REGULATED RIVERS: RESEARCH & MANAGEMENT
Regul. Rivers: Res. Mgmt. **16**: 421–432 (2000)

FISH LARVAE AND THE MANAGEMENT OF REGULATED RIVERS

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ABSTRACT

Alterations to the natural hydrologic regime in regulated rivers can disrupt cues that initiate the maturation and spawning of riverine fish, or they can change the conditions which are suitable for the recruitment of larvae into juvenile populations. Observations of fish larvae have the potential to provide insights into the effects of flow regulation, showing whether it has had a greater impact on fish by preventing spawning or by reducing or eliminating recruitment. We investigated historical and current records of native fish in the highly regulated Campaspe River and the moderately regulated Broken River, Murray-Darling Basin, Australia, and compared these with the results from sampling of fish larvae over three consecutive years to assess the likely impact that river regulation has had on fish populations in lowland Australian rivers. Of the 12 native species of fish that have been recorded historically from the Campaspe River, eight still occur, generally in low abundance, but only three of these were recorded as larvae in this experiment. From recent records, ten native fish species are extant in the Broken River from a suite of 15 that have been recorded there; of these, nine were collected as larvae. The presence of Murray cod larvae in this river was a significant finding. Thus, the less regulated Broken River is in a much healthier state than the Campaspe River. The results of sampling in both rivers indicated that most species of fish spawned each year, despite high inter-annual variation in antecedent hydrological conditions. This suggests that for the species present in these two rivers, the hydrology (pattern of daily discharge) during the winter and spring preceding breeding was unlikely to be a cue for final maturation and spawning. These findings are only preliminary, but they may show that river regulation has had more of an impact on post-spawning recruitment than on prevention of spawning. This has important implicatons for the remediation of the effects of river regulation, with targeting of recruitment processes and the factors influencing these, a priority. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: larval fish; lowland river; Murray-Darling Basin; recruitment; reproduction; river regulation

INTRODUCTION

Many rivers in Australia are regulated, either by upstream reservoirs or by direct abstractions. Although river regulation for hydroelectricity generation is well established in Australia, it is the storage and release of water for irrigation purposes that is by far the most important form of regulation in the Murray-Darling Basin. Indeed, approximately 80% of the mean annual discharge of the River Murray itself is diverted annually, with the majority of this being used to irrigate pasture, crops, grape vines and orchards (Close, 1990; Australian Department of Industry, Science and Tourism, 1996; Crabb, 1997). The direct effect of this type of river regulation is to reduce overall flow volume, decrease within- and between-year variability and alter the timing of flows, often enhancing normally-low summer flows and reducing normally-high winter flows (Close, 1990). Indirectly, river regulation can reduce the temperature of water downstream of reservoirs (Petts, 1984; Walker, 1985), produce barriers to the upstream and downstream movement of organisms (Petts, 1984) and alter the nature of the transport of particulate organic and inorganic matter (Webster *et al*., 1979; Kondratieff and Simmons, 1984; Petts, 1984; Puig *et al*., 1987).

River regulation in general has a detrimental effect on native fish populations while often enhancing conditions for introduced species, especially those which are habitat generalists (Cadwallader, 1978, 1990;

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Received 23 February 1999
Revised 8 May 1999
Accepted 25 July 1999

Walker, 1985; Gehrke *et al*., 1995). There is much evidence implicating river regulation in the fragmentation of populations (Dynesius and Nilsson, 1994) and also in the disruption of life cycles (Ward and Stanford, 1979; Jackson, 1989; Pardo *et al*., 1998). The life cycles of fish are intrinsically linked to their environment. The annual hydrologic, temperature and photoperiodic cycles provide a basis on which fish reproductive cycles have evolved to coincide with conditions most suitable to the survival and recruitment of their offspring (Bye, 1984; Nesler *et al*., 1988). If the nature of the hydrologic regime of a river is changed, environmental conditions that cue fish to migrate, mature and spawn may not occur and so fish may not reproduce (Mackay, 1973; Welcomme, 1979, 1985, 1989; Jackson, 1989). On the other hand, if maturation and spawning are related more to circa-annual rhythms, fish may produce offspring, but if environmental conditions are not suitable, recruitment into juvenile populations may be poor or not occur at all (Petts, 1984; Harris, 1988; Mion *et al*., 1998). Both scenarios will result in depleted fish populations.

This paper describes the use of fish larvae as one step in identifying some of the causes of the decline of fish populations in regulated rivers. Investigations of the Campaspe and Broken rivers, in the southern region of the Murray-Darling Basin, Australia, were used in a case study, to obtain preliminary results on the occurrence of fish larvae over three successive breeding seasons.

USE OF FISH LARVAE IN ASSESSMENT OF THE EFFECTS OF RIVER REGULATION

River regulation can affect fish through: (i) reproductive effects, i.e. by removing appropriate conditions for gonad maturation, for migrations, for pre-spawning interactions or for spawning; or (ii) recruitment effects, i.e. by decoupling the occurrence of larvae and the environmental conditions needed to sustain them until they become juveniles (this may include desiccation of eggs or larvae, dispersal of eggs or larvae or availability of habitats).

If river regulation has 'reproductive' effects, the result will be that fish fail to spawn or that spawning will not be successful in producing viable eggs or larvae. If there are inappropriate conditions leading up to and immediately preceding spawning, a proportion of eggs may become atretic or, in some cases of high stress, fish may not spawn at all (Jobling, 1995).

The result of 'recruitment' effects will be, in most cases, that larvae are produced but do not survive to become juveniles. However, in the case of successful spawning that includes viable eggs but conditions inappropriate for egg survival (such as low oxygen levels or desiccation) or hatching (some species require specific discharge levels for eggs to hatch, e.g. *Galaxias brevipinnis*; O'Connor and Koehn, 1998), non-production of larvae would occur, despite the operation of recruitment effects.

Clearly the presence of larvae in a river during the breeding season indicates that fish have spawned. The absence of larvae during the normal breeding season, however, may indicate that fish have not spawned at all (reproductive effects); or that fish have spawned but the eggs are not viable because of antecedent conditions (reproductive effects); or that fish have spawned but the eggs do not develop properly or hatch successfully (recruitment effects).

This last point is unlikely to explain the absence of larvae in the Campaspe and Broken rivers, because no studies have indicated that specific discharge levels are required for egg development or hatching (Koehn and O'Connor, 1990). If desiccation of eggs by rapid changes in river height were to be a potential threat to survival, eggs would have to be attached in shallow habitats and have relatively long incubation periods. The incubation periods of the eggs of many species of fish that occur in the Murray-Darling Basin are extremely short, usually only a matter of hours or at most a few days (Koehn and O'Connor, 1990; Humphries *et al*., 1999). Those fish which have incubation periods extending over several days tend to spawn in relatively deep habitats, and the male is thought to guard and fan eggs to maintain adequate levels of oxygen (Koehn and O'Connor, 1990; Humphries *et al*., 1999).

For the rehabilitation of degraded rivers, it is important to identify whether river regulation has affected fish more in terms of reproduction or recruitment. For example, it may be possible to release appropriate discharges at the right time and temperature to get fish to mature and spawn or to stock the river with fingerlings. However, to identify improved conditions for recruitment, links must also be established between parameters such as food, habitat, predation, and water quality on the one hand and survival of eggs and larvae on the other.

It is possible to sample adult fish in such a way as to distinguish between the reproduction and recruitment alternatives, but it involves collecting fish in the act of spawning or soon after. Several Murray-Darling Basin species, such as golden perch, *Macquaria ambigua*, can maintain ripe gonads for considerable periods without spawning and can, in fact, resorb their gonads should appropriate conditions not occur during that season (Cadwallader, 1990). For species such as this, it would be necessary to collect fish relatively frequently over the potential spawning period and examine them for atretic follicles. More importantly, it is often very difficult to obtain permits to collect the adults of threatened or endangered species. Indeed, it is not desirable to sacrifice species such as Murray cod, some of which weigh more than 50 kg and can be more than 30 years old (Harris and Rowland, 1996). Cannulation of ovarian tissue is an option, but the potential for damage or stress to fish near spawning time is always a risk.

An alternative to sampling adult fish is to use the presence of fish larvae as an indication that fish have spawned (Gale and Mohr, 1978; Brown and Armstrong, 1985; Corbett and Powles, 1986; Nesler *et al*., 1988). Moreover, some studies have established significant relationships between the abundance of larvae (in the drift) and the biomass of mature females (e.g. Johnston *et al*., 1995), while others have correlated the abundance of larvae with intensity of adult spawning activity (e.g. Nesler *et al*., 1988). The latter study identified peak spawning times of adult Colorado squawfish, *Ptychocheilus lucius*, based on peak abundance of larvae in the drift over several years, and related both to baseline flow spikes in early summer. For the most part, however, fish larvae have been used to provide evidence for the effects of river regulation mainly through degradation of nursery habitats (Schiemer *et al*., 1991; Scheidegger and Bain, 1995). There has been little investigation of their utility for determining the direct influences of river regulation on reproduction.

Collection of fish larvae provides evidence for which species have spawned and also when and where they spawned, confirms that at least a portion of the eggs spawned are viable, indicates that the origins of fish are from the target water body, since juveniles and/or adults may have been stocked or colonized from elsewhere and can generally be carried out quantitatively. The disadvantages of sampling fish larvae are: (i) that sampling must take place frequently, at least monthly, because of variation in the behaviour of larvae of different species of fish; (ii) that a variety of methods may need to be used for sampling; and (iii) that sorting of samples and identification of species can be laborious.

A CASE STUDY: THE CAMPASPE AND BROKEN RIVERS

Description of rivers

The Campaspe River, northern Victoria, is located in the southern Murray-Darling Basin and is a tributary of the River Murray (Figure 1). It is heavily regulated; about 50% of the mean annual discharge of approximately 2×10^8 m^3 has been diverted, mostly for irrigation, since the early 1960s. The main regulating storage, Lake Eppalock, and two smaller weirs, impede fish movement. The entire river downstream of Lake Eppalock experiences reduced duration of high flows in winter because of the filling of the storage. The upper and middle sections of the river, delineated by weirs, experience approximately 6 and 2 months of enhanced summer flows, respectively. Records indicate that the Campaspe River once supported a diverse native fish population, including the highly prized Murray cod *Maccullochella peelii peelii*, silver perch *Bidyanus bidyanus*, freshwater catfish *Tandanus tandanus*, and golden perch, and was known to be one of the best rivers for Macquarie perch *Macquaria australasica*, in the state (Table I) (Anonymous, 1973). Recent evidence (Humphries, unpublished data), however, suggests the fish fauna is in a highly degraded state, dominated by two introduced species, the common carp *Cyprinus carpio* and

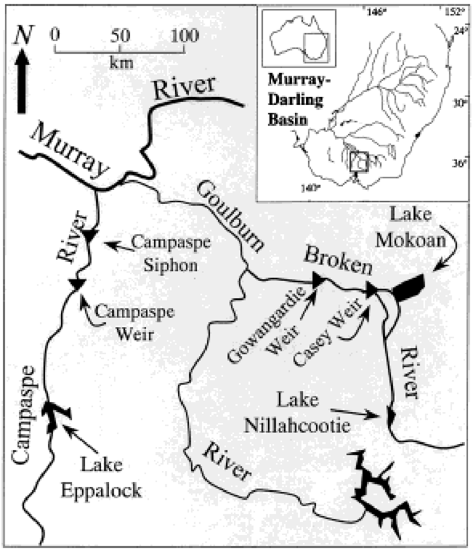

Figure 1. Map of the Campaspe and Broken rivers

European perch *Perca fluviatilis*. Periodic stockings of Murray cod and golden perch, popular angling species, probably help to sustain populations of these two species (Department of Natural Resources and Environment, unpublished data), but there is now no sign of the once abundant Macquarie perch.

An environmental flows experiment is currently under way in the Campaspe River. The aims are to describe in detail the state of the fish fauna of that river, and to attempt to rehabilitate the river through a redistribution of flows from Lake Eppalock (Humphries and Lake, 1996; Smith and Humphries, 1997). Discharge was targeted as having a major role, since, despite some isolated saline pools, water quality in the river is apparently adequate for native fish (McGuckin, 1990) and physical habitat and food appear plentiful (Humphries and Lake, 1996; J. Growns, personal communication). The impetus for the design of the experimental release was the paradigm that several species of Murray-Darling Basin fish require rises in river height or discharge to move upstream, mature and spawn (Lake, 1967; Rowland, 1983; Arumugam and Geddes, 1987; Geddes and Puckridge, 1988; Lloyd *et al*., 1989; Puckridge and Walker, 1990). There is evidence to show that species such as golden perch commence vitellogenesis in winter, accompanied by a rise in oestradiol, and that this might be influenced by ambient conditions (B. Ingram, personal communication). The concept behind the experiment was that the diminished duration of high winter and spring flows in the Campaspe River may have contributed to the failure of those species of fish known to require rises in daily discharge, to mature and spawn. We sought to test the hypothesis that a redistribution of flows, that would extend the winter/spring high flow period, would enhance conditions for these fish to mature and spawn.

The much less regulated Broken River nearby was also used to provide additional data on the occurrence of spawning and presence of fish larvae. In a depauperate river like the Campaspe, stocks of some species may be insufficient for fish to find a mate or to guarantee the collection of larvae. The Broken River is a tributary of the Goulburn River, which itself is a tributary of the River Murray (Figure 1). It is less regulated than the Campaspe River, with only about 10% of its mean annual discharge of 2×10^8 m^3 diverted for offstream use. Two reservoirs, Lake Nillahcootie and Lake Mokoan, are the primary regulating bodies; however, there are two weirs downstream (Casey and Gowangardie weirs) which provide barriers to movement of fish. Like the Campaspe, the water quality and physical habitat of the Broken River appear in good condition, although upstream of the study reaches, remedial works are currently under way to replace snags removed some time ago as a result of previous ‘river improvement’ work (P. Brown, personal communication). Human-induced deposits of sand are present in the Broken River and have no doubt reduced the diversity of habitats available to fish through infilling

Table I. Species of fish recorded from the Campaspe and Broken rivers, ca. 1850–1998, during the current study as adults (adult), and during the current study as larvae (larvae)

Common name	Species	Campaspe			Broken		
		1800s–1998	Adult	Larvae	1800s–1998	Adult	Larvae
Native species							
Australian smelt	*Retropinna semoni*	+	+	+ + +	+	+	+ + +
Mountain galaxias	*Galaxias olidus*	+			+	+	0 ? ?
Spotted galaxias	*Galaxias truttaceus*	+*	+				
Flathead galaxias	*Galaxias rostratus*	+*	+		+		
Crimson-spotted rainbowfish	*Melanotaenia fluviatilis*	!			+	+	+ + +
Silver perch	*Bidyanus bidyanus*	+	+		+		
Golden perch	*Macquaria ambigua*	+	+		+	+	0 0 +
Macquarie perch	*Macquaria australasica*	+			+		
Murray cod	*Maccullochella peelii peelii*	+	+		+	+	+ + +
Trout cod	*Maccullochella macquariensis*	!			+	+	
River blackfish	*Gadopsis marmoratus*	+			+	+	×
Western carp gudgeon	*Hypseleotris klunzingeri*	+	+	0 ? 0	+	+	+ + +
Lake's carp gudgeon	*Hypseleotris sp. 5*				+*	+	+ + +
Midgleys's carp gudgeon	*Hypseleotris sp. 4*				+*	+	+ + +
Flathead gudgeon	*Philypnodon grandiceps*	+	+	+ + +	+		
Freshwater catfish	*Tandanus tandanus*	!			+		
Bony herring	*Nematalosa erebi*	+					
Introduced species							
Common carp	*Cyprinus carpio*	+	+	+ + +	+	+	+ + +
Goldfish	*Carassius auratus*	+	+		+	+	
Tench	*Tinca tinca*	+			!		
European perch	*Perca fluviatilis*	+	+	+ + +	+	+	+ + +
Brown trout	*Salmo trutta*	+	+		+	+	×
Rainbow trout	*Oncorhynchus mykiss*	+			+	+	×
Gambusia	*Gambusia holbrooki*	+	+	×	+	+	×
Weatherloach	*Misgurnus anguillicaudatus*	+*	+				

+, recorded; +*, recorded for the first time during current study; !, within range but not recorded; ?, uncertain of identification of larvae; ×, unlikely to be collected as larvae; under 'Larvae': + + +, species present in 1995–1996, 1996–1997 and 1997–1998, respectively; 0, not present in the corresponding year.

of pools (P. Humphries, personal observation). Nevertheless, the fish fauna of this river is known to be diverse: there have been recent observations of the endangered trout cod *Maccullochella macquariensis*, and anglers' reports suggest the existence of healthy populations of golden perch and Murray cod (P. Humphries, unpublished data), both of which are stocked in the Broken River in most years.

Adult and larval fish sampling

Adult fish were collected between October 1995 and February 1998 and fish larvae were collected between October 1995 and April 1998. Adult fish were sampled bimonthly from the Campaspe River from eight run reaches (characterized by non-turbulent flow, relatively shallow water and moderately fast currents) using a Smith–Root backpack electrofisher (usually 250 m reach electrofished) and ten fyke nets (seven 35 mm mesh, three 4 mm mesh) and from two pool reaches (characterized by relatively deep water with slow currents) using a Smith–Root electrofishing boat (usually 250 m reach electrofished) and 10 fyke nets (seven 35 mm mesh, three 4 mm mesh). Fyke nets were set for approximately 24 h. Adult fish were not specifically sampled in the Broken River, but records of species in this river were obtained from anglers, from bycatch at larval fish sampling (below) and from recent surveys by the Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, Victoria (T. Raadik, unpublished data).

Fish larvae were sampled in the Campaspe River (six run reaches, two pool reaches) and the Broken River (four run reaches, two pool reaches) monthly between August and April, and in June. A single overnight drift net sample (0.5 m diameter, 500 μm mesh), five light trap samples (modified Quatrefoil; Secor *et al.*, 1992) and three seine net samples (2 m wide × 1 m high, 1 mm mesh) were taken in each run reach. Three 5-min samples by trawl net (0.5 m diameter, 500 μm mesh) and five light trap samples were taken in each pool reach. All passive methods were set before dark and retrieved next morning, whereas active methods (trawls and seines) were carried out after dark.

Species recorded as adults and larvae

A total of 12 native and eight introduced species of fish have been recorded in the Campaspe River between the first records in the mid-1800s and the present day (Table I). Three species, including flathead

Table II. Total number and biomass of adult fish collected from the Campaspe River bimonthly between October 1995 and February 1998

Common name	Total no.	%	Total biomass (g)	%
Australian smelt	201	11.9	328.8	0.1
Mountain galaxias	3	0.2	8.9	<0.1
Spotted galaxias	1	0.1	30.0	<0.1
Flathead galaxias	1	0.1	11.0	<0.1
Carp gudgeon	12	0.7	4.3	<0.1
Flathead gudgeon	519	30.6	1230.1	0.3
Murray cod	16	0.9	7253.5	1.7
Golden perch	125	7.4	51 539.0	12.1
Silver perch	3	0.2	168.0	<0.1
Common carp	267	15.8	309 005.6	72.7
Goldfish	29	1.7	7074.4	1.7
Goldfish/carp hybrid	2	0.1	2477.0	0.6
Brown trout	15	0.9	7798.1	1.8
European perch	406	24.0	38 291.5	9.0
Gambusia	93	5.5	63.0	<0.1
Weatherloach	1	0.1	*	
Grand total	1694		425 283.2	

* Weight not measured.

galaxias *Galaxias rostratus*, weatherloach *Misgurnus anguillicaudatus*, and spotted galaxias *Galaxias truttaceus*, were first recorded during the present study and the last had not been recorded previously from the Murray-Darling Basin. Although crimson-spotted rainbowfish *Melanotaenia fluviatilis*, trout cod, river blackfish *Gadopsis marmoratus*, and freshwater catfish have not been recorded from the Campaspe, the river is within their natural range and it is likely that they once occurred in this river. Thus, a total of 15 native species would have probably occurred in this river in the past. From the bimonthly collections between October 1995 and February 1998, it was found that eight native fish species remain in the river (Table I); however, only Australian smelt *Retropinna semoni*, flathead gudgeon *Philypnodon grandiceps*, and golden perch contribute more than 5% by number, and only golden perch more than 5% by weight (Table II). The introduced common carp and European perch make up approximately 40% of the total number and more than 80% of the total biomass of fish collected.

Of the eight native species occurring in the Campaspe River, three were recorded as larvae, although carp gudgeon (*Hypseleotris* sp.) larvae were only collected in one of the 3 years (Table I). Australian smelt and flathead gudgeon larvae were collected in each of the 3 years of sampling and the latter contributed approximately 70% to the total larvae collected (Table III). Common carp and European perch larvae were also represented in samples from each year.

A total of 15 native and seven introduced species of fish have been recorded from the Broken River to date (Table I). In all, three species of carp gudgeon have now been recorded from this river; however, problems with the taxonomy of this genus makes the exact number uncertain and a fourth species may also occur here (Syahfullah, and P. Unmack, personal communications). Ten of the 15 recorded native fish species still occur in the Broken River (Table I), although sources of these data preclude any estimates of percentage contribution. Information from anglers suggests that golden perch are abundant and that Murray cod are commonly caught, and there is anecdotal evidence of many large fish still present in the river.

Of the 10 native species occurring in the Broken River as adults, nine were collected as larvae (Table I). There is some uncertainty of the identification of galaxiid (Galaxiidae sp.) larvae, but these are most likely mountain galaxias *Galaxias olidus*, because this is the only species currently caught as adults. Although river blackfish larvae were collected in the first year, the larvae of this species are guarded by the males in nests in hollow logs (Jackson, 1978) and would not normally be expected to be caught as larvae. Larvae of this species were caught in drift nets, so it is likely that a flush dislodged some individuals from the nest and swept them downstream. In addition to the native species, common carp, European perch and gambusia larvae were also collected from the Broken River. The larvae of most of the native and introduced species were collected consistently in each of the years studied. Golden perch

Table III. Total number of larval fish collected from the Campaspe and Broken rivers between October 1995 and April 1998

Species	Campaspe River		Broken River	
	Total no.	%	Total no.	%
Australian smelt	1408	17.66	3906	73.12
Flathead gudgeon	5760	72.23		
Carp gudgeons	18	0.22	709	13.27
Murray cod			228	4.27
Blackfish			4	0.08
Rainbowfish			41	0.77
Galaxias sp.			57	1.07
European perch	662	8.30	28	0.53
Common carp	126	1.58	358	6.70
Gambusia			9	0.17
Golden perch			2	0.04
Grand total	7974		5342	

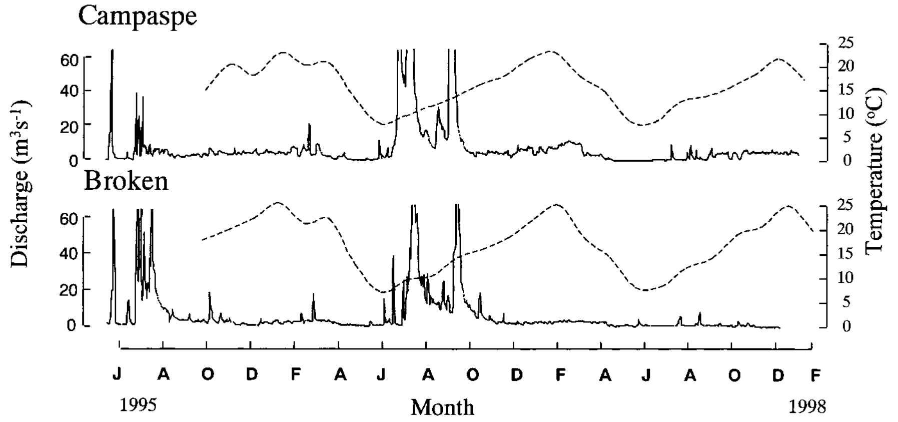

Figure 2. Discharge (solid line) and water temperature (dashed line) for the Campaspe River (at Barnadown) and Broken River (at Casey weir) between June 1995 and January 1998; discharge has been truncated at 60 $m^3 s^{-1}$

larvae, however, were only collected in the 1997–1998 season. The Broken River larval fish fauna was dominated by Australian smelt, with smaller but significant contributions from carp gudgeons, Murray cod and common carp (Table III).

Discharge and temperature

Mean daily discharge records were obtained from a gauging station above Campaspe Weir in the Campaspe River and for a gauging station above Casey Weir in the Broken River between June 1995 and January 1998 (Goulburn-Murray Water, unpublished data). Temperature was recorded in these same sections of each river using a Horiba U-10 Water Quality Checker once per month at two stations.

The Campaspe and Broken rivers follow very similar patterns, because both rivers are under the influence of the same climatic conditions and their catchments are relatively close (Figure 2). Temperature showed some variation throughout the 3 years of study. Temperatures reached their maximum in January in 1996 and 1997, but 1 month earlier the following year. Temperatures were usually above 20°C between December and February in each year. Minimum temperatures occurred in June at approximately 7°C.

The pattern of daily discharge varied considerably among the 3 years (Figure 2). The winter of 1995 experienced about average rainfall, both rivers had periods of high flow between June and late August, and Lake Eppalock spilled for a short time. Above-average rainfall in the winter and spring of 1996 resulted in two periods, August and October, of close to bankfull or over-bank flows in both rivers. Billabongs (oxbow lakes) and anabranches (anastomosing channels) were connected to the main stems of the rivers for several weeks in total. Low daily discharge levels did not set in until about December of that year. The following winter had very little rain, and consequently discharge throughout this time in both rivers was extremely low. These conditions persisted throughout summer, although there were irrigation releases in the upper two sections of the Campaspe River and below the Lake Mokoan outlet in the Broken River.

DISCUSSION AND CONCLUSIONS

The state of the fish fauna of the Campaspe River is poor. This is evident from the results of adult and larval fish sampling. Indeed, the dominant species recorded as adults were also dominant as larvae. The difference in proportions of these two groups almost certainly relates to the temporal scale of sampling and the duration of spawning and therefore occurrence of larvae of each species. In other words, flathead gudgeon and smelt, two small native species, spawn for between 5 and 7 months, whereas common carp and European perch spawn for only 1 or 2 months. Thus, the larvae of the former two species contribute more, simply because of the extended duration of their occurrence in the river. The other species, such as Murray cod, golden perch and silver perch, which were collected as adults from the Campaspe, did not occur as larvae. No large native fish were found to have spawned in the Campaspe River in any of the years studied.

Although the records for the adult fish in the Broken River are not as good, it can be stated with confidence that the fish fauna of this river is in a much healthier state than that of the Campaspe. A much greater proportion of those species known to exist as adults in the river occurred as larvae. Notable was Murray cod, whose larvae were collected in each of the 3 years. Notable by its absence, except in the last year, was golden perch.

There was remarkable inter-annual consistency in those species of fish that occurred as larvae in each of the rivers studied. It is uncertain why some species, which were caught as adults, were not found as larvae. It may be that they were so sparse that the sampling did not coincide either temporally or spatially with the larvae. Or it may be that their populations are so small that they cannot find a mate at the right time or, alternatively, that the right spawning cues no longer exist. If either of the last two explanations is true, it is apparent that fish larvae provide a reliable indication of which species spawned during each breeding season. This fact in itself is important for the assessment of the viability of populations of fish under regulated conditions. Indeed, fish larvae are very useful in the evaluation of the health of river systems in general, primarily because of the specific habitat, flow and food requirements of this life stage (Sheaffer and Nickum, 1986; Schiemer *et al*., 1991; Scheidegger and Bain, 1995). There is also complete certainty that the fish larvae are derived from the river in which they were found, unlike juvenile and adult fish which may be the result of stocking or migration.

The results from the Broken River, which include several native species, suggest that the considerable inter-annual variation in daily discharge and temperature in the months immediately preceding the breeding season have little effect on which species spawn. This suggests that variables other than daily discharge, *per se*, govern when fish spawn. On the other hand, golden perch were only found as larvae in the last year of the study. Their occurrence in this year, which coincided with extremely poor winter rains before the breeding season and low daily discharge throughout summer, is in complete contradiction to previous work which has suggested that this species requires a rise in flow to initiate spawning (Lake, 1967; Mackay, 1973; Cadwallader, 1990). However, the origins of the larval golden perch are not clear. Only a handful was collected from the Broken River and these occurred approximately 500 m upstream of the mouth of a channel that links the river with Lake Mokoan, an off-river water storage. It is unlikely that the larvae could have been carried out of Lake Mokoan by the current and then swum against that current upstream into the weir pool for this distance, but the possibility cannot be ruled out. The larvae collected were probably only 1–2 days old, because they still had large yolk sacs. Whatever the origins of the larvae, a post-larval golden perch was caught in a drift net approximately 10 km downstream of the weir pool, providing further evidence of successful spawning and at least some recruitment of this species during the breeding season of 1997–1998.

What do the fish larvae in the Campaspe and Broken rivers tell us about the relative influences of river regulation on the reproduction or recruitment of fish in these types of lowland rivers? The results from the moderately regulated Broken River suggest that fish will continue to spawn despite the considerable variation in the daily discharge that prevails around the time when they normally spawn. On the other hand, in this river there may have been strong selection for those species that are cued to mature and spawn under a variety of conditions and therefore only those species survive. This strategy, of annual spawning, is apparently widespread among the Murray-Darling fish fauna, with only golden and silver perch thought to delay spawning if conditions are not appropriate in any one year (Cadwallader, 1990; Humphries *et al*., 1999). Assuming that most species of fish will spawn each year and that the results can be extrapolated from the Broken River to the Campaspe, the absence or low abundance of a species in that river should indicate a history of poor recruitment. With the initiation of regulation, fish may have continued to spawn; however, with the construction of barriers preventing movement, and low recruitment, it may not have taken many years for numbers of fish to decline to levels which would have also made successful spawning difficult.

Other workers have suggested that recruitment in species through their larvae can be affected by hydrological conditions as well as by the influence of flow regulation on the nature of, and links with, rearing habitat (Scheidegger and Bain, 1995; Copp, 1997a,b; Kennedy and Vinyard, 1997). Apart from the disruptive effects of flow regulation, many regulating storages have hypolimnetic releases of cold water, a common occurrence in south-eastern Australia (Gippel and Finlayson, 1993; Finlayson *et al*., 1994). Although Lake Eppalock depresses the temperature of water downstream during summer by up to 5°C, the Campaspe River still maintains temperatures above 20°C for several months each year, which should be warm enough for most fish to spawn. Previous work in hatcheries has shown that golden perch require temperatures above 23°C to cue spawning; however, this has not been confirmed in the wild. For most other species, temperatures above 20°C appear sufficient for spawning to occur (Lake, 1967). A shorter period of warm water, however, may also play a role in reducing the window of opportunity for recruitment of some species.

It is clear that there is a need to understand the influence of hydrology on recruitment in lowland river fish. If spawning is consistent from year to year but recruitment is not, future investigations should focus first on determining how environmental conditions correlate with recruitment, and then on determining mortality schedules for the early life stages of fishes. Then we can identify when fish are most at risk and when they can be said to have recruited. Finally, the hydrology-driven processes that influence recruitment need to be identified. Mortality is extremely high during the early life stages of a fish and small changes in density of food, intensity of predation, access to rearing habitats or water quality can mean the difference between recruitment success and failure. If we hope to improve riverine fish populations through enhanced recruitment we need to understand how the hydrology of a river influences each of the above variables, and in turn how these variables interact to influence the survival and growth of young fish.

This study has indicated that the occurrence of the larvae of most species of fish is a predictable event in two lowland Australian rivers, despite considerable inter-annual variation in hydrologic regime, and is likely to be a reliable indicator of those species that spawn within each system. Fish larvae are thus able to provide some crucial insights into the effects of river regulation on fish populations and communities: whether river regulation has prevented fish from spawning or, alternatively, reduced recruitment or eliminated it entirely. We suggest that fish larvae are a useful initial indicator of the effects of river regulation and recommend that follow-up studies on the mechanisms influencing recruitment be included in future remedial studies.

ACKNOWLEDGEMENTS

The authors thank Luciano Serafini and Alison King for assistance with larval fish sampling, and Paul Brown, John Douglas, Andrew Pickworth and Russel Strongman from the Marine and Freshwater Resources Institute, Snobs Creek, for providing much of the juvenile and adult fish data for the Campaspe River. Tarmo Raadik from the Freshwater Ecology Division of Marine and Freshwater Resources Institute kindly supplied historical records of fish collected from the Campaspe and Broken rivers. The authors are grateful to two anonymous referees for their comments on the manuscript. This study was partly funded by the Land and Water Resources Research and Development Corporation, and Environment Australia.

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