silver perch and flatheaded galaxias in the lower and middle section, but not in the upper
section. Parallel work on larval fish, using methods more suitable for capturing
Australian smelt, indicated that this pelagic, shoaling species was as abundant in the
upper section of the river as it was in the other two sections (Humphries et al., 2002). On
the other hand, from the results presented here and from observations over many years,
we believe that the absence of the other species from samples in the upper Campaspe is a
true reflection of their absence or rarity in that section (Humphries et al., 2002;
Humphries, unpublished data). Alien species tended to be more extensive in their spatial
distribution in the Campaspe River than did native species. Common carp, European perch and goldfish occurred in each section, albeit in decreasing abundance with increasing distance upstream.

*Fish fauna and hydrology*

There are few studies in Australia or the rest of the world where changes to the fish fauna of a river can be attributed directly to flow alteration (Lloyd *et al.*, 2003; Lytle & Poff, 2003). The main reason for this is because of the impracticality of conducting rigorously designed - controlled and replicated - experiments in anything but the smallest systems. Nevertheless, we can gain substantial insight into the influence of flow by comparisons across broad geographic areas in streams which differ in their flow regimes and associated characteristics (Lamaroux & Cattaneo, 2006). Similarly, in our study we have been able to compare characteristics of the fish fauna of the Campaspe River among three river sections that experience contrasting hydrologies. We have also been able to describe relationships between fish-related variables and hydrological variables and to contrast the Campaspe River and the similar, but less regulated Broken River. An important point to note, however, is that much of the study reported here occurred during an extended dry period and that the patterns observed were without doubt a function of both natural climatic and anthropogenic influences.

Our analysis of the fish fauna during the 7 ½-year study indicated that the lower section of the Campaspe River was consistently the most species rich; again confirming our prediction that the greater degree of regulation the fewer native species occurring, since this section was the least regulated of the three. When access to the Campaspe
River from the Murray River is possible, this means that this section will potentially be more accessible than at least the upper section. These patterns in species richness by section were, however, not reflected in relationships between threshold discharge levels for upstream movement over weirs and species richness in the lower section, although species richness was positively related to high flow variables in the middle section of the river. Thus, our prediction that fish-related variables, such as richness, would respond to high or threshold flows was not confirmed. The general lack of significant relationships between hydrology and richness is not entirely surprising, given the rarity of the upstream connection between the Murray River and the lower Campaspe and between the lower and middle Campaspe (about a month in total in 1996 and for 3-4 d in 2000) and between the middle and upper sections (2-3 d in 1996) and because of the relatively small pool of species in the river.

Irrespective of the potential for movement between river sections, greater species richness in the lower Campaspe River is consistent with the widely held view of a positive relationship between species richness and stream order (see Matthews, 1986). However, what fish are responding to is the subject of ongoing debate; it may relate to diversity of habitat (Gorman & Karr, 1978), rates of immigration and emigration (Power et al., 1988) or drainage basin size or stream length, width or gradient (Lake, 1982; Grenouillet, Pont & Hérissé, 2004). In contrast to the Campaspe River, despite the presence of two substantial weirs, there was no decline in number of species evident with increasing distance upstream in the Broken River. Indeed, our prediction that there would be more native species, and that they would comprise a larger proportion of the fish fauna in the Broken than in the Campaspe River, was confirmed. It is thus unlikely
that the decline in species with distance upstream from the Murray River confluence can be explained solely by the presence of weirs in the Campaspe River. We have little doubt, however, that there will be some species, especially those thought to move considerable distance as part of their normal life history (Reynolds, 1983; Koehn, 1997; Koehn & Nicol, 1998; Koehn, Stuart & Crook, 2003), which will not be in abundance above barriers without regular stocking.

The high degree of regulation in the upper section of the Campaspe River has been proposed by Humphries et al. (2002) as having a deleterious effect on the fish fauna of this system. Differences in physico-chemical variables between the Campaspe and Broken Rivers, mainly turbidity and conductivity, and between the upper and the middle and lower sections of the Campaspe River, seem unable to explain the differences observed. In addition, temperature depression, as a result of low-level releases from Lake Eppalock, is relatively minor and inconsistent, compared with other systems, like the Goulburn and Murray Rivers (McMahon & Finlayson, 1995), and is also unlikely to explain the observed differences. As circumstantial evidence for the impacts of flow alteration, Humphries et al. (2002) cited the absence of carp gudgeons, a species considered vulnerable to river regulation (Gehrke, 1997), in the upper section of the Campaspe River, the dominance of small, opportunistic, short-lived native species which breed over a protracted period and the success of generalist alien species. These authors proposed that the enhanced flows over the spring/summer period in the upper section of the Campaspe did not prevent spawning for most species but reduced the area of slackwater rearing habitats. Recent experiments in a lowland river, in which slackwaters were ‘destroyed’, through diverting current into existing slackwater patches, showed that
simulating the effects of irrigation flows displaced larvae from slackwaters (Humphries et al., 2006). River regulation has also been shown generally to affect recruitment in other rivers systems in the world (Robinson, Clarkson & Forrest, 1998; Liebig et al., 1999; Merigoux & Ponton, 1999; Schiemer et al., 2001).

The Campaspe River’s fish fauna is, however, depauperate throughout its length downstream of Lake Eppalock; not just in the upper section, where most of the irrigation releases occur. It is logical, especially for highly mobile organisms such as fish, and for rivers that are longitudinally connected, that the effects of flow alteration on fish faunas will extend beyond the immediate area that is heavily regulated. Some clues to how flow affects this river’s fish fauna may, perhaps, be gained from sporadic recordings of species during our study and how they relate to flow conditions. The only major high flow event which occurred during the 7 ½-year study was in the winter/spring of 1996, although a brief period of relatively high flow also occurred in late 2000. For several weeks between August and October of 1996, Lake Eppalock spilled, the river was very high and filled billabongs and anabranches and broke its banks in places, and this was the same time during which we estimate that threshold levels of discharge were reached sufficient for fish to move into both the lower and middle sections of the river and, possibly, for 2-3 days into the upper from the middle section. Downstream movement, even from above Lake Eppalock, was possible during these high flow events. During that time, or in the months following the high flow period, several species were collected that had not been recorded prior to this, which were mostly not recorded for the rest of the study and which responded to high flow events by moving considerable distances upstream or downstream. Therefore, there is qualitative evidence that our prediction that fish will
respond to high or threshold flows through movement over weirs may have some validity. Under unregulated conditions, only small rises in flow would have allowed unimpeded movement throughout much of the length of the Campaspe River. Since Lake Eppalock was built, however, movement between river sections would be limited predominantly to when the storage filled and spilled; prior to 1996, approximately every two years, but since that time, never.

Despite the likely effect of high flow events on fish movement, there was no quantitative relationship between the overall composition of the Campaspe River fish fauna and any hydrological variables, which is contrary to our predictions. This was somewhat unexpected, considering the large inter-annual differences in discharge during the study. Thus, the composition was stable over a period, which included, as stated above, a high flow year, a moderate flow year and five years when flows were very low. However, again, there is a relatively small suite of species which is driving the overall composition, and these are species – both native and alien – are known to have broad habitat and water quality tolerances and life histories which allow them to breed and recruit under a range of conditions (Humphries et al., 2002). There has been much effort expended on the question of how stable fish assemblages are and the mechanisms behind their variability (see e.g. Grossman, 1982; Matthews, Cashner & Gelwick, 1988; Schlosser & Ebel, 1989; Grossman, Dowd & Crawford, 1990; Grossman et al., 1998; Poff & Allan, 1995). There seems to be general agreement, however, that flow variability - high flows in general (and short spates in particular) – affect fish assemblage variability (Schiemer et al., 2001; Oberdorff, Hugueny & Vigneron, 2001; Koel & Sparks, 2002; Li & Gelwick, 2005), although this agreement is not universal (see e.g.
Moyle & Vodracek, 1985). It appears that the nature of the differences among the three river sections of the Campaspe and the nature of the species which remain in this degraded system outweigh any among-year differences in their influence on characteristics of the fish fauna.

When the abundances of individual species and life stages were examined, however, several were significantly related to hydrological variables. For example, the abundance of golden perch in winter in the lower section was positively related to the duration of 10th percentile flows and above, suggesting the potential for movement upstream from the Murray River in response to high flows. Total fish abundance in the lower section in winter, on the other hand, was positively related to the duration of 90th percentile flows and a measure of variability in flow. The reason for this is uncertain. Indeed, it is hard to come to general conclusions regarding fish/hydrology relationships for the fish fauna, the river and hydrological seasons. This could be due to the fact that the duration of the study was still too short for robust investigation of relationships, the fact that each section of river has a distinct hydrology and therefore is probably operating differently and so we would expect relationships between hydrology and fish to be different among river sections, or that these types of rivers have high inter-annual variability in flow and antecedent conditions, perhaps extending for many years, play a role in the abundances that we see in any one year.

An example, perhaps, of the complexities of fish/hydrology relationships is of the recruitment of common carp. Abundance of YOY carp showed two peaks: a minor one in 1996/97, during a year of high rainfall, high flows and extended periods of connection for the river system below Lake Eppalock and a major one in 2000/01, when rainfall and
flows were much higher than in the last three years, but considerably lower than in 1996. This resulted in the apparently contradictory positive relationship between YOY carp abundance and the number of spells of 90th percentile flows in the lower section of the river. But this is explainable by the fact that it was the 1996/97 and 2000/01 years which influenced the significance of the relationship, and that in these two recruitment years, YOY carp abundance was lowest during the higher of the two flows and highest during the lower of the two. Strong carp recruitment was also reported in major floodplain wetlands of the Murray River in the 2000/01 breeding season, in response to an environmental water release (Brown et al., 2005; Crook & Gillanders, 2006). Indeed, this species seems to respond to inundation of previously dry habitat by spawning in many locations in the Murray-Darling Basin (King et al., 2003; Smith & Walker, 2004; Driver et al., 2005).

In conclusion, we have found evidence that the differences that exist in the fish fauna of the three sections of the Campaspe River are likely to be due to differences in hydrology and that the fish fauna of this river as a whole is in a poorer state than the less regulated Broken River. This adds weight to the call for more sensitive management of rivers, especially for rivers which are heavily regulated and which have for decades been managed solely as irrigation conduits. Providing periodic moderate-to-high flows and threshold flows over barriers or – better still – allowing fish passage through fishways or removal of weirs altogether will mean that fish will be able to move into and out or areas for life history purposes, for the acquisition of food, to recolonise river sections and to escape potentially harmful conditions, such as blackwater events. Despite some progress in understanding, our 7 ½ - year study is apparently still of insufficient duration for
proper investigation of fish/hydrology relationships. It is sobering to realise that for this to be accomplished, riverine fish studies of 20+ years are probably needed. These are rare in the world (although see e.g. Daufresne et al. 2003) and entirely absent in Australia. With the likelihood of reduced streamflows in south-eastern Australia and increased temperatures associated with climate change, it is all the more imperative that long-term studies are initiated now in order to understand the link between fish and flow and to make predictions for the future.

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Figure legends

Figure 1. Map of Campaspe and Broken Rivers, showing major storages and delineating upper, middle and lower sections of each river included in study.

Figure 2. Median mean monthly discharges for the (a) upper section and (b) lower section of the Campaspe River prior to the construction of Lake Eppalock (pre-dam, 1885-1908) and after the construction of Lake Eppalock (post-dam, 1977-1994).

Figure 3. Discharge, temperature, conductivity, turbidity, dissolved oxygen and pH measurements taken for the upper (dotted line), middle (dashed) and lower (solid) sections of the Campaspe River between October 1995 and February 2003. Vertical dashed line represents when bimonthly sampling changed to sampling in October, December, February and June.

Figure 4. Occurrence of native and alien fishes in the Campaspe River, as recorded during fyke netting and electrofishing, superimposed over discharge between October 1995 and February 2003. Gaps in the figure after June 2000 (dashed line) exist because bimonthly sampling changed at this time to sampling in October, December, February and June.
Figure 5. Non-metric multidimensional scaling analysis plot of fish assemblage data for the three sections and seven years from the Campaspe River.

Figure 6. Mean + 1SE of (a) species richness and log_{10}(x+1) abundance of (b) total fish, (c) golden perch, (d) flathead gudgeon (e) common carp and (f) European perch for the lower (black columns), middle (hatched) and upper (white) sections of the Campaspe River between 1996 and 2002.

Figure 7. Proportion of young-of-year (white bars) and older (black bars) (a) common carp, (b) European perch and (c) golden perch collected in the Campaspe River between the 1995/96 and 2002/03 spawning seasons. YOY were defined as carp < 124 mm (Brumley 1996; Villizi & Walker 1999), European perch < 100 mm (Shafi & Maitland 1971) and golden perch < 200 mm (Anderson, Morison & Ray 1992).

Figure 8. Discharge, temperature, conductivity, turbidity, dissolved oxygen and pH measurements taken for the upper (dotted line), middle (dashed) and lower (solid) sections of the Broken River between October 2000 and February 2003. Note: discharge is presented for the upper section (dotted line) and the middle and lower sections combined (solid line) of the Broken River, because of where the rivers is gauged.