

Downstream transport of larval and juvenile fish in the Murray River

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NRMS Project No. R7019
July 2003

NSW Fisheries Final Report Series
No. 50
ISSN 1440-3544



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Authors: Dean Gilligan and Craig Schiller
Published By: NSW Fisheries
Postal Address: PO Box 21, Cronulla NSW 2230
Internet: www.fisheries.nsw.gov.au

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ISSN 1440-3544

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ACKNOWLEDGEMENTS

This research was supported by the Murray-Darling Basin Commission through the Natural Resources Management Strategy. We thank Keith Breheny, Andrew Bruce, Michael Rodgers and Ian Wooden for technical assistance. We also thank the steering committee which consisted of John Harris, Paul Humphries, Gerry Quinn, John Koehn and Lance Lloyd.

Paul Humphries provided advice on larval fish sizes. The Department of Land & Water Conservation provided flow and temperature data from gauging stations throughout the reach of the Murray River studied. The Department of Land & Water Conservation, Goulburn-Murray Water and Murray Irrigation provided data on water extraction volumes.

Thanks also goes to the land owners and management bodies who provided permission to access survey sites.

Lee Baumgartner, Bob Creese, Stuart Rowland, Mark Lintermans and Jim Barrett provided helpful comments on the draft report.

This research was conducted under ACEC approval number 99/2.

Several ichthyoplankton sampling techniques were used: light traps (to sample backwaters and areas of low flow), fyke nets (to sample benthic drifting fish in addition to fish migrating upstream), and drift nets (to sample pelagic drifting fish). Intensive sampling was done in the first 2 years; in the final year of sampling (November 1999), a modified drift net design was used to sample multiple levels within the water column and at four periods throughout the day. A subsample of drifting fish were aged by sectioning their otoliths and counting annual bands.

A total of 35,064 fish, and 1,585 fish eggs were sampled from the Murray River during this study. Species caught comprised five alien fish species, five native fish species and three native fish genera that were not identified to species level; carp gudgeons, flat-headed gudgeons and freshwater cod. No golden perch larvae were caught, and only one larval silver perch was sampled. Eggs caught in the nets were not readily identified to species level, but a subsamples of eggs subsequently hatched at the Narrandera Fisheries Centre were identified as those of golden perch and silver perch.

There were significant differences between the fish communities sampled from the 12 sites within the river. However, the only consistently different fish community was that which occurred within the Torrumbarry weir-pool, which was dominated by carp gudgeons.

Significant differences were detected between fish communities sampled by each of the sampling gears used. Carp gudgeons and Australian smelt were sampled more frequently in backwater areas than in either pelagic or benthic drift samples. In contrast, cod, carp and eggs were more abundant in drift samples. Cod, carp and eggs were sampled by both drift nets and fyke nets but carp and eggs were more abundant in the pelagic drift net samples while cod were more abundant in the benthic drift nets. In contrast, drifting carp gudgeons, Australian smelt and flat-headed gudgeons were never sampled in the pelagic drift nets and were only captured in the benthic fyke nets.

Comparison of fish moving upstream against the flow with those drifting downstream, demonstrated that large numbers of carp gudgeons and Australian smelt were moving upstream during the sampling period. Fish species that predominantly moved downstream were cod and carp. Eggs were not included in this analysis, as all eggs sampled were moving in the downstream direction as expected.

The study confirmed that larval cod (Murray cod and/or trout cod), juvenile carp and both golden and silver perch eggs drift downstream as part of the ichthyoplankton. Densities of each of these drifting taxa were up to 44.49 per Megalitre (ML^{-1}) (mean \pm SE = 2.89 ± 0.75) for cod, 1,704.29 ML^{-1} (mean \pm SE = 50.97 ± 23.68) for carp and 156.63 ML^{-1} (mean \pm SE = 4.14 ± 2.09) for perch eggs. These densities are within the ranges observed by other studies of drifting ichthyoplankton.

Cod larvae commenced drifting in late October and had settled from the drift prior to late December in both 1997 and 1998. Therefore, the period over which downstream drift occurs is approximately two months. However the greatest abundance of drifting cod occur during a four week period throughout November. The presence of cod larvae, and therefore cod reproduction, was patchily distributed within the section of the Murray River studied, and reproductive outputs at each site were not consistent over the two breeding seasons sampled. The ages and sizes of cod larvae suggest that larvae drifting downstream had recently commenced dispersal and had spent little time drifting downstream. This suggests that larval cod are likely to undergo downstream drift for a short period of only a few days. Cod larvae were not found to move upstream following their short period of larval drift. Nor were they found to settle into backwaters or low flow habitats. A possible hypothesis is that following a small amount of downstream drift, larval cod settle onto the bottom and make no further upstream or downstream movements. No relationship

between flow and cod spawning was identified. In contrast to expectations, cod reproduction was greatest in 1997, when spawning occurred at basal flows.

Larval and juvenile carp began downstream drift in early October and continued to occur in the drift until February. A vast majority of drifting carp appeared at the beginning of the season in mid October, with smaller peaks throughout November. The period of time over which carp larvae and juveniles occurred in the drift was much longer than that observed for cod. The age of carp sampled drifting downstream ranged from 10-53 days with a mean of 32 ± 2 days. This provides further evidence that carp undergo a much longer period of downstream dispersal than cod. As a result, there is greater potential for carp to travel and disperse further downstream than for the more localised downstream movements of cod larvae. Within the section of the Murray River surveyed, the Barmah-Millewa forest was identified as a major source of carp reproduction. This has also been reported from studies of carp undertaken by the Arthur Rylah Institute (Victoria). In contrast, very little carp reproduction occurs between Yarrowonga and the Barmah-Millewa forest. In contrast to cod, carp spawning activity is closely associated with inundation of the floodplain habitats within the Barmah-Millewa forest. Flows in excess of 9,500ML from early September are likely to result in substantial carp spawning. Dispersal of carp larvae/juveniles was found to be closely associated with the receding tails of flow peaks. Therefore, subsequent flow peaks or flow peaks sustained for 5-14 days are likely to result in substantial dispersal of carp juveniles from wetland habitats into the main river channel. This knowledge may assist with developing informed harvest of aggregating adults or dispersing juveniles from this and other key locations of carp reproduction.

There was a virtual absence of golden perch or silver perch larvae, despite the fact that the sampling strategy had been specifically designed to sample drifting larvae of these two species. However, subsamples of drifting eggs were positively identified as those of golden and silver perch. Eggs occurred in the drift between mid October and late January. In contrast to expectations, there was no evidence that spawning activity of golden or silver perch is associated with high flow events as all spawning activity in the Murray River in 1997 and 1998 was at stable regulated flows.

We found no evidence that Torrumbarry Weir significantly obstructed the downstream drift of cod larvae within the Murray River. In contrast, there were significant differences in the densities of carp, with highest densities in the river and significantly lower densities in the weir-pool and below Torrumbarry Weir. This suggests that carp may settle from the drift under the low flow conditions of the weir-pool. The occurrence of larval cod and larval/juvenile carp immediately below Torrumbarry Weir at equivalent densities to their occurrence in the weir-pool suggests that both species may pass through Torrumbarry Weir during downstream drift. Although the weir itself was not found to significantly obstruct downstream drift, settlement of ichthyoplankton in the associated weir pool may have implications for recruitment. However, rather than weir-pools providing sub-optimal rearing habitats, they may provide habitats and resources which could potentially improve recruitment for drifting fish. This results from weir-pools simulating the naturally low flows which would have been experienced by spawning and recruiting fish during the breeding season under non-regulated flow conditions.

Large scale water extraction can have serious adverse effects on species of fish with downstream drifting larvae. Drifting cod larvae and the eggs and larvae of golden and silver perch can be entrained in water extracted from the river. As this water is not returned to the river system, water extraction during the breeding season has the potential to remove large numbers of potential recruits from the ecosystem. Density data and extraction records suggest that millions of cod larvae and eggs of golden and silver perch are removed from the Murray River annually. However, as cod have a highly predictable larval drift period within the months of October – December, reduction in the volume of water extracted during these months will enhance

recruitment of cod and may result in substantial rehabilitation of cod populations. Further, larval drift is a nocturnal behaviour in most species of fish studied. If this applies to Australian native fish, restricting water extraction from the river to hours of daylight, may result in further substantial benefits for fish communities within the river system whilst having little impact on extraction volumes.

1. INTRODUCTION

The early life-history stages of fishes, from egg to juvenile, have a disproportionately high influence on population dynamics (Chambers & Trippel 1997; Gadomski & Barfoot 1998). Eggs and larvae may be more sensitive to environmental effects than older life-stages (Childs *et al.* 1998). Environmental degradation of freshwater ecosystems, such as cold water pollution, river regulation, habitat loss and pollution, can have serious consequences for recruitment. As a result of environmental degradation of river systems within the Murray-Darling Basin, the distribution and abundance of native fish has declined significantly over the last ~50 years (Reynolds 1976; Cadwallader 1978). Most studies aimed at assessment of these impacts have been directed at adult fish populations and predominantly those large species which are commercially or recreationally important. Only recently has research been undertaken on the critically impacted early life stages of fish within the Murray-Darling Basin (Humphries *et al.* 1999; Humphries & Lake 2000; Humphries *et al.* 2002; King 2002; Meredith *et al.* 2002).

1.1. Downstream larval drift

It is well established that migration is essential for a number of fish species occurring in the Murray-Darling Basin (Mallen-Cooper 1989; Mallen-Cooper *et al.* 1995) and Australian rivers in general (Horwitz 1999; Thorncraft & Harris 2000; Koehn 2001; Gehrke *et al.* 2002). A great deal of effort is being made to reinstate fish passage, with several million dollars allocated to install fishways on all major barriers on the Murray River downstream of Hume Weir (Murray River Fishway Assessment Program, 2002). Fishway research and resultant management actions are intended to assess and improve upstream migrations of adult and juvenile fish. However, downstream dispersal of eggs and larvae, termed larval drift, has received little attention (but see Humphries & Lake 2000; Humphries *et al.* 2002; Meredith *et al.* 2002) despite its potentially important role in dispersal of some migratory species (Reynolds 1983; Mallen-Cooper *et al.* 1995). World-wide, the downstream drift of eggs and larvae is an important life history process for a wide variety of fish (Brown & Armstrong 1985). Within the Murray-Darling Basin, several species with either an obligatory or facultative larval drift stage have been identified (Humphries *et al.* 2002).

The timing and conditions for spawning of riverine fish are likely to have evolved to optimise the survival and development of eggs and larvae. For example, some species of drifting taxa are thought to be reliant on river rises to act as spawning cues (Lake 1967a; Reynolds 1983; Schiller & Harris 2001). Others are cued by ambient conditions such as temperature or photoperiod (Humphries *et al.* 1999; Schiller & Harris 2001; Humphries *et al.* 2002; Meredith *et al.* 2002). The evolved responses of each species to conditions of flow and temperature make riverine fish susceptible to river regulation and associated effects (Humphries *et al.* 2002). One of these effects is the alteration of the way regulated flows transport eggs and larvae downstream (Humphries *et al.* 2002).

1.2. Reproductive biology of riverine fish species with drifting larvae

1.2.1. *Murray cod and trout cod*

Murray cod (*Maccullochella peelii*) and the closely related trout cod (*Maccullochella macquariensis*) are both thought to be temperature cued spawners, with Murray cod spawning at temperatures of 16 - 20°C and trout cod at 16°C (Lake 1967a; Rowland 1983a; Ingram & Rimmer 1992; Rowland 1998b; Humphries *et al.* 2002). Therefore, the timing of spawning for Murray cod is likely to vary throughout its distribution, with spawning occurring earlier in the warmer northern

areas of the Murray-Darling Basin. If spawning does not commence, extended exposure to temperatures of 16 - 20°C causes damage to the oocytes which are rapidly reabsorbed (Lake 1967a; Ingram & Rimmer 1992). Rowland (1998b) reported that by December, gonads of wild fish are either spent or re-absorbing. As a result, spawning opportunities for freshwater cod species are restricted to a narrow window of opportunity for any one population. This 'season' could be as short as 4-5 weeks (Rowland 1998b). It is known that Murray cod do not require a rise in flow to trigger a spawning event (Rowland 1998b). The flow requirements of trout cod are less clear. Unlike Murray cod, this species will not spawn in hatchery ponds without hormone treatment, despite the seasonal (winter) gonadal maturation being similar in both species (Ingram & Rimmer 1992; Rowland 1998b). Hatching of Murray cod commences 5 - 9 days after fertilisation (Lake 1967a; Ingram & Rimmer 1992) and larval cod remain 'clumped' within the spawning site (Cadwallader & Gooley 1985; Ingram & Rimmer 1992). Following yolk sac absorption, 21 - 25 days after fertilisation and at a size of 12 - 13 mm (Lake 1967b; Ingram & Rimmer 1992; Rowland 1992), larvae disperse and are known to drift in the current (Koehn & Nicol 1998; Humphries *et al.* 2002).

1.2.2. *Golden and silver perch*

Golden perch (*Macquaria ambigua*) and the threatened silver perch (*Bidyanus bidyanus*) are unrelated taxa that have adopted similar reproductive strategies. Both species are thought to have a temperature threshold of around 22.5°C required for spawning (Rowland 1983; Battaglione 1991; Rowland 1996). However, unlike cod, it is considered that they depend on a river rise to stimulate aggregation and spawning activity (Lake 1967a; Mackay 1973; Cadwallader 1977; Rowland 1983; Mallen-Cooper 1996; Stuart and Jones 2002). Spawning is believed to be preceded by a substantial upstream migration in both species (Reynolds 1983; Battaglione 1991; Mallen-Cooper *et al.* 1995). Unlike cod, golden and silver perch are able to maintain gonadal maturity for an extended period, and do not reabsorb oocytes until February or March (Lake 1967a; Rowland 1983; Cadwallader 1990; Battaglione 1991). However, breakdown of oocytes occurs gradually if fish are exposed to temperatures above 23°C for several weeks (Lake 1967a).

Eggs of both species are semi-buoyant due to the existence of oil droplets (Lake 1967a). Their pelagic eggs drift with the current for a short incubation period of 24 - 46 hours (Lake 1967b; Rowland 1984; Rowland 1996; Neira *et al.* 1998). The larvae are small (2.5 - 3.7 mm) (Lake 1967a, Lake 1967b, Neira *et al.* 1998), poorly developed at hatching, and continue to drift in the current (Lake 1967b; Rowland 1996). The yolk sac is absorbed after 5 days at sizes < 6 mm in length (Gehrke 1990a; Gehrke 1990b; Rowland 1996). At 12 - 15 days old, larvae are no longer positively buoyant (Gehrke 1990b). Metamorphosis occurs at 18 - 25 days (Lake 1967b; Gehrke 1990b). At up to 25 days old, golden perch larvae still showed no rheotactic behaviour (swimming against the flow) and could not hold their position in the water flowing at 5 mm s⁻¹, but a small proportion of silver perch showed rheotactic behaviour at this age (Gehrke 1990b). Eggs and larvae of both species are likely to drift in the current but few larval fish studies have sampled them (Koehn & Nicol 1998; Humphries *et al.* 2002).

1.2.3. *Carp*

The introduced carp (*Cyprinus carpio*) also has a dispersal phase through downstream drift. The potential for reliance of carp on temperature or photoperiod as spawning cues is weak as they have an extended spawning period and may spawn over several days (Mills 1991) and a number of times each year (Adamek 1998; Brown *et al.* 2003). Rising river levels are not required for spawning, but these conditions enhance spawning activity through the inundation of spawning habitat such as floodplains or riparian vegetation (Mills 1991; Roberts & Ebner 1997; Adamek 1998; Vilizzi 1998; Brown *et al.* 2003). The eggs of carp are adhesive (Mills 1991) and hatch within 2 - 6 days. The 5 mm long larvae remain attached to vegetation for a further 2 - 8 days by cement glands on their heads (Schoonbee & Prinsloo 1984; Roberts & Ebner 1997). Free-

swimming larvae appear 4 - 14 days after spawning and are reported to be poor swimmers with little ability to maintain their position against currents (Mills 1991). Spawning habitats are largely restricted to off-channel or low-flow habitats. However, at some stage in development, larval carp leave their vegetated habitats and disperse downstream via larval drift.

1.2.4. Bony herring

The reproductive strategy of bony herring (*Nematalosa erebi*) has received little attention (Puckridge & Walker 1990). Bony herring are in the same family as the North American gizzard shad (Clupeidae: Dorosomatinae) (Puckridge & Walker 1990), for which larval drift is recognised as an important process (Muth & Schmulbach 1984). *Nematalosa erebi* is extremely fecund (Puckridge & Walker 1990). Spawning occurs between October and February and is not flow dependent (Llewellyn 1983; Puckridge & Walker 1990; Humphries *et al.* 1999; Meredith *et al.* 2002; Wooden pers. obs.). Newly stripped eggs are adhesive and demersal, but the eggs do contain an oil droplet and have been sampled in a semi-buoyant state (Puckridge & Walker 1990). Spawning involves aggregations of adult fish at spawning sites, usually open sandy substrata (Puckridge & Walker 1990), but spawning has also been observed over submerged macrophyte beds (Wooden pers. obs.). Larvae hatch at 3 mm and are initially difficult to distinguish from larval Australian smelt.

1.2.5. Facultative drifting species

Humphries *et al.* (2002) identified the flat-headed gudgeon (*Philypnodon grandiceps*) as a facultative drifting species. This species has a protracted spawning season and is potentially a serial spawner (Humphries *et al.* 2002). It is not known to exhibit any predictable spawning behaviour in response to cues such as temperature or flow.

1.3. The impact of river regulation on downstream larval drift

Numerous dams, weirs and other barriers regulate and divert flow in the major tributaries of the Murray-Darling Basin (Horwitz 1999; Blanch 2001; Young 2001), creating flows in regulated rivers that are significantly altered from unregulated conditions (Walker 1985; Maheshwari *et al.* 1995; Walker 2001). If the hydrological regime or water quality conditions are changed, as they are by river regulation, species that rely on flow or temperature cues to initiate maturation and spawning may be affected (Mackay 1973; Jackson 1989; Humphries & Lake 2000). Alternatively, spawning may occur, but conditions may be unsuitable for larval survival and recruitment (Rowland 1983a; Mion *et al.* 1998; Humphries & Lake 2000). An example is seasonal flow reversal in the lower Murray-Darling Basin. Altered flows and water extraction during spawning, hatching and larval developmental periods of species which exhibit downstream larval drift will contribute to changes in the distribution and abundance of populations within a river system (Bishai 1960).

Results from tag-recapture studies demonstrate that adult fish are capable of successfully moving downstream past low-level weirs within the Murray-Darling Basin (O'Connor *et al.* 2003). However, O'Connor *et al.* (2003) demonstrated that Murray cod and golden perch exhibited significant behavioural avoidance to passing downstream at Torrumbarry and Kennedy's Weirs. Northern hemisphere studies have suggested that weirs prevent the downstream migration of juvenile salmonids (Bell and DeLacy 1972; Haro *et al.* 1998; Jepson *et al.* 1998). Mallen-Cooper *et al.* (1995) identified the process whereby drifting larvae are carried over weirs or dams as a potential cause of increased larval mortality. Further, the concentration of eggs and consequent settlement of large numbers of larvae in weir pools because of reduced flow in these environments could also lead to poor downstream transport. Lastly, water extraction could potentially result in the removal of eggs and larvae from the river system (Koehn & Nicol 1998).

Identifying the spatial scale and timing of downstream transport of eggs, larvae and juvenile fish, the species composition of the drifting larval assemblage and the impacts of river regulation on larval fish could identify critical management requirements for fish communities in regulated rivers.

1.4. Natural processes affecting downstream larval drift

Understanding the potential for dispersal and the level of control that larvae and small fishes have over the timing and extent of their entrainment within flowing water may provide a basis for assessing the effects of river regulation and water extraction. Diel drifting behaviour has been demonstrated in many species of freshwater fish (Clifford 1972, Gale & Mohr 1978; Muth & Schmulbach 1984, Flecker *et al.* 1991; Gehrke 1992; Childs *et al.* 1998). Similarly, rheotaxis (swimming against the flow) is also documented for the larvae of a number of fish species (Bishai 1960; Gehrke 1990*b*; Gehrke 1992). As a result, behaviour of larval fish can influence the rate, and therefore the extent, of dispersal and their ability to exhibit active habitat choice and settlement from the drift in appropriate locations.

1.5. Objectives

This study aimed to describe aspects of the downstream transportation of eggs, larval and juvenile fish. In doing so, we aimed to assess the timing and spatial scale of downstream drift and the impacts of barriers and water extraction on downstream migration.

2. METHODS

2.1. The Murray River between Mulwala and Barham

The Murray River between Yarrowonga and Barham (Figure 1) supports breeding populations of six of the seven species thought to undertake larval drift: Murray cod, trout cod, golden perch, silver perch, flat-headed gudgeon and carp. The seventh species, bony herring, do occur in the Murray River but are not abundant within this reach. Further, it is not known if this species spawns this far up the Murray River catchment. Twelve sites were selected over a 450-kilometre reach of the Murray River (Table 1, Figure 1). Distances between sites ranged from 25 to 58 km (Table 1).

Two migration barriers, Yarrowonga Weir and Torrumbarry Weir, exist within this section of the river. Water extraction within this reach occurs at the Yarrowonga, Mulwala and Corurgan canals (upstream of site 10), the National channel and Toupna Creek offtakes (Torrumbarry) and a small un-named offtake (downstream of site 11).

2.2. Sampling periods

Sampling was undertaken over three consecutive years, 1997 to 1999. For the first two years, sampling was undertaken between October and February, which comprises a majority of the reproductive period for most species in the Murray River (Humphries *et al.* 2002). During this period, flow is regulated by release from Hume Weir, and water is extracted from the river.

Sites were sampled fortnightly, in sequence from downstream to upstream, throughout the 1997-1998 sampling period. More than one site was sampled per day in the 1998-1999 season. Consequently, sites were sampled every 7.5 ± 0.8 days. Two sites not sampled in the initial sampling season were added for the 1998-1999 season. Site 11 (Koondrook) was added to extend the length of river sampled and site 3.5 (Wills Bend) was added to give greater resolution for assessment of weir pool effects. Sampling at site 6 (Bull paddock) was discontinued in the 1998-1999 season.

Only sites 5 and 7 were sampled in the 1999-2000 season. Both sites were sampled for a single 48 hour period in November 1999.

2.3. Sampling methods

Several types of ichthyoplankton sampling techniques were used. Ichthyoplankton nets have been used widely to collect fish eggs and larvae (Gale & Mohr 1978; Gallagher & Conner 1983; Muth & Schmulbach 1984; Brown & Armstrong 1985; Flecker *et al.* 1991; Franzin & Harbicht 1992; Kelso & Rutherford 1996; Pavlov *et al.* 1996; Robinson 1998; Humphries *et al.* 2002; Meredith *et al.* 2002). A combination of sampling equipment was used at each site (Table 2). Equipment was set overnight and the mean set time for each type of equipment was $16:59 \pm 0:04$ hours. In the second sampling season, two sites were sampled per day on several occasions. When this occurred, the number of nets deployed was reduced at one of the sites. The term 'partial set' refers to the modified equipment layout (Table 2).

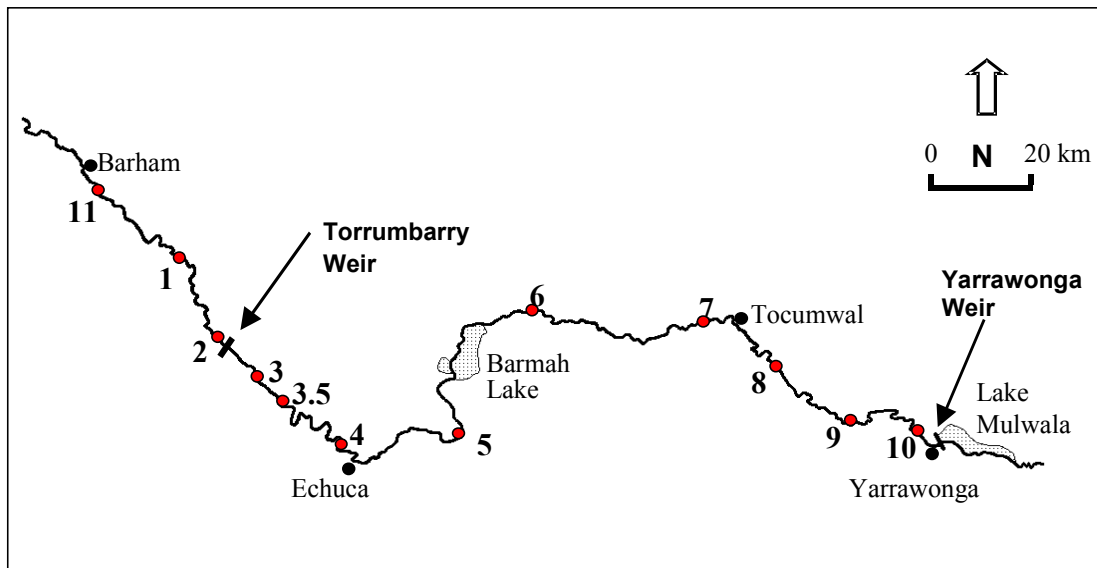


Figure 1. Survey sites within the Murray River, New South Wales, Australia.

Table 1. Site numbers, names and locations sampled from November 1997 to November 1999. Reach length describes the distance between each site and the next site upstream.

Site No.	Site Name	Longitude	Latitude	Distance from mouth (km)	Reach length (km)	Comments
11	Koondrook	144 ⁰ 09' 20"	35° 39' 40"	1,532	40	
1	Nursery bend 3	144 ⁰ 20' 30"	35° 46' 00"	1,572	52	
2	Torrumbarry	144 ⁰ 26' 40"	35° 56' 00"	1,624	26	Below weir
3	Tabs Tavern	144 ⁰ 30' 40"	35° 59' 45"	1,650	30	Weir-pool
3.5	Wills bend	144 ⁰ 36' 00"	36° 01' 45"	1,680	25	Above weir-pool
4	Echuca	144 ⁰ 43' 15"	36° 06' 10"	1,705	51	
5	Jepsoms Nursery	144 ⁰ 59' 00"	36° 03' 15"	1,756	58	
6	Bull Paddock	145 ⁰ 07' 30"	35° 49' 00"	1,814	57	
7	Ulupna Island	145 ⁰ 28' 15"	35° 48' 35"	1,871	37	
8	Race course	145 ⁰ 37' 30"	35° 53' 00"	1,908	40	
9	Burkes Beach 3	144 ⁰ 49' 30"	35° 59' 00"	1,948	34	
10	Yarrowonga	145 ⁰ 59' 59"	36° 01' 09"	1,982	0	Below weir

Table 2. Sampling equipment used at each site per sampling season.

Equipment per site	Sampling season			1999-00
	1997-98	1998-99 Full Set	Partial Set	
2mm Fyke net	4	4	0	0
3mm Fyke net	4	0	0	0
Drift net (high flow)	1	1	1	0
Drift net (medium flow)	1	1	1	0
Drift net (low flow)	1	1	1	0
Quatrefoil light traps	10	8	4	0
Triple-rigged drift nets	0	0	0	2

2.3.1. *Drift nets*

Drift nets were 1.5 m long cones constructed from 250 µm mesh. The circular opening was 40 cm in diameter and had a single funnel trap. The surface area to mouth ratio of 10:1 was more conservative than that recommended by Kelso & Rutherford (1996) to minimise debris blockage within the net. The net entrance was covered with a 40mm mesh exclusion screen to prevent the entry of large animals and debris. These nets were set facing upstream in the upper parts of the water column as previous studies had demonstrated that larvae are found at greater densities near the surface (Brown & Armstrong 1985; Franzin & Harbicht 1992).

Flow meters (*General Oceanics*) were positioned in the entrance of all drift nets in the first year of sampling. Due to the increased number of nets in the following season, not all nets had flow meters attached. Flow meters in the drift nets enabled estimation of the volume of water filtered by the net.

2.3.2. *Triple-rigged drift net*

A series of three drift nets supported by a frame was used to assess larval densities at various depths within the water column. The sampling gear was set in water depths of around 2.5 m. Spacers were used to modify the depth of each net within the apparatus. The top net was set at the surface, the bottom net was set 5 cm above the substratum and the middle net was set at half depth.

Two triple-rigged nets were set at each of the two sites used for this component of the study, one in fast flow and the other in a low flow area. Each of the three nets in the fast flow set was fitted with a flow meter. In the low flow set, only the mid depth net was fitted with a flow meter. Flow readings were recorded on each retrieve. Nets were set for 48 hours and cleared on a 6 hourly basis at 3:00, 9:00 15:00 and 21:00 (Australian daylight savings time).

2.3.3. *Fyke nets*

2 mm Fyke nets

The rectangular entrance hoop of these nets was 66 cm wide and 48 cm deep and had a single funnel trap fitted with a large mesh exclusion screen. Two 2 m long wings with a drop of 75 cm were fitted to the sides of the entrance hoop and were set with their ends spaced 2 m apart projecting forward from the entrance. These nets were set on the river bed facing upstream to capture fish moving downstream with the flow. The ratio of surface area to mouth area was greater than 4:1.

3 mm Fyke nets

These nets were identical to the 2 mm nets but were constructed from slightly larger mesh. In contrast to the 2 mm fyke nets, these were set facing downstream to sample fish moving upstream against the flow. 3 mm fyke nets were used in the 97-98 season only.

2.3.4. Light traps

Perspex Quatrefoil traps (Secor *et al.* 1992) were set with a 12 hour yellow cyalume light stick. These traps were set in low flow areas such as backwaters and often amongst macrophytes.

2.3.5. Sorting and identification

A reference collection of approximately 200 larvae of a range of positively identified specimens was available for identification. Sorting and identification was undertaken in the laboratory using stereoscopic microscopes. Larvae of most species were identifiable to species level, with the exception of carp gudgeons (*Hypseleotris* spp.), flat-headed gudgeons (*Philypnodon* spp.) and freshwater cods (*Maccullochella* spp.) which, due to the difficulty of positively identifying larvae, were only identified to the level of genus¹.

Reference specimens of hatchery produced golden perch and silver perch eggs were used to differentiate eggs of these species. No distinction was made between the eggs of either golden or silver perch. To support identification, a subsample of eggs ($n \approx 50$) collected on the 14th October 1998 were hatched at the Narrandera Fisheries Centre and positively identified as those of golden perch and silver perch.

Samples were preserved in 70% ethanol.

2.3.6. Flow and water diversion volumes

Flow data (megalitre (ML)/day) and water temperatures from gauging stations at Yarrawonga (409025), Tocomwal (409202) Torrumbarry (409207) and Barham (409005) were provided by the NSW Department of Sustainable Natural Resources. Water diversion volumes from the Murray River between Mulwala and Barham (ML per month) were provided by Murray Irrigation, the Department of Sustainable Natural Resources and Goulburn-Murray Water.

The time taken for flows to travel from Yarrawonga, through Tocomwal and Torrumbarry to Barham was estimated by counting the number of days taken by flow peaks and troughs to travel between adjacent gauging station and calculating the mean number of days across all flow events.

2.3.7. Water quality

During sampling, temperature, pH, dissolved oxygen (DO), conductivity and turbidity were measured using a Horiba U10 Water Quality Checker. Readings were taken in a representative section of the sample site in mid-river at a depth of 0.5 m.

¹ Cod and gudgeon larvae may be identified to species level by mitochondrial DNA analysis if required.

2.4. Age evaluation of drifting larval fish

Seventy-eight larval cod and 46 larval carp were aged at the Central Aging Facility (Marine and Freshwater Resources Institute, Victoria). Methods are described in Appendix 1 along with the results from this analysis.

2.5. Data analysis

2.5.1. Comparison of gear types and fish communities at sampling sites

Catches from replicate 2 mm fyke nets (benthic drift), drift nets (pelagic drift) and quatrefoil light traps (backwaters) were pooled within samples from the 97-98 and 98-99 seasons. All data were standardised to catch per unit effort (CPUE – no. of fish caught per hour of sampling) for each gear type. Samples with zero catches were removed from the data-set as the analyses used could not cope with null data. Bray-Curtis similarities (Bray and Curtis, 1957) between fish sampled by each gear type at different sites were calculated based on 4th-root transformed catch data using PRIMER 5.1.2 (Plymouth Marine Laboratory). A two-way crossed ANOSIM (Analysis of similarities) (Clarke, 1993), with ‘site’ and ‘gear type’ as factors was used to assess differences in fish community composition. Permutation tests to estimate the probability of the observed results used 999 randomisations. SIMPER (similarity percentages) analyses were used to identify species most responsible for the observed relationships between fish communities at the various sites.

Average CPUE for each site over the 97-98 and 98-99 breeding seasons were $\ln(x+1)$ transformed prior to Pearson’s correlation in S-Plus 2000.

2.5.2. Upstream migration

Catches from 4 replicate 2 mm fyke nets (downstream movement) and 4 replicate 3 mm fyke nets (upstream movement) were pooled within samples from the 97-98 sampling season. Samples with zero catches were removed from the data-set as the analyses used could not cope with null catches. Bray-Curtis similarities (Bray and Curtis, 1957) between fish sampled by each gear type at different sites were calculated based on 4th-root transformed catch data using PRIMER 5.1.2 (Plymouth Marine Laboratory). Multi-dimensional scaling (MDS) ordinations identified a single outlier which was removed from the data-set prior to further analysis (2 mm fyke nets at site 5 on the 21/02/98: Catch = 3 oriental weatherloach (*Misgurnus anguillicaudatus*)). Eggs were not included in this analysis as all eggs sampled were moving in the downstream direction as expected. Differences between the fish communities sampled moving upstream and downstream were examined using one-way ANOSIM. Permutation tests to estimate the probability of the observed results used 999 randomisations. SIMPER analyses were used to identify species most responsible for the observed differences between upstream and downstream moving fish.

2.5.3. Length at age and growth throughout the spawning season

The age of cod and carp larvae (estimated by otolith microsection) was regressed against fish length (mm) in S-Plus 2000 to determine length at age relationships. Similarly, the length (mm) of cod and carp larvae (mm) was regressed against number of days within the drifting season to determine whether there was an increase in fish length as the spawning season progressed. Data was normally distributed and no transformation was necessary.

2.5.4. *Impacts of river regulation on downstream larval drift*

The impact of instream barriers on downstream drift was assessed by comparison of the density (fish per megalitre (ML) of larval cod and larval/juvenile carp in the Murray River above Torrumbarry weir-pool (sites 3.5 and 4), within the weir-pool (site 3) and downstream of Torrumbarry Weir (site 2). Density of pelagic eggs was not analysed as no eggs were sampled at sites 3.5 and 4 above Torrumbarry weir-pool, thereby preventing analyses of egg data. Data were analysed using Kruskal-Wallis tests in S-Plus 2000. A non-parametric test was used as the data could not be normalised by transformation. Analyses were only conducted on samples collected during the drift period of 4/11/97- 20/12/97 and 24/10/98 – 20/12/98 for cod, and 4/11/97-20/12/97 and 8/10/98 – 20/12/98 for carp.

2.5.5. *Spatial and temporal distribution within the drift.*

Data for cod from triple-rigged drift nets were analysed using fixed effects ANOVA in S-Plus 2000. Site (5 and 7), level in the water column (top, middle and bottom) and sampling period (3:00am-9:00am, 9:00am-15:00pm, 15:00pm-21:00pm and 21:00pm-3:00am) and their interactions were used as factors. Data were transformed to $\ln(x + 1)$ to stabilise variances.

3. RESULTS

3.1. Community composition

A total of 35,064 fish and 1,585 fish eggs were sampled from the Murray River during this study. The species composition comprised five alien fish species, five native fish species and three native fish genera that were not identified to species level as larvae: carp gudgeons, flat-headed gudgeons and cod (potentially seven native species) (Table 3). No golden perch larvae and only one silver perch larva were collected despite the sampling strategy being designed specifically to sample drifting larval fish. However, a small subsample of the eggs collected during the study were subsequently hatched at the Narrandera Fisheries Centre and were positively identified as those of both golden perch and silver perch.

There were significant differences between fish communities sampled from 12 sites within the Murray River (ANOSIM, Global $R = 0.179$, $p = 0.001$). However, the only consistent pattern of fish community change between sites was evident for the Torrumbarry weir-pool (site 3) which was different from all other sites ($p = 0.0002$), driven largely by the high abundance of carp gudgeons, and the consistent similarity of all sites between Yarrawonga (site 10) and Bull paddock (site 6) upstream of the Barmah-Millewa Forest.

3.2. Drift behaviour

Significant differences were detected between fish communities sampled by each gear type used (ANOSIM, Global $R = 0.357$, $p = 0.001$). Carp gudgeons and Australian smelt were sampled more frequently in backwater areas (ie with non-drifting light traps) than in either pelagic or benthic drift samples (Table 4). In contrast, cod and carp larvae and perch eggs were more abundant in drift samples (Table 4). Cod, carp and eggs were sampled by both drift (pelagic) nets and fyke (benthic) nets, but carp and eggs were more abundant in the pelagic drift net samples while cod were more abundant in the benthic nets. Drifting carp gudgeons and Australian smelt were never sampled in the pelagic drift nets and were only captured in the benthic fyke nets (Table 4).

3.3. Upstream migration

Significant differences were detected in the fish communities moving upstream and downstream at each site (ANOSIM: Global $R = 0.185$, $p = 0.001$). Differences were due to a large proportion of carp gudgeons and Australian smelt moving upstream (Table 5). Fish species that predominantly moved downstream were cod and carp. All eggs were moving in a downstream direction as expected.

Table 3. Fish sampled in each of the 1997-1998, 1998-1999 and 1999-00 sampling seasons (not standardised by sampling effort).

Scientific name	Common name	1997-1998	1998-1999	1999-2000	Lengths (mm)	
					Smallest	Largest
<i>Bidyanus bidyanus</i>	Silver perch	1				12.1
<i>Carassius auratus</i>	Goldfish	26			13.2	36.3
<i>Craterocephalus fluviatilis</i>	Murray hardyhead	70	14		12.0	42.0
<i>Cyprinus carpio</i>	Carp	523	23,547	2	3.8	167.0
<i>Gadopsis marmoratus</i>	River blackfish	1			11.7	11.7
<i>Gambusia holbrooki</i>	Gambusia	187	2		20.0	35.5
<i>Hypseleotris</i> spp.	Carp gudgeons	7327	1187		8.3	66.7
<i>Maccullochella</i> spp.	Murray and/or trout cod	441	265	189	6.1	72.2
<i>Melanotaenia fluviatilis</i>	Crimson spotted rainbowfish	111			13.4	45.4
<i>Misgurnus anguillicaudatus</i>	Oriental weatherloach	8	41		60.0	147.0
<i>Perca fluviatilis</i>	Redfin perch	45	9		18.0	96.0
<i>Philypnodon</i> spp.	Flat-headed gudgeons	165	86		5.6	61.0
<i>Retropinna semoni</i>	Australian smelt	564	250	2	6.0	60.0
Eggs		222	1363			

Table 4. Contributions of individual species to the dissimilarity between fish communities sampled by each of the gear types used; drift nets (pelagic drift), 2mm fyke nets (benthic drift), and quatrefoil light traps (non-drifting – backwaters). The consistency ratio indicates the consistency of each species at discriminating between communities at each site. % is the percentage of total dissimilarity between fish communities that is contributed by each species individually. D% is the dissimilarity of the fish communities being compared. Data have been combined across all sampling occasions. Data was transformed to the 4th root.

Species	Mean abundance (nos. per net)		Consistency ratio	%	D%
	Benthic drift	Pelagic drift			
<i>Benthic drift versus pelagic drift</i>					
	Benthic drift	Pelagic drift			
<i>Cyprinus carpio</i>	3.63	8.73	1.13	29.80	80.07
<i>Hypseleotris</i> spp.	0.25	0.00	1.05	19.80	
<i>Maccullochella</i> spp.	0.23	0.14	0.91	16.87	
Eggs	0.08	0.26	0.59	11.08	
<i>Retropinna semoni</i>	0.04	0.00	0.64	8.28	
<i>Benthic drift versus non-drifting</i>					
	Benthic drift	Non-drifting			
<i>Hypseleotris</i> spp.	0.25	1.92	1.28	29.71	69.73
<i>Cyprinus carpio</i>	3.63	0.03	0.77	18.82	
<i>Retropinna semoni</i>	0.04	0.05	0.90	14.22	
<i>Maccullochella</i> spp.	0.23	0.00	0.73	13.81	
<i>Pelagic drift versus non-drifting</i>					
	Pelagic drift	Non-drifting			
<i>Hypseleotris</i> spp.	0.00	1.92	1.56	31.58	90.26
<i>Cyprinus carpio</i>	8.73	0.03	1.02	26.46	
<i>Maccullochella</i> spp.	0.14	0.00	0.76	13.08	
<i>Retropinna semoni</i>	0.00	0.05	0.78	9.96	
Eggs	0.26	0.00	0.50	9.26	

Table 5. Contributions of individual species to the dissimilarity between fish communities moving upstream and downstream within the Murray River. The consistency ratio indicates the consistency of each species at discriminating between communities in each region. % is the percentage of total dissimilarity between fish communities that is contributed by each species individually. D% is the dissimilarity of the fish communities being compared.

Species	Mean abundance		Consistency ratio	%	D%
	Upstream	Downstream			
<i>Hypseleotris</i> spp.	69.90	6.73	1.32	31.28	66.51
<i>Retropinna semoni</i>	6.73	0.95	1.03	20.21	
<i>Maccullochella</i> spp.	0.08	6.64	0.79	16.89	
<i>Philypnodon</i> spp.	1.58	0.41	0.76	10.91	
<i>Cyprinus carpio</i>	0.11	11.52	0.48	8.21	
<i>Perca fluviatilis</i>	0.42	0.05	0.43	4.28	

3.4. Characteristics of downstream drift

3.4.1. Cod species

Cod larvae were sampled in all three sampling seasons. Larvae were already drifting on commencement of sampling on 4th November 1997 and continued to occur in the drift until 19th December 1997. In the following year, cod appeared in the drift on 21st October 1998 and continued to occur until 15th December 1998 (Figure 2). Water temperatures during periods of larval drift for cod were 20.1°C – 24.7°C in 1997 and 19.9°C – 26.0°C in 1998 (Figure 2). Drifting cod larvae were more abundant in the 1997 breeding season (Figure 3). Larval drift peaked around 16th November in 1997 at a temperature of 22.9°C. In the following year, drift peaked a week earlier, on 9th November 1998, at a temperature of 21.2°C. The majority of cod larvae (86.8%) occurred within the drift over a 4 week period.

As spawning is expected to have occurred 21-25 days prior to the occurrence of free swimming larval cod (Lake 1967*b*; Ingram & Rimmer 1992; Rowland 1992), it was possible to infer the date and environmental conditions at the time of spawning. Spawning peaked around 24th October 1997 and 17th October 1998 at temperatures of 18°C and 17°C. No high flow events occurred in the 63 days prior to the occurrence of drifting cod larvae in the Murray River in 1997 (Figure 2). In contrast a high flow occurred 22 days prior to the first occurrence of drifting cod larvae in 1998 (Figure 2). However, peak cod abundance did not occur until 41 days after this flow event (Figure 2). Further, larval cod abundance was lower in the high flow 1998 season than in the 1997 season where spawning occurred at stable regulated flows (Figure 3).

There was no significant relationship between length of drifting cod larvae and the number of days throughout the drifting period in either 1997 ($p = 0.55$) or 1998 ($p = 0.52$) seasons (Figure 4).

Drifting cod larvae were patchily distributed within the surveyed sections of the Murray River (Figure 5). The abundance of cod at each site in the 1997-98 and 1998-99 breeding seasons was not significantly correlated ($r = 0.17$, $p = 0.67$). In 1997, cod larvae were most abundant at sites 11 (near Barham), site 4 (near Echuca) and between sites 10 and 6 (Yarrawonga – above Barmah). In 1998-99 cod larvae were most abundant at site 7 (Ulupna Island) and between sites 11 and 2 (below Torrumbarry), but were always less abundant than in the previous breeding season.

Otoliths extracted from cod larvae sampled in the drift indicated that the age of drifting fish ranged from 10 – 23 days with a mean \pm SE of 14.4 ± 0.3 ($n = 68$) (see Appendix 1). The mean total length of drifting cod sampled was 11.0 ± 0.1 mm with a range of 6.1 – 23.7 mm (Figure 6). There was a significant length at age relationship for cod larvae ($\text{age}(\text{days}) = 2.59 + 1.06(\text{length}(\text{mm}))$), $F_{1,67} = 15.88$, $p = 0.0002$, $R^2 = 0.19$) (Figure 7).

Using the age-at-length relationship above to infer the ages of cod given in figure 6, a large proportion of cod larvae (95%) sampled from the drift are 12 – 16 days old. Therefore, the period of time spent in the drift is less than four days for a majority of the population.

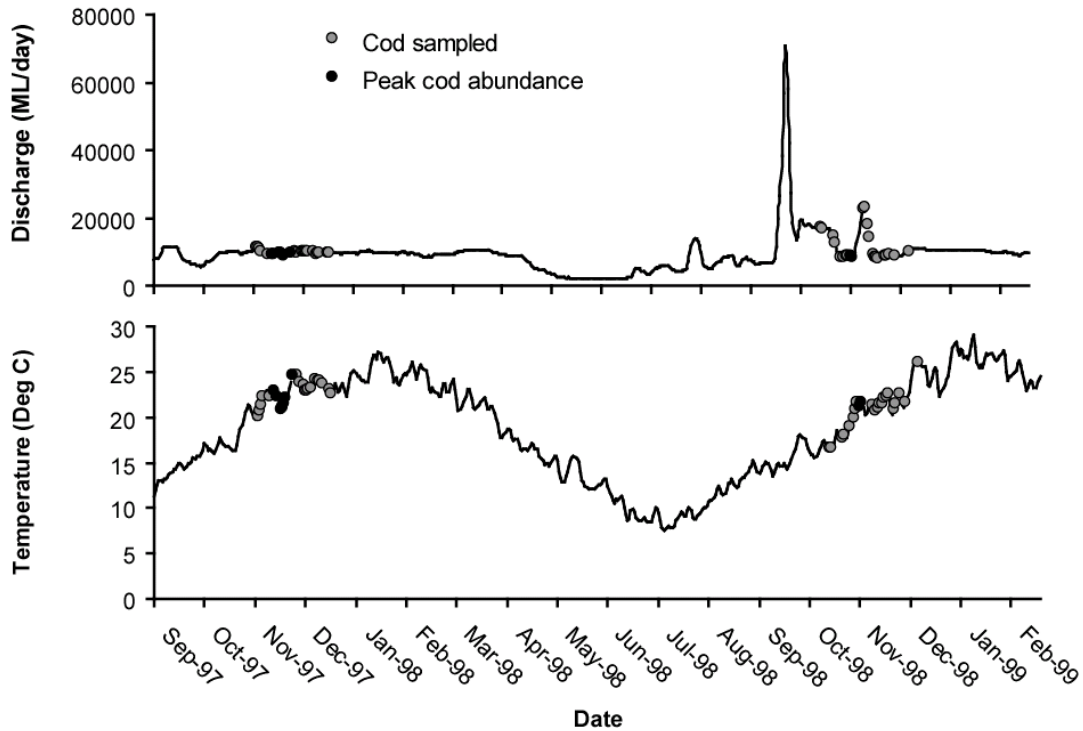


Figure 2. Occurrence of drifting larval cod in samples from the 1997-98 and 1998-99 sampling seasons plotted against flow (top graph) and temperature (lower graph) (Tocumwal gauging station: 409202). Each point represents a sampling occasion where drifting cod were sampled. Black points indicate samples with high larval cod abundance. Grey points indicate capture of drifting larval cod but only at moderate to low abundance.

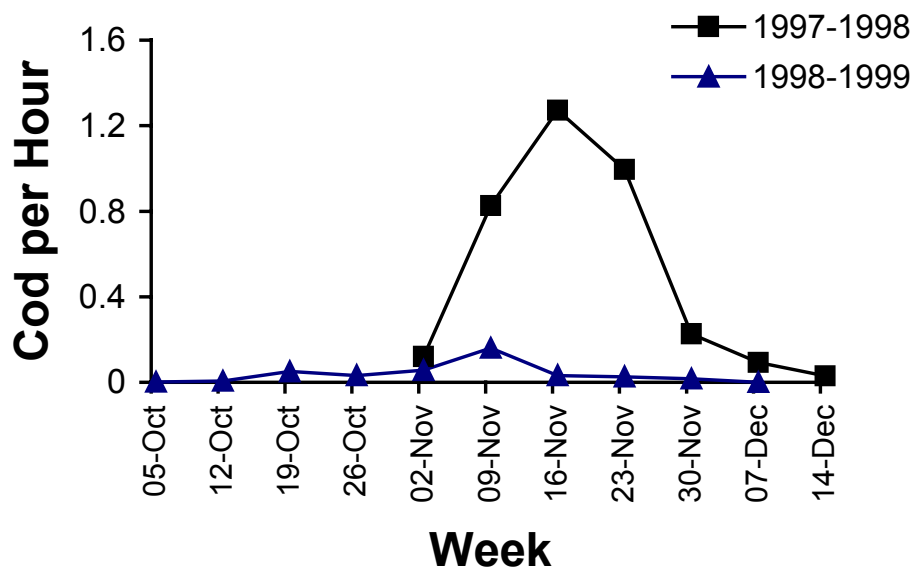


Figure 3. Abundance of drifting cod larvae (cod per hour averaged for each week) throughout the 1997-98 and 1998-99 breeding seasons. Data from all sampling techniques have been combined.

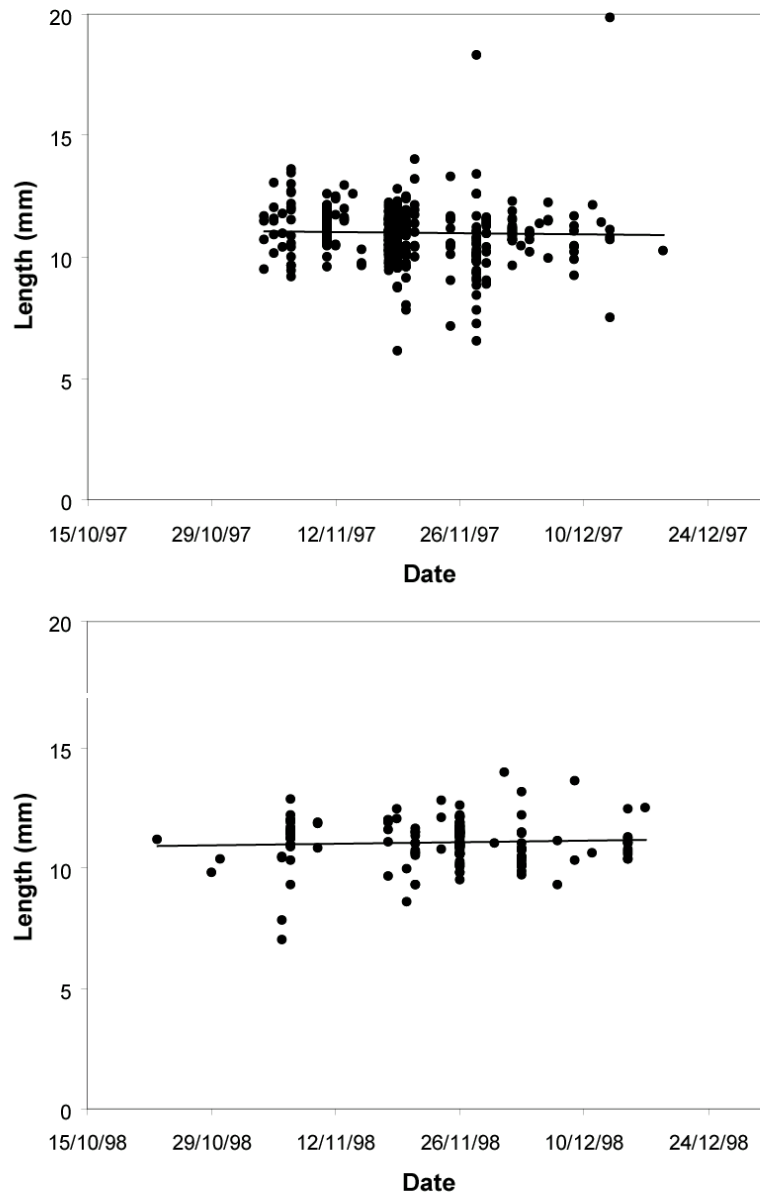


Figure 4. Length of cod larvae sampled throughout the 1997 and 1998 spawning seasons. Length was not significantly related to date in either year (1997: $p = 0.55$, 1998: $p = 0.52$).

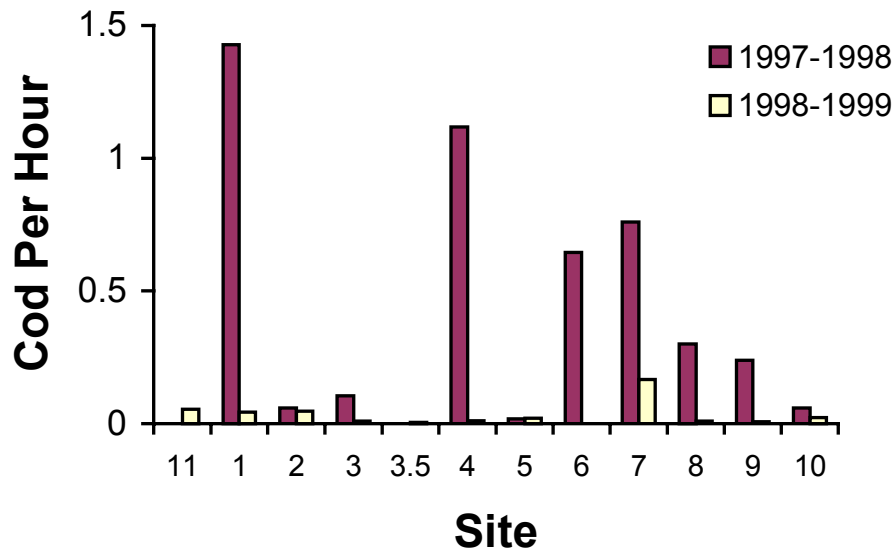


Figure 5. Abundance of drifting cod larvae (cod per hour averaged over entire sampling season) at sites sampled throughout the Murray River using data combined for all sampling techniques.

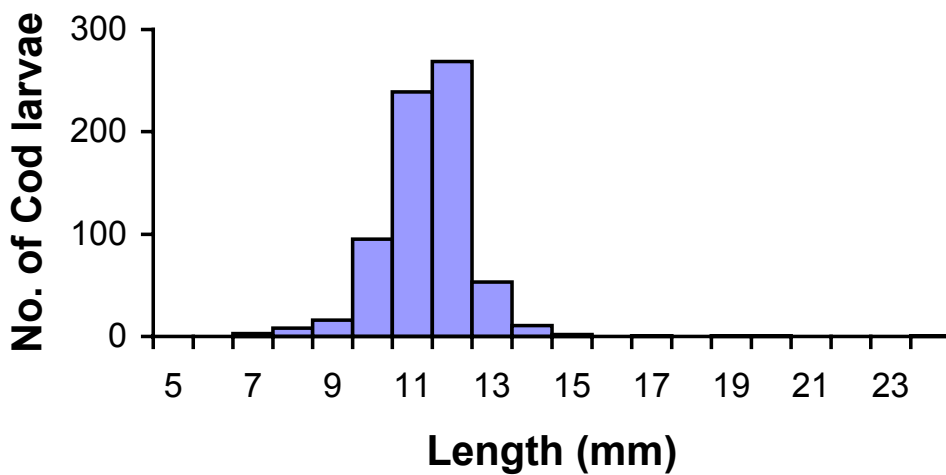


Figure 6. Length frequency distribution (total length) of drifting cod larvae sampled throughout the project.

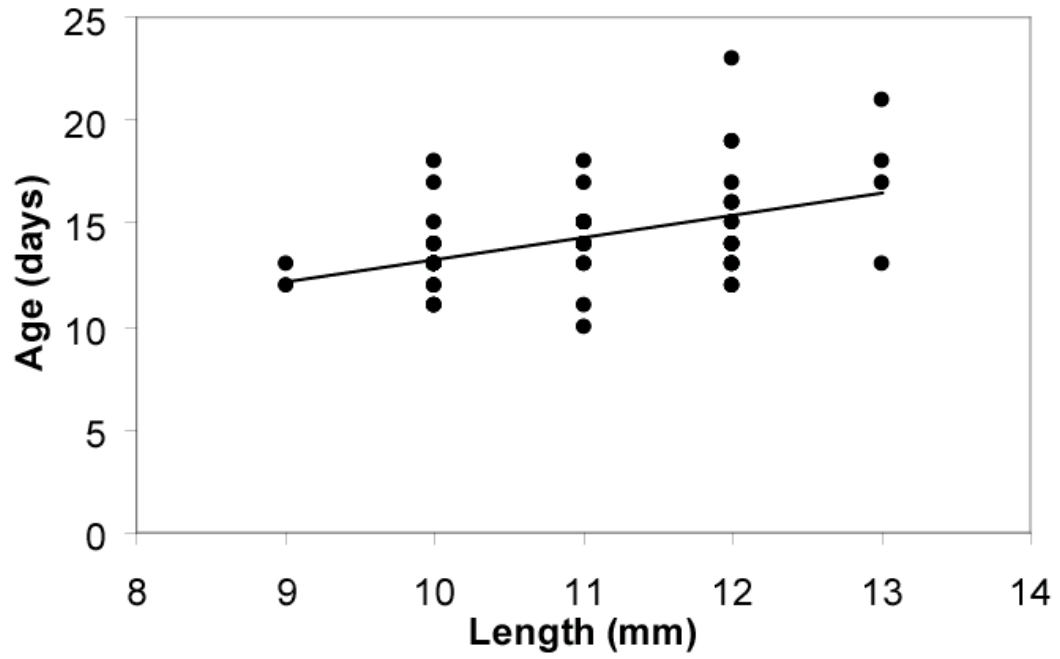


Figure 7. Length at age relationship for cod larvae.

3.4.2. *Carp*

Drifting carp were sampled in both the 1997-98 and 1998-99 breeding seasons but not in the small number of samples collected in November 1999. In the 1997-98 season, the first carp larva captured was on 6th November 1997. As sampling only began on 4th November 1997, carp larvae may have started to drift before this date. Although most captures of carp had occurred by 13th December 1997, carp continued to occur in the drift until 7th February 1998. In the following year, carp appeared in the drift from 8th October 1998 until 15th December 1998 (Figure 8). Water temperatures during periods of drift for carp were 20.6°C – 26.1°C in 1997-98 and 15.6°C – 25.2°C in 1998-99.

Drifting carp were significantly more abundant in the 1998 breeding season. This may have been because of the earlier start to sampling in 1998-99. In 1998-99 a large peak in carp abundance occurred on 12th October 1998. Sampling in 1997 did not begin until late October and may have 'missed' the peak in carp drift observed in the following year. Although less abundant in the 1997-98 season, carp were still more abundant than cod larvae. Carp drift peaked around 23rd November in 1997 at a temperature of 21.5°C (Figure 9). In the following year, the very large peak in drift occurred on the 12th October 1998 at a temperature of 15.2°C, with much smaller peaks on 2nd November and 16th November at 17.6°C and 20.8°C respectively (Figure 9).

The occurrence of drifting larval/juvenile carp was most frequently associated with the declining flows of flood peaks (Figure 8). This makes interpretation of spawning cues more difficult than for cod, as carp, which spawn in off-stream habitats, may spawn at any time, with juveniles remaining within wetlands until rising flood waters lead to dispersal into the river channel. Despite this, the high densities of carp juveniles sampled on the tail of the flow peak in October 1998 were preceded by a flow peak 12 days prior to the dispersal event (Figure 8). As free-swimming carp can occur between 5-14 days post-spawning, this could implicate the preceding flow peak in the substantial carp spawning event observed. In contrast, the high flow in August 1998 did not result in the dispersal of drifting carp larvae in the following flow peak in October 1998 (Figure 8). This suggests that carp spawning did not occur during the August flow event. Similarly, the low numbers of dispersing carp in receding flow of the November 1997 flow peak suggest that the high flow in September 1997 (69 days prior to peak carp abundance in that year) did not result in substantial carp spawning.

There were significant relationships between length of drifting carp larvae/juveniles and the number of days throughout the drifting period in both 1997 ($F_{1,278} = 21.46, p < 0.0001$) and 1998 ($F_{1,818} = 1760.66, p < 0.0001$) seasons (Figure 10). This indicates both a short-term spawning event and a longer drift period than for cod larvae.

Drifting carp were predominantly sampled at sites downstream of the Barmah-Millewa Forest, with greatest abundance at sites 4 and 5 (below Barmah to Echuca) (Figure 11). Very low abundances of drifting carp were detected in the upper reaches between Yarrawonga and Barmah (Figure 11). The abundance of carp at each site in the 1997-98 and 1998-99 breeding seasons was not significantly correlated ($r = 0.61, p = 0.08$). However, a clear trend in the data was obvious, suggesting that the locations of carp reproduction are more predictable than those of cod and are centred around the Barmah-Millewa Forest.

Otoliths extracted from carp sampled in the drift indicated that age ranged from 10 – 53 days with a mean \pm standard error (SE) of 31.545 ± 2.03 ($n = 33$) (see Appendix 1). The mean length of drifting carp sampled was 18.6 ± 0.19 mm with a range of 3.76 – 51.00 mm with two outlying individuals of 74.85 and 167 mm (Figure 12). There was a significant length at age relationship for carp larvae/juveniles ($\text{age}(\text{days}) = 10.15 + 0.85(\text{length}(\text{mm}))$), $F_{1,31} = 58.05, p < 0.001, R^2 = 0.65$) (Figure 13).

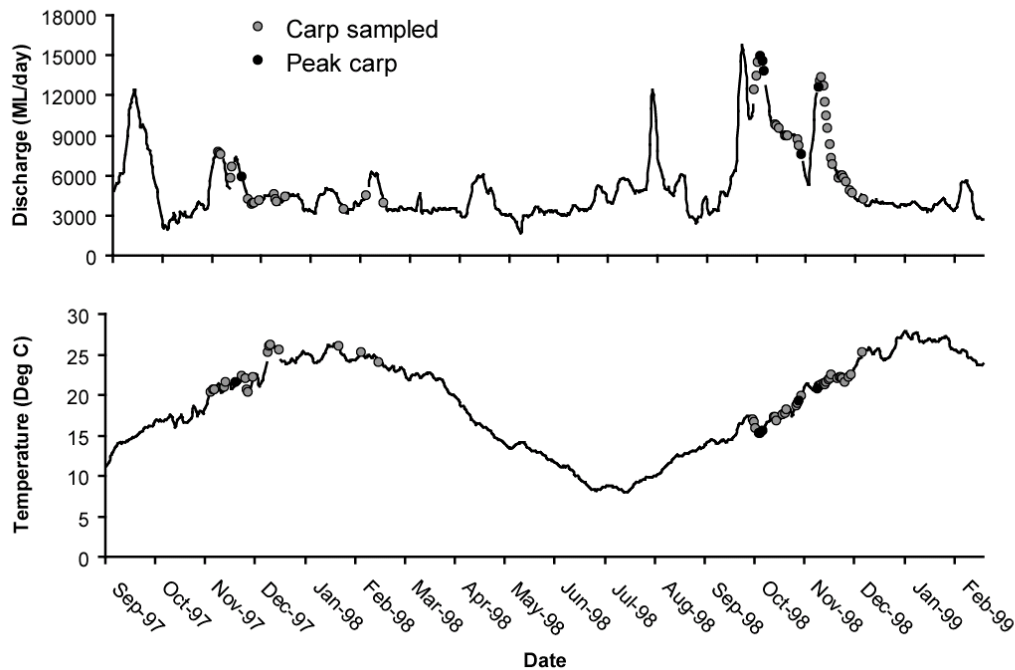


Figure 8. Occurrence of drifting carp larvae/juveniles in samples from the 1997-98 and 1998-99 sampling seasons plotted against flow (top graph) and temperature (lower graph) (Torrumbarry gauging station: 409207). Each point represents a sampling occasion where drifting carp were sampled. Black points indicate samples with high carp abundance. Grey points indicate capture of drifting carp but only at moderate to low abundance.

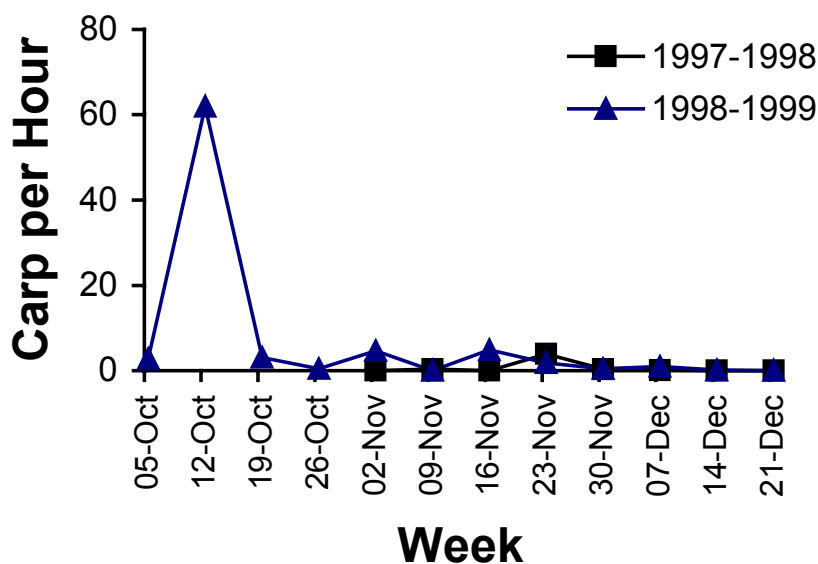


Figure 9. Abundance of drifting carp larvae/juveniles (carp per hour averaged for each week) throughout the 1997-98 and 1998-99 breeding seasons.

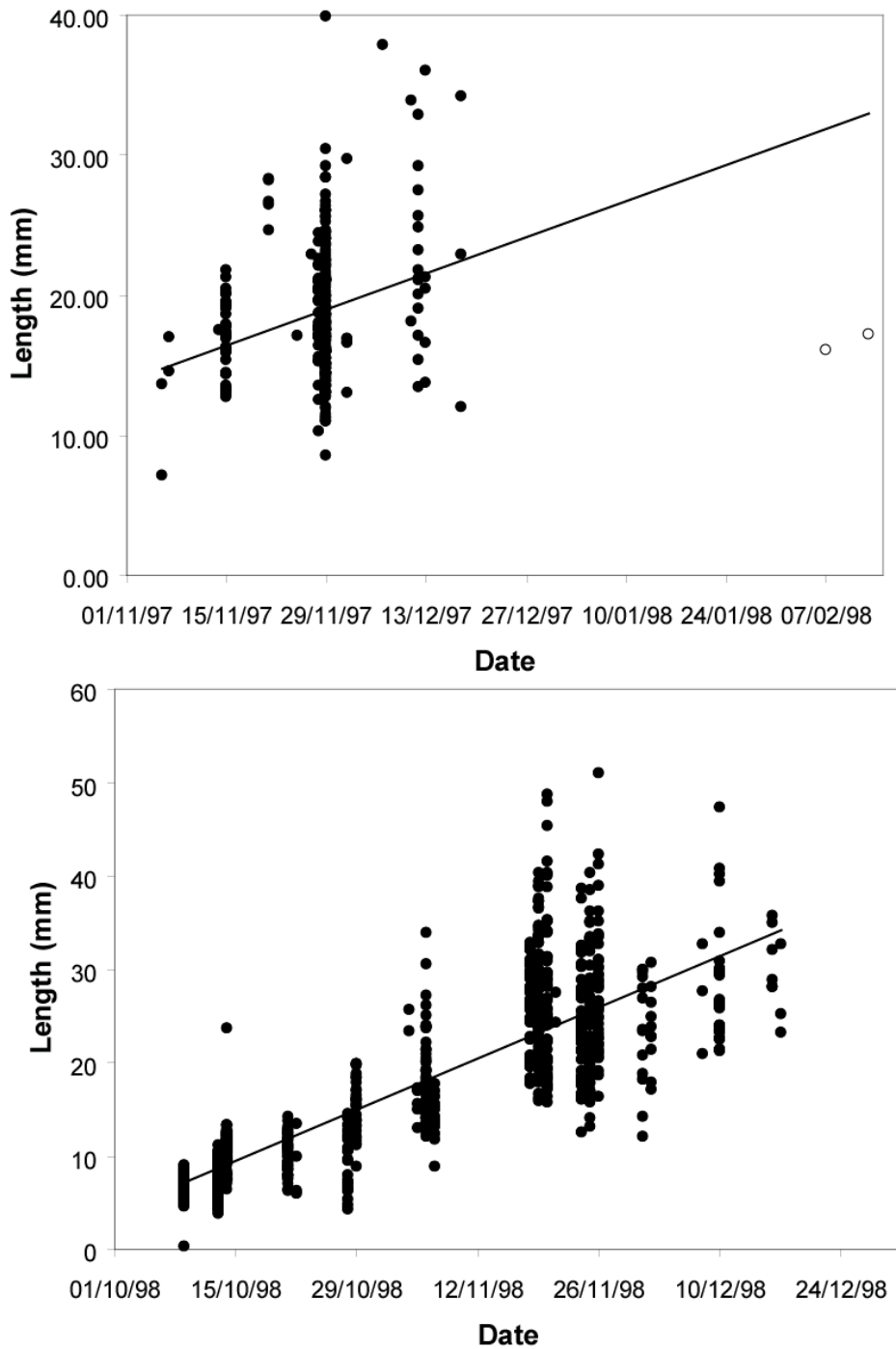


Figure 10. Length of carp larvae/juveniles sampled throughout the 1997 and 1998 spawning seasons. Length was significantly related to date in both years (1997: $p < 0.0001$, 1998: $p < 0.0001$), but the relationships were not very strong in the first year (1997: $R^2 = 0.07$, 1998 $R^2 = 0.68$). The two outliers (open dots) in the upper graph were omitted from the analysis.

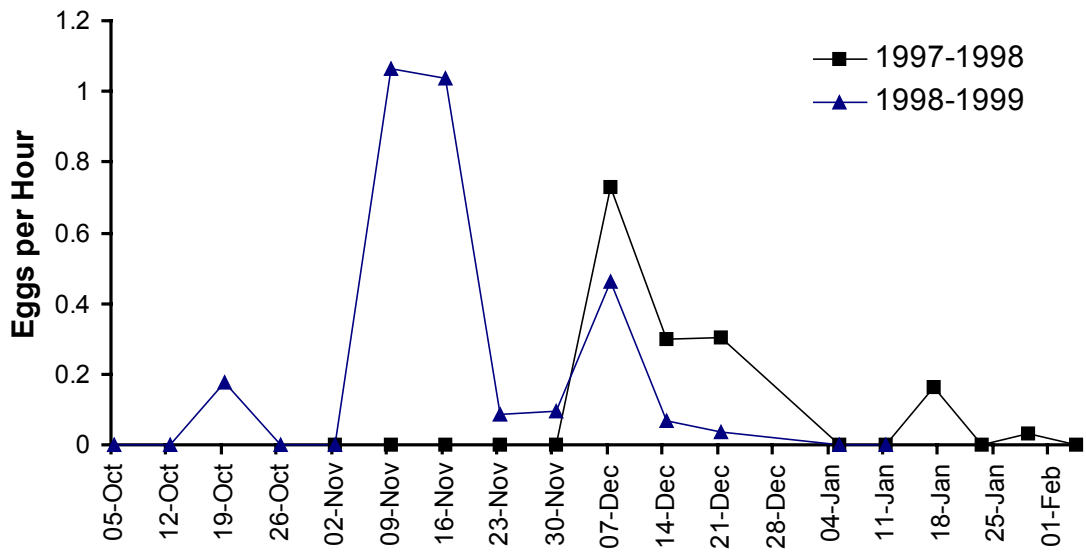


Figure 11. Abundance of drifting carp larvae/juveniles (carp per hour averaged over entire sampling season) at sites sampled throughout the Murray River using data combined for all sampling techniques.

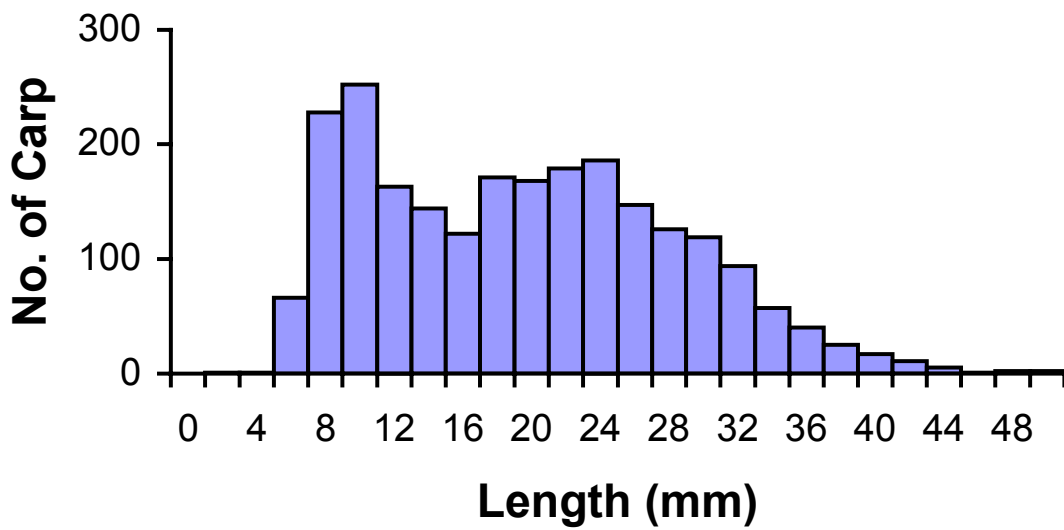


Figure 12. Length frequency distribution (fork length) of drifting carp sampled throughout the project.

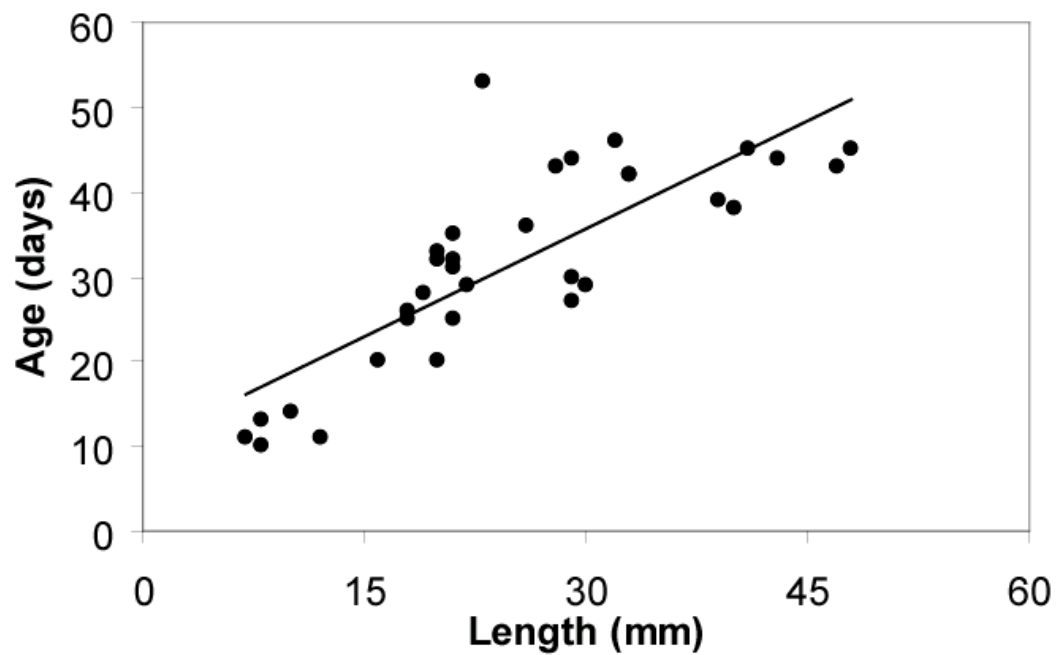


Figure 13. Length at age relationship for carp larvae/juveniles.

3.4.3. Eggs (golden perch & silver perch)

Eggs were sampled in drift nets over a two month period in both seasons sampled, but not during the same two month period in each year; ie from 3rd December 1997 to 29th January 1998, and from 12th October 1998 to 11th December 1999 (Figure 14). A single larval silver perch (12.1mm) was sampled on 19th November 1997. No golden perch larvae were sampled. Water temperatures during periods of occurrence of eggs in the drift ranged from 15.7°C to 27.1°C over both years. The larval silver perch was sampled at a temperature of 21.1°C.

Drifting eggs were sampled in relatively low abundance in both years (Figure 15). However, there was a peak in abundance during mid November 1998 (at 20.8°C) with smaller peaks in the first weeks in December of 1997 (at 22.9°C) and 1998 (at 22.6°C) (Figure 15).

As eggs only have a 24 - 46 hour incubation period (Lake 1967*b*; Rowland 1984; Rowland 1996; Neira *et al.* 1998), and the occurrence of eggs was not restricted to within one or two days of flow peaks, the data presented suggests that silver perch and golden perch are not flood cued spawners as has previously been suggested. Instead, peak eggs abundances occurred at stable regulated abundances of flows, despite a substantial flow peak in November 1998 (Figure 14). Perch spawning was detected several weeks before and after this flow event, with no peak in spawning activity associated with the potentially ideal flow event itself.

Drifting eggs were predominantly sampled at sites upstream of the Barmah-Millewa Forest, with greatest abundance at sites 7, 8 and 9 (Figure 16). However, the abundance of eggs at each site in the 1997-98 and 1998-99 breeding seasons was not significantly correlated ($r = 0.41$, $p = 0.28$).

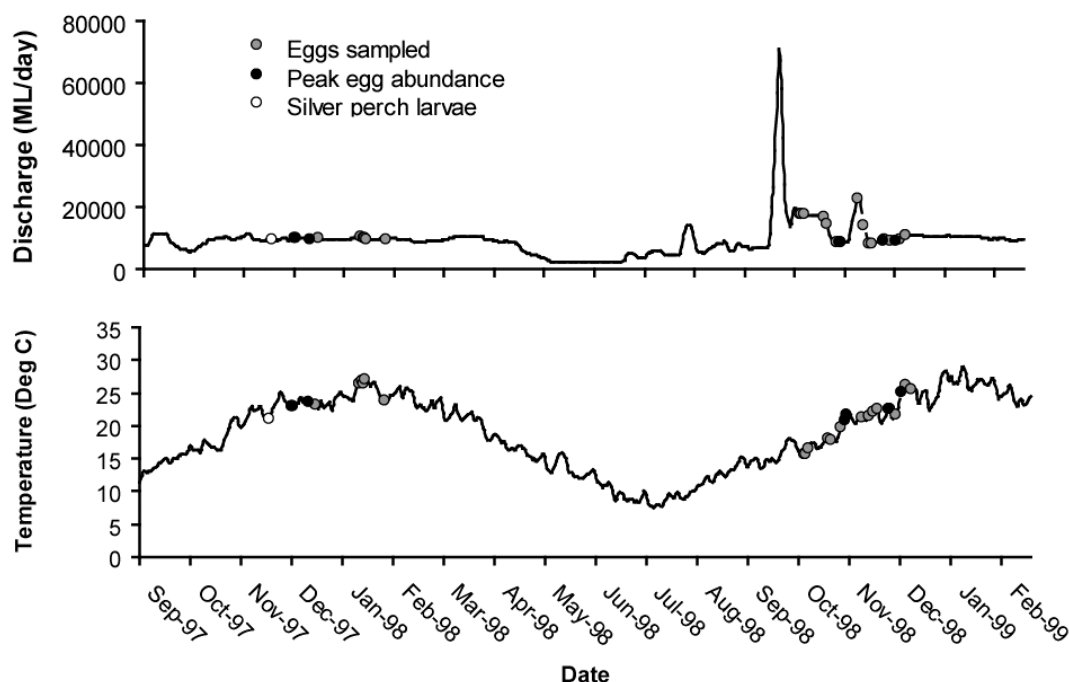


Figure 14. Occurrence of drifting eggs and a single silver perch larva in samples from the 1997-98 and 1998-99 sampling seasons plotted against flow (upper graph) and temperature (lower graph) (Tocumwal gauging station: 409202). Each point represents a sampling occasion where drifting eggs were sampled. Black points indicate samples with high egg abundance. Grey points indicate occurrence of eggs but only at moderate to low abundance. White point represents the sampling of silver perch larva.

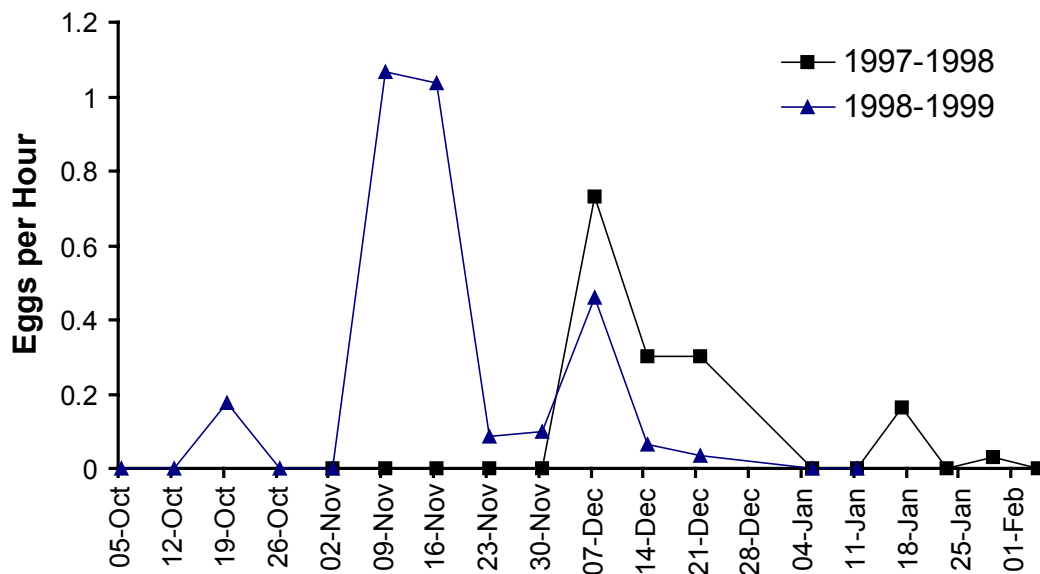


Figure 15. Abundance of drifting eggs throughout the 1997-98 and 1998-99 breeding seasons.

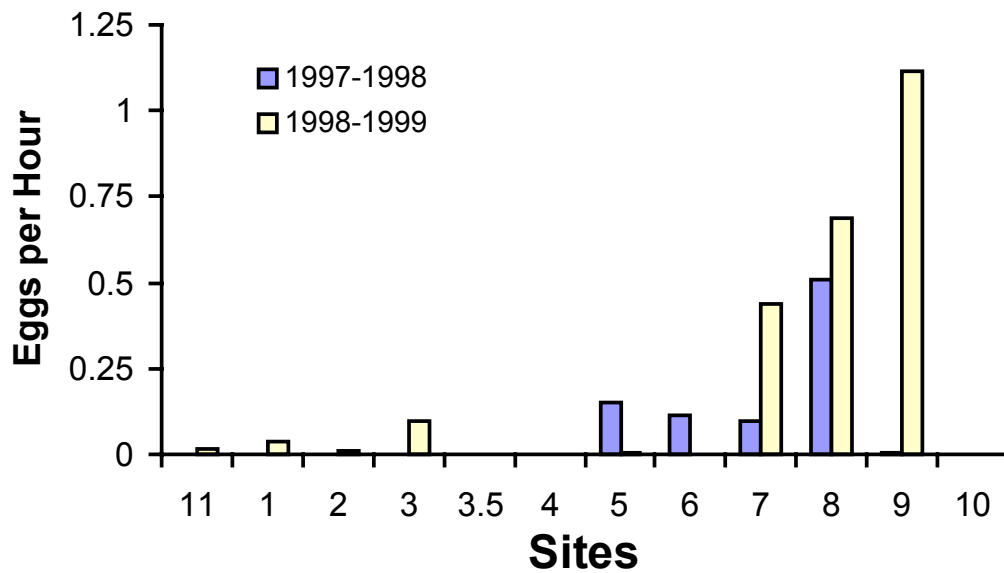


Figure 16. Abundance of drifting eggs at sites sampled along the Murray River downstream from Yarrowonga.

3.5. Effects of weirs

Significant differences were identified in the number of carp (Kruskal-Wallis: $\chi^2_2 = 6.73$, $p = 0.035$) sampled per hour in the Murray River above Torrumbarry weir-pool, within the weir-pool and below Torrumbarry Weir. Carp abundance was significantly greater in the river and lowest in the weir-pool. No significant differences in the number of drifting cod larvae were found at these three sites. However, like carp, cod larvae were less abundant in the weir-pool and below the weir than in the river upstream.

As lower numbers in the weir-pool may result from lower flows, and therefore less water being filtered per hour, data were also standardised to number per ML of water filtered. These analyses also found significant differences in the number of drifting carp ($\chi^2_2 = 9.11$, $p = 0.011$) but no significant differences for cod ($\chi^2_2 = 1.06$, $p = 0.59$) per ML of water filtered. The result for carp was consistent with the result based on CPUE, with significantly greater densities in the river upstream of the weir-pool, and lower densities in the weir-pool and below Torrumbarry weir (Figure 17).

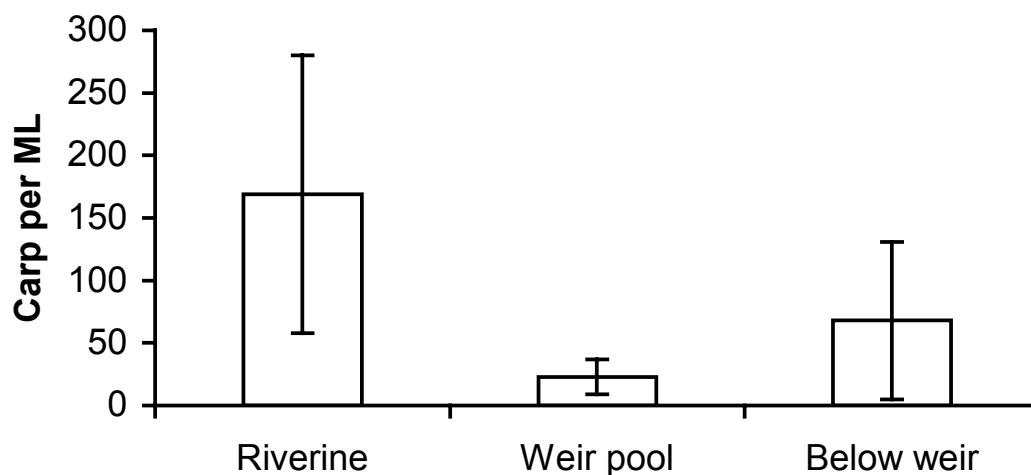


Figure 17. Average density of carp per Megalitre (ML) in the Murray River above Torrumbarry weir-pool, within the weir-pool and directly below Torrumbarry Weir.

3.6. Effects of water extraction

Average densities (ML^{-1}) of drifting cod, carp and eggs are given in Table 6. Densities of all three groups were extremely variable within and between years. Extrapolation of average densities per ML to the known volumes of water diverted from the Murray River between Yarrawonga (including Yarrawonga and Mulwala canals) and Barham during each taxa's drifting season, provides a crude estimate of the number of cod larvae, carp and perch eggs that might be lost from the Murray River as a result of water extraction.

Table 6. Average densities (per ML) of drifting cod larvae, carp larvae/juveniles and perch eggs sampled in the spring/summers of 1997-98, 1998-99 and in November 1999. Estimates are based on the average densities for all samples between the first and last occurrence of each species in each year and volume extracted from the river during the dispersal period identified for each species. Estimated numbers of cod larvae, carp larvae/juveniles and perch eggs potentially lost from the Murray River as a result of water diversion are based on the assumptions that larvae are uniformly distributed throughout cross sectional area of the stream and that densities are uniform at all water extraction points.

Species	n	Fish per ML	Volume extracted during drifting season (ML)	Potential recruits lost	
<i>Cod larvae</i>	1997-1998	7	7.3 ± 4.9	(Oct-Dec) 1,366,866	9,978,122
	1998 – 1999	59	0.14 ± 0.03	1,277,707	178,879
	1999	55	5.3 ± 1.4	900,458	4,763,423
<i>Carp</i>				(Oct-Dec) <i>Water extracted below Barmah-Millewa Forest only</i>	
	1997 – 1998	7	2.1 ± 1.0	355,270	753,172
	1998 – 1999	81	55.2 ± 25.7	360,583	19,900,576
<i>Eggs</i>				(Oct- Jan)	
	1997 – 1998	19	16.8 ± 9.9	1,873,969	31,520,159
	1998 – 1999	75	0.9 ± 0.4	1,875,372	1,744,096

3.7. Spatial and temporal distribution of drifting cod

In November 1999, there was a significant difference in the relative abundance of cod drifting during four time periods throughout the day (ANOVA $F_{3, 76} = 9.77, p < 0.0001$). Drifting cod larvae were significantly more abundant in sampling periods between 3:00am and 15:00pm, with peak catches in the 3:00-9:00am sampling period at both sampling sites 5 and 7 (Figure 18). Relative catch rates between 15:00pm and 3:00am were very low, particularly in the 9:00am-15:00pm sampling period (Figure 18). No significant differences in larval abundance were observed across levels within the water column (ANOVA, $F_{2, 76} = 0.14, p = 0.87$). Further, the level in the water column was not dependent on the time of sampling as indicated by a non-significant interaction term between time of drift and level within the water column (ANOVA $F_{6, 76} = 0.35, p = 0.91$).

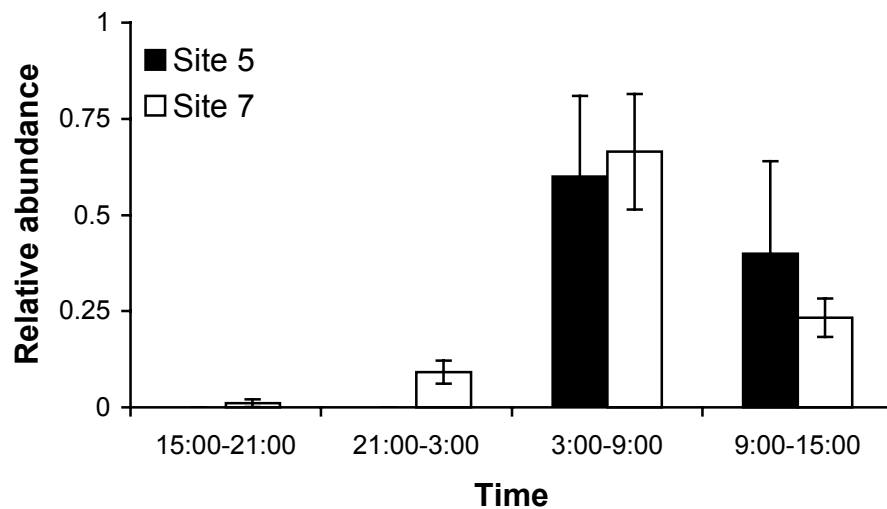


Figure 18. Relative abundance of drifting cod larvae (\pm SE) sampled during four time periods in November 1999 at 2 sites on the Murray River. Data have been combined across levels in the water column.

4. DISCUSSION

4.1. Importance of downstream drift

Downstream drift is an important dispersal mechanism for many fish species around the world (Clifford 1972; Gale & Mohr 1978; Gallagher & Conner 1983; Muth & Schmulbach 1984; Brown & Armstrong 1985; Flecker *et al.* 1991; Harvey 1991; Winnell & Jude 1991; Jurajda 1998). High densities of drifting fish per megalitre (ML) have been recorded in a number of studies, with average or maximum densities of 58 ML⁻¹ (Muth & Schmulbach 1984), 127 ML⁻¹ (Gale & Mohr 1978), 323 ML⁻¹ (drum) (Muth & Schmulbach 1984), 383 ML⁻¹ (Winnell & Jude 1991), 1,477 ML⁻¹ (Gale & Mohr 1978), 2,789.5 ML⁻¹ (Gallagher & Conner 1983), 8,430 ML⁻¹ (Jurajda 1998), 31,000 ML⁻¹ (Harvey 1991), and up to > 250,000 ML⁻¹ (Flecker *et al.* 1991) being reported.

Within Australia, densities of drifting fish within the Murray-Darling Basin have been reported as 76.7 ML⁻¹ in the Campaspe River and 2.7 ML⁻¹ in the Broken River (Humphries *et al.* 2002). Of the 11 species of larval fish sampled by Humphries *et al.* (2002) in the Campaspe and Broken Rivers, eight species were sampled from drift nets; the native Australian smelt, carp gudgeons, flat-headed gudgeon, Murray cod, river blackfish, and the introduced redfin perch, carp and gambusia. Despite the high number of species captured in drift nets, samples were dominated by flat-headed gudgeons (96.7%) in the Campaspe River and Murray cod (75.8%), Australian smelt (6.7%) and carp (14.4%) in the Broken River (Humphries *et al.* 2002). In this study, 12 of the 13 fish taxa, as well as eggs, were sampled using drift nets (benthic and pelagic), with river blackfish being the only species that was not sampled moving downstream. Although a wide diversity of taxa were sampled drifting (or swimming) downstream, drift samples were significantly dominated by carp, cod (Murray cod and/or trout cod) and eggs (golden perch and/or silver perch). These taxa were infrequently sampled from backwater habitats which were dominated by carp gudgeons and Australian smelt. In contrast to the results of Humphries *et al.* (2002), flat-headed gudgeons were not abundant in either drift samples or backwater habitats within the Murray River.

Comparisons of fish populations moving upstream against the flow with those drifting downstream, demonstrated that large numbers of carp-gudgeons (83% of individuals) and Australian smelt (89% of individuals) were moving upstream during the sampling periods.

This study has confirmed that larval cod (Murray cod and/or trout cod), carp and eggs drift downstream as part of the ichthyoplankton. Densities of each of these drifting taxa were up to 44.49 ML⁻¹ (mean \pm SE = 2.89 \pm 0.75) for cod, 1,704.29 ML⁻¹ (mean \pm SE = 50.97 \pm 23.68) for carp and 156.63 ML⁻¹ (mean \pm SE = 4.14 \pm 2.09) for eggs. These densities are within the range of those observed by other studies of drifting ichthyoplankton.

4.1.1. Murray cod and trout cod

Koehn & Nicol (1998), Humphries *et al.* (2002) and Meredith *et al.* (2002) have also reported downstream drift of larval Murray cod. The present study sampled drifting cod larvae in all three sampling seasons. Cod larvae commenced drifting in late October and had settled from the drift prior to late December in both 1997 and 1998. Therefore, the period over which downstream drift occurs is approximately two months but is concentrated within a four week period in November. The drifting season for each of the two species separately may be somewhat shorter as trout cod may commence to spawn at lower temperatures, and therefore earlier than Murray cod (Lake 1967a; Ingram & Rimmer 1992; Rowland 1998). Hence, trout cod larvae might be expected to occur towards the start of the drift period with Murray cod larvae occurring towards the end.

Cod larvae, and therefore cod reproduction, was patchily distributed within the section of the Murray River studied and reproductive outputs at each site were not correlated over each of the breeding seasons sampled.

Spawning activity of cod was not found to be associated with changes in flow. Further, of the two breeding seasons assessed, the abundance of drifting cod larvae was greatest in the year with consistent regulated irrigation flows with no flow peaks to act as spawning cues. The spawning season is inferred to be largely confined to the month of October but ranged from late September through to November, peaking at temperatures of 17 - 18°C.

Hatchery rearing experiments suggest that cod larvae disperse from the 'nest' following yolk-sac absorption 21-25 days post-fertilisation, at a length of 12-13mm (Lake 1967b; Ingram & Rimmer 1992; Rowland 1992). The ages (10-23 days) and average length (11 ± 0.01 mm) of cod larvae sampled from the Murray River suggest that larvae sampled drifting downstream had only recently emerged from the 'nest' and had spent little time drifting downstream. A majority (95%) of sampled from the drift were aged between 12 and 16 days. This suggests that larval cod are likely to undergo downstream drift for a short period of up to and around four days. This is supported by the fact that no increase in the size of cod larvae was detected over the course of the breeding season (Figure 10). This not only suggests that cod spent little time in the drift but also suggests that no obvious 'peak spawning period' occurred which would indicate a distinct environmental trigger to spawning activity (such as a flow peak).

Cod larvae were not found to move upstream following their short period of larval drift. Nor were they found to settle into backwaters or low flow habitats. A possible hypothesis to explain this is that, following a small amount of downstream drift, larval cod settle onto the substratum and make no further upstream or downstream movements. This is supported by a further hypothesis that juvenile cod feed on benthic invertebrates within the river channel (King 2002) as opposed to the diet dominated by planktonic crustaceans under hatchery pond conditions (Rowland 1992).

The small spatial scale of downstream drift observed for cod larvae suggests that larval drift may not be a significant dispersal mechanism for cod. It has been hypothesised that downstream larval drift was required to counteract upstream spawning migrations undertaken by adult Murray cod (Reynolds 1983; Koehn & Nicol 1998). In light of the small spatial scale of downstream drift, and protracted spawning period, it may be appropriate to assess the generality of upstream spawning migrations of adults. Radio-tracking of trout cod suggests that this species does not undertake large scale movements (Koehn & Nicol 1998). In contrast, Reynolds (1983) and Koehn & Nicol (1998) concluded that upstream movements of Murray cod were spawning migrations, with fish moving greater distances upstream during higher flows. However neither of these papers provides conclusive evidence that these movements are associated with spawning activity. Figures presented in Koehn & Nicol (1998) do not show an increase in upstream movement preceding the spawning months of October and November, with subsequent downstream migration in November and December, as would be expected under a model of upstream spawning migrations for Murray cod.

4.1.2. *Carp*

Downstream drift of carp has been reported in introduced populations in North America (Gale & Mohr 1978; Muth & Schmulbach 1984; Brown & Armstrong 1985). The drift season identified in those populations was short, with drift only observed in early June, corresponding to the first month of summer in the Northern Hemisphere. In our study, carp began downstream drift in early October and continued through to late December, with occasional samples collected through until February. A vast majority of drifting carp appeared at the beginning of the season in mid October,

with smaller peaks throughout November. A large peak in carp drift was not observed in 1997. Stuart and Jones (2002) assessed carp dispersal in the same section of the Murray River as this study and reported the occurrence of drifting carp between September and January. Larval carp were found within Barmah Lake in September 2000 but did not disperse into the river and anabranches until late October (Stuart and Jones 2002). Brown *et al.* (2003) reported carp spawning at Barmah between August-September 1999 and September-October 2000 as water increases from 12-18°C. However they reported that across their range, the carp spawning period is much longer, with some populations spawning serially (Brown *et al.* 2003).

Within the section of the Murray River surveyed, the Barmah-Millewa forest was identified as a major source of carp reproduction. This was also reported by Stuart and Jones (2002). However, Stuart and Jones (2002) also sampled carp larvae upstream of the Barmah-Millewa forest at Cobrawonga (near site 9 of this study) but in relatively low numbers. Based on these results, we speculate that very little carp reproduction occurs within the Murray River between Yarrawonga and the Barmah-Millewa forest.

Both in this study and that of Brown *et al.* (2003), larval/juvenile carp abundance was greatest in a year of sustained and extensive flooding relative to periods of minor flooding. The Barmah-Millewa floodplain environment is inundated above flows of 9,500ML per day (Stuart and Jones 2002). As a result, the first flow event exceeding this level in September - October is highly likely to result in a large carp spawning event, as the occurrence of drifting carp larvae/juveniles was closely associated with the receding tails of flow peaks. The dispersal of these larvae from the wetland habitats can be expected to occur in the following flow peak. This provides some opportunity for the targeted harvest of dispersing juvenile carp.

Both this study and that of Stuart and Jones (2002) found that the length of drifting carp increased over time throughout the breeding season. Similarly, Stuart and Jones (2002) also identified only single peaks in the length-frequency histograms of carp in the Barmah area. These data suggest that the period of time over which the majority of carp larvae were spawned is much shorter than believed. It is highly likely that mass spawning events occur as a result of floodplain inundation within the Barmah-Millewa forest, with little spawning under stable regulated flow conditions and no serial spawning in this population.

Carp larvae become free swimming 2-8 days after hatching (Roberts & Ebner 1997). The age of carp sampled drifting downstream ranged from 10-53 days with a mean of 32 ± 2 days. Therefore carp remain in the drift for a much longer period of time than larval cod. As a result, there is greater potential for carp to travel and disperse further downstream than for the more localised downstream movements of cod larvae. This is exacerbated by the majority of carp dispersing from wetland nurseries under flood peak conditions.

Unlike Holland (1986) and Sheaffer & Nickum (1986), we found no evidence that carp settled within backwater habitats within the river as demonstrated by very small catches of carp in quatrefoil light traps in comparison with the catches from drift samples. Instead, settlement was observed in weir pool habitats, with significant reductions in the density of carp captured in drift samples under weir-pool conditions.

4.1.3. Eggs (golden perch and silver perch)

Our sampling, like that of Humphries *et al.* (2002) and Koehn & Nicol (1998) failed to sample large numbers of golden perch or silver perch larvae. However, subsamples of the drifting eggs collected in this project were positively identified as those of golden and silver perch. Both golden and silver perch have previously been thought to require temperatures above 22.5°C in addition to a river rise to initiate spawning (Lake 1967a, Cadwallader 1977; Rowland 1983; Battaglione 1991;

Rowland 1996). Although these species can maintain gonadal maturity for an extended period of time, spawning in either species is unlikely to occur over a protracted period.

Under this hypothesis, drifting eggs of these species should appear following flow peaks and in very high abundances. Further, as the incubation period is very short, from 24 - 46 hours (Lake 1967*b*; Rowland 1984; Rowland 1996; Neira *et al.*, 1998), eggs of these species should not remain in the drift for very long. However, pelagic eggs were collected from mid October through to late January during our study. This suggests that the Murray River populations of golden and/or silver perch do not require a temperature of 22.5°C to initiate spawning, and that spawning occurs at lower temperatures and over longer periods of time than previously believed. This is supported by the sampling of the single silver perch larva at a temperature of 21.1°C. Although not accurately aged, at 12.1mm this fish was likely to be several weeks old. Therefore the spawning event from which this fish arose probably occurred at a temperature of < 19.0°C in 1997. Further, the peak egg abundance observed at the beginning of sampling in spring 1998 was found to be a silver perch spawning event as indicated by the identification of hatchlings in the laboratory. Therefore spawning is likely to have occurred at temperatures of around 16.5°C in 1998.

Stuart and Jones (2002) sampled drifting eggs of golden perch following a flow peak in late October 2000 (at a temperature of 17°C) and a smaller number of eggs following a flow peak in late November 2000 (at a temperature of 21°C). In contrast, we found no evidence that spawning of golden and silver perch was associated with high flows. In this study, all peaks in egg abundance occurred during periods of stable regulated flow. For example, peaks in spawning activity were detected at stable regulated flows both two weeks before and two weeks after a river rise of 14,000ML in mid November 1998, with little spawning activity being associated with the hypothesised preferred high flow conditions. However, both these species are highly fecund and the low sample sizes of eggs collected in this study could indicate that no significant flood-response spawning events of either species occurred during the study period in the section of the Murray River sampled. Further sampling during appropriate large flood events could result in the collection of much greater abundances of the eggs and larvae of these species. Despite the low number of eggs collected for this study, the data suggests that spawning of these two perch species was not associated with river rises in this section of the Murray River.

Two studies addressing the relationship between recruitment success and flow for golden perch (Moffat 2003) and both golden and silver perch (Mallen-Cooper and Stuart 2003) further question the relationship hypothesised under the flood-recruitment model. Mallen-Cooper and Stuart (2003) compared data on cohort strength and with flow during the breeding season in each year, and suggest that years of high recruitment are not necessarily associated with floodplain inundation. Most years of high recruitment were associated with variable 'within-channel' flows. Further, recruitment of golden perch was negatively related to floodplain inundation (Mallen-Cooper and Stuart 2003). Mallen-Cooper and Stuart (2003) also revisited the data for those studies upon which the flood-recruitment model was established and found that this seminal data could be re-interpreted to support their model of significant recruitment in non-flood years. Moffat (2003) also reported that the strength of each year class of golden perch is not significantly correlated with flow in the year of spawning and recruitment. Both studies provide further evidence that these species are not obligate flood-cued spawners as previously believed (Lake 1967*a*; Mackay 1973; Cadwallader 1977; Rowland 1983*b*; Mallen-Cooper 1996; Stuart and Jones 2002).

A radio tracking study of golden perch in the Murray River by O'Connor *et al.* (2003) found that the movement of adult fish was negligible between May and September with a substantial increase in movement in September-October 2000 following a river rise. The response of fish varied with some moving upstream (24%), some downstream (52%) and others not moving (24%). By the end of December, a majority of the fish had returned to their original location. In the following year (2001), 85% of fish did not move with 15% travelling downstream in October (18°C). The

movements were interpreted by the authors to represent downstream spawning migrations. However a survey of the reproductive condition of 10 females in the following year indicated that none had spawned by December 2001. An equally plausible hypothesis is that adult golden perch move downstream following and preying upon the downstream drifting larvae of other fish or invertebrate taxa. These prey items could possibly be larval/juvenile carp dispersing from wetland spawning habitats on the receding tails of the coinciding flow peaks. As a result, downstream movements in September-October should not be considered spawning migrations until further evidence is available.

The results of this study, which support the findings of Mallen-Cooper and Stuart (2003) and Moffat (2003), demonstrate that golden and silver perch should not be considered obligate flood-cued spawners. High flow events were not associated with spawning activity over the period of time sampled for this study. Further, these studies do not support the model of flood-recruitment whereby recruitment success is dependant on inundation of the floodplain. In this study, all peaks in spawning activity were at relatively stable regulated flow conditions.

4.2. Effects of weirs

River regulation through the construction of dams, weirs and levee banks within major tributaries of the Murray-Darling Basin has altered natural flow and temperature regimes (Reynolds 1976; Cadwallader 1978, Walker *et al.* 1978; Walker 1979). River regulation has been shown to enhance conditions for alien species (Moyle & Williams 1990; Walker 1992; Harris and Gehrke 1997), alter food webs (Power *et al.* 1996; de Merona & Albert 1999), fragment populations (Gehrke *et al.* 1999), prevent spawning (Tomasson *et al.* 1984, Cambray *et al.* 1997; King *et al.* 1998) and reduce or eliminate recruitment (Robinson *et al.* 1998; Liebig *et al.* 1999; Merigoux & Ponton 1999; de Merona & Albert 1999). Childs *et al.* (1998) suggested that river regulation was most detrimental to larval fish as rapid fluctuations in river level would impact on littoral habitats which are actively sought and favoured by young fish (Petering and Johnson 1991; Brown & Coon 1994; Copp 1997; Baras & Nindaba 1999; Ponton *et al.* 2000), or areas of low flow which provide important nursery habitat (Sager 1987; Schiemer & Spindler 1989; Schiemer *et al.* 1991; Sempeski & Gaudin 1995; Watkins *et al.*, 1997; Sempeski *et al.* 1998). In addition, thermal pollution may retard development and swimming performance (Childs *et al.* 1998).

Humphries *et al.* (2002) interpreted their results as showing that river regulation did not affect spawning but did affect recruitment. They argued that only opportunistic species such as flat-headed gudgeons, Australian smelt, carp and redfin perch would flourish under regulated conditions.

We found no evidence that Torrumbarry Weir significantly obstructs the downstream drift of cod larvae within the Murray River. In contrast, there were significant differences in the densities of carp, with highest densities in the river and significantly lower densities in the weir-pool and below Torrumbarry Weir. This suggests that carp may settle from the drift under low flow conditions in the weir-pool. The occurrence of larval cod and carp below Torrumbarry Weir at equivalent densities to their occurrence in the weir-pool suggests that both taxa can pass Torrumbarry Weir during downstream drift.

Although the weir itself was not found to significantly obstruct downstream drift, settlement of ichthyoplankton in the associated weir pool may have implications for recruitment. Studies of the diet and availability of prey suggest that weir pools may provide suitable conditions for the growth and development of larval native fishes. Under hatchery pond conditions, cod and golden perch larvae feed selectively on crustacean zooplankton in preference to abundant rotifers in larval rearing ponds (Rowland 1992, Rowland, 1996). Rotifers generally dominate riverine zooplankton communities, while the preferred crustacean zooplankton dominate billabongs, backwaters and impoundments (Shiel 1978; Shiel 1979; Shiel 1980; Geddes 1984). Further, zooplankton biomass is positively correlated with water residence time (Basu & Pick 1996) and low flows in rivers (Pace *et al.* 1992; Thorp *et al.* 1994; Robertson 1995; Basu & Pick 1996) and is therefore greatest under low flow conditions (Ferrari *et al.* 1989). These arguments support the low-flow hypothesis of Humphries *et al.* (2002) in that impounded conditions within the river channel mimic the low flow conditions that would have naturally occurred in the Murray River prior to river regulation.

Impounded waters may therefore play an important role in the survival of larvae (Rowland 1992, Rowland 1996). This was demonstrated by Bulak *et al.* (1997), who found that striped bass recruitment success was greater for eggs that hatched within Lake Marion (USA), rather than in tributary streams. Therefore, the settlement of drifting cod, carp and eggs within Torrumbarry weir-pool may improve recruitment for these species rather than detract from it.

4.3. Spatial and temporal variation in downstream drift

Many studies have demonstrated that downstream drift is largely a nocturnal process (Hoar 1953; Woodhead 1957; Northcote 1962; Lindsey & Northcote 1963; Elliot 1966; Geen *et al.* 1966; Priegel 1970; Clifford 1972; Gale & Mohr 1978; Pavlov *et al.* 1978; Thayer *et al.* 1983; Muth & Schmulbach 1984; Brown & Armstrong 1985; Corbet & Powles 1986; Naesje *et al.* 1986; Iguchi & Mizuno 1990; Flecker *et al.* 1991; Winnell & Jude 1991; Franzin & Harbicht 1992; Pavlov *et al.* 1996; Johnston 1997; Jurajda 1998; Gadomski & Barfoot 1998; Marchetti & Moyle 2000). Some studies report a diel vertical migration with ichthyoplankton and invertebrate taxa drifting in the surface layers during the night and at lower levels in the water column during the day (Woodhead 1957; Clifford 1972; Gale & Mohr 1978; Pavlov *et al.* 1978; Gallagher & Conner 1983; Muth & Schmulbach 1984; Brown & Armstrong 1985; Copp & Cellot 1988; Wurtsbaugh & Neverman 1988; Richmond & Kynard 1995; Pavlov *et al.* 1996). There are exceptions to this nocturnal strategy (Gallagher & Conner 1983; Muth & Schmulbach 1984; Iguchi & Mizuno 1990; Robinson *et al.* 1998), but they are much less frequent. Nocturnal drifting behaviour has been reported for carp with densities of 30 ML⁻¹ recorded during the day and 66.7 ML⁻¹ at night (Gale & Mohr 1978). This general pattern of nocturnal activity of larval fish may be a result of loss of visual orientation under darkness (Hoar 1953; Northcote 1962; Lindsley & Northcote 1963), a mirroring of diel vertical migrations undertaken by zooplankton, which is the primary prey of larval fish (Shiel *et al.* 1982; Bayly 1986; Shiel 1986; Haney 1988), or predator avoidance (Richmond and Kynard 1995).

We identified significant differences in the number of cod larvae drifting downstream during four periods throughout the day. Drifting cod larvae did not preferentially drift at a particular depth within the water column. Further, depth in the water column was not dependent on time of day. Although we detected significant temporal variation, we are unable to conclusively state that drifting cod larvae are either diurnally or nocturnally active, as the time intervals assessed were neither wholly nocturnal or diurnal, and contained dusk and dawn periods.

Diel drift behaviour is also likely to be important for golden perch and silver perch, as both species have been demonstrated to respond to light by swimming downwards, but not towards shade (Lake 1967a; Gehrke 1990b).

4.4. Extent of drift

Stuart and Jones (2002) suggest that at an average flow rate of 20,000 ML per day, larvae would travel at 45km per day within the Murray River between Barmah and Torrumbarry. At that rate, and assuming that larval fish travel at the same rate as the flow peak, up to 8 days of drift are required to transport larval cod from below Yarrowonga Weir to Torrumbarry Weir. If cod larvae only remain in the drift for up to four days (as suggested by the data), only cod spawned within around 180 km upstream of Torrumbarry are likely to be impacted by a weir or weir-pool conditions. However a combination of the temporally variable drift behaviour observed for cod larvae, and observation of rheotaxis up until 19 days of age (Breheny, unpublished data) suggests that they may well drift at a much slower rate than that of flow peaks between gauging stations. Therefore, only cod larvae spawned within short distances upstream of weirs and weir-pools are likely to be influenced (positively or negatively) by the existence of these structures and habitats.

In contrast to cod larvae, carp drift for a much longer period and have a greater probability of exposure to weirs and weir-pools during downstream drift. However Stuart and Jones (2002) reported that carp larvae/juveniles took approximately one month to travel 144km whilst a flow rate of 45 km per day suggests that they should have made the journey in under 4 days.

4.5. Water extraction

Temporal variability in drift behaviour has important implications for management of cod within the Murray River. Koehn & Nicol (1998) recognised the potential effects of large scale water extraction on Murray cod reproduction and the possibility of high mortalities of larval fish passing through the hydroelectric plant or through the weir gates at Yarrawonga Weir. Cod larvae and the eggs and larvae of golden and silver perch can be entrained in water extracted from the river. As this water is rarely returned to the river system, water extraction during the breeding season has the potential to remove large numbers of potential recruits from the ecosystem (Koehn & Nicol, 1998).

Density data applied to extraction records from the study reach suggest that millions of cod larvae and eggs of golden and silver perch are potentially removed from the Murray River annually (Table 6).

As cod have a highly predictable drifting period within the months of October – December, reduction in the volume of water extracted during these months could enhance recruitment and may result in substantial rehabilitation of cod populations. If further assessment identifies that larval cod are nocturnally active, restricting water extraction from the river to hours of daylight, may result in further substantial benefits for fish communities within the river system whilst having little impact on extraction volumes.

5. RECOMMENDATIONS FOR FURTHER RESEARCH

5.1. Native fish

Water extraction during the breeding season was identified as a factor potentially responsible for the loss of a considerable number of recruits per year. This is particularly important for trout cod which are a nationally listed endangered species and silver perch which are listed as critically endangered in Victoria and vulnerable in New South Wales (and nationally). As a result, further assessments are suggested, to inform decisions about the management of water extraction during the breeding seasons of these species. These assessments could:

1. Assess the relative abundance of drifting eggs and larvae extracted from the river through water diversion and report on its importance to fish populations.
2. Clarify the diel behaviour of drifting larvae and report on its relevance to the management of water extraction during the breeding season.
3. Genetic identification of trout cod and Murray cod larvae to ‘tease-out’ differences in the spawning and reproductive biology of these two sympatric species.

5.2. Carp

This study demonstrated that carp spawning does not occur uniformly throughout river systems. Within the Murray River, the Barmah-Millewa forest was identified as a key location for carp recruitment. This information suggests that carp control initiatives undertaken in this wetland will considerably reduce the level of carp recruitment within the middle to upper reaches of the Murray River.

Commercial harvest of spawning aggregations in August-October, or exclusion of adults from these wetlands may significantly reduce the pool of mature spawning fish. In addition, this study identified that dispersal of young carp occurs on the receding tail of flow peaks following the initial spawning event. Therefore, commercial harvest of dispersing juvenile carp can be timed by regularly monitoring the hydrograph or by actively initiating dispersal behaviour by implementing environmental flows. To enable a targeted harvest, it is important to:

1. Identify and map the key locations of carp recruitment throughout the Murray-Darling Basin and establish the uniformity of dispersal behaviour of carp larvae/juveniles across these sites.

Further, the daughterless carp gene technology initiative will require information of the density of carp larvae/juveniles (fish per ML) produced each breeding season. This information is required to ensure that stocked genetically modified carp comprise a sufficient proportion of natural recruitment to ensure maintenance and spread of the daughterless gene throughout the Murray-Darling Basin. The sampling strategy developed for this project is ideal for:

2. Assess and monitor the density of carp larvae/juveniles (fish per ML) produced at key locations of carp recruitment throughout the Murray-Darling Basin.

6. REFERENCES

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7. **APPENDIX 1**

Marine and Freshwater Resources Institute

Counts of Daily Growth Increments in the Otoliths of
Juvenile Murray Cod (*Maccullochella peelii*) and Carp
(*Cyprinus carpio*).

The Central Ageing Facility

September 2000

Introduction

A sample of 78 juvenile Murray Cod, *Maccullachella peelii* and 46 Carp, *Cyprinus carpio* were supplied by NSW Fisheries (Narrandera Fisheries Centre) for daily estimation by the Central Ageing facility. Samples were collected between 1997 and 1999 Table 1.

Table 1. Batches of Murray Cod and European Carp sent to the CAF for daily age estimation.

Species	Batch	Date of Collection	Sample N
Murray Cod	50	97/98	29
Murray Cod	51	98/99	24
Murray Cod	52	97/98	25
		<i>Totals</i>	78
Carp	114	Unknown	9
Carp	115	97/98	16
Carp	116	98/99	21
Carp			
		<i>Totals</i>	46

Methods

Samples

Samples were received as whole juveniles stored in alcohol. Each specimen was allocated an identification number relating to the date of capture and fish length. Total length was measured to the nearest mm using electrical calipers.

Preparation of Otoliths

A dissecting microscope and transmitted polarised light was used to excise the otoliths from the fish. Otoliths were located in the auditory capsule by making a dorso-ventral cut from the top of the head through the preopercle using a scalpel blade. Sagittae were removed from the Murray Cod and stored on numbered microscope slides. The whole set of otoliths (lappilli, sagittae and asterisci) were excised for a sub sample of carp for preliminary evaluation of their comparative value for age interpretation (Brothers, 1987; David et al 1994). As no micro-increments could be detected in either the asterisci or sagittae, only the lappilli was used. The lappilli was extracted from the remaining carp samples.

The preparation of the otoliths was similar for both species. No preparation was required for otoliths with approximately <10 daily increments. Otoliths with >10 microincrements were ground down in a two stage process to obtain sections \equiv 50 μ m thick. Otoliths were attached to heated glass slides using clear thermal glue (Crystal Bond). Otoliths were arranged with the proximal face down and the distal face was ground down to the primordia with 1000 & 1200 carbide lapping film. The otolith was then turned over and the proximal face was ground down until the daily growth increments were visible over the whole otolith surface.

The ground surface were covered in immersion oil and viewed under a compound microscope. Magnification varied between 100 and 1000x depending on the size of the otolith. All ages were made without reference to either date of collection or fish length.

Readability

Each otolith sample was assigned a readability score between one and five. Readability is dependent on the clarity of the incremental structure. Readability score of one indicated the sample exhibited clear incremental structure throughout the whole otolith. Whereas a readability of five was assigned to a sample if it was unable to be assigned an age. This may include samples whose incremental structure was not clear enough to enable accurate age estimation or the samples that were either missing or broken.

Precision

Because of the difficulty in accurately counting daily growth increments, samples were aged up to three times where necessary to obtain a constant age estimate.

Results and Discussion

A total of 68 Murray cod sagittae were prepared and aged and 33 carp lapilli were examined. The remaining samples either could not be located within the fish sample or were damaged during preparation. Of the 13 carp that were not prepared and aged 10 were from fish smaller than 12mm total length (TL). Carp otoliths are extremely small and were difficult to extract from very small fish. Additionally these fish seemed to be effected by the high tannin environment that they were sampled from. These two factors influenced the availability of age estimates for carp under 12mm.

The ground section of the sagittal otoliths of the Murray Cod displayed clear contrasting light and dark zones (Figure 1). Age estimation was made along the anterior half as this area displayed the clearest and most unambiguous zones. Approximately the first 10 increments were, relatively dark, circular and concentric about the primordium. After approximately 10 days the increments became wider and increasingly less concentric.

The ground preparation of the Carp lapilli were quite circular up to approximately 20 days old increments were easily recognisable on all areas of the otolith. However, with increasing number of increments the otolith becomes progressively more elliptical and increments are the clearest along the posterior and anterior axis (Figure 2). The first 15-20 increments are relatively dark, circular and concentric around the primordium, whereas after approximately 10 days the increments become narrower and progressively more elliptical around the primordia. The edge of the otolith often proved to be the most difficult to interpret as the increments became narrow.

Assigned ages for Murray cod ranged from 10 to 23 days with a modal age of 14 days (Figure 3). Estimates from Carp ranged from 10 to 46 days (Figure 5). Length versus age plots indicate a positive relationship for both Murray Cod and Carp growth (Figure 5) Age estimates are presented in Appendix 1.

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Figure 1. Murray cod ground otolith, fish number 15 (Batch 51), indicating anterior (A) and posterior (P) sectors. Length 13mm, estimated age 13 days.

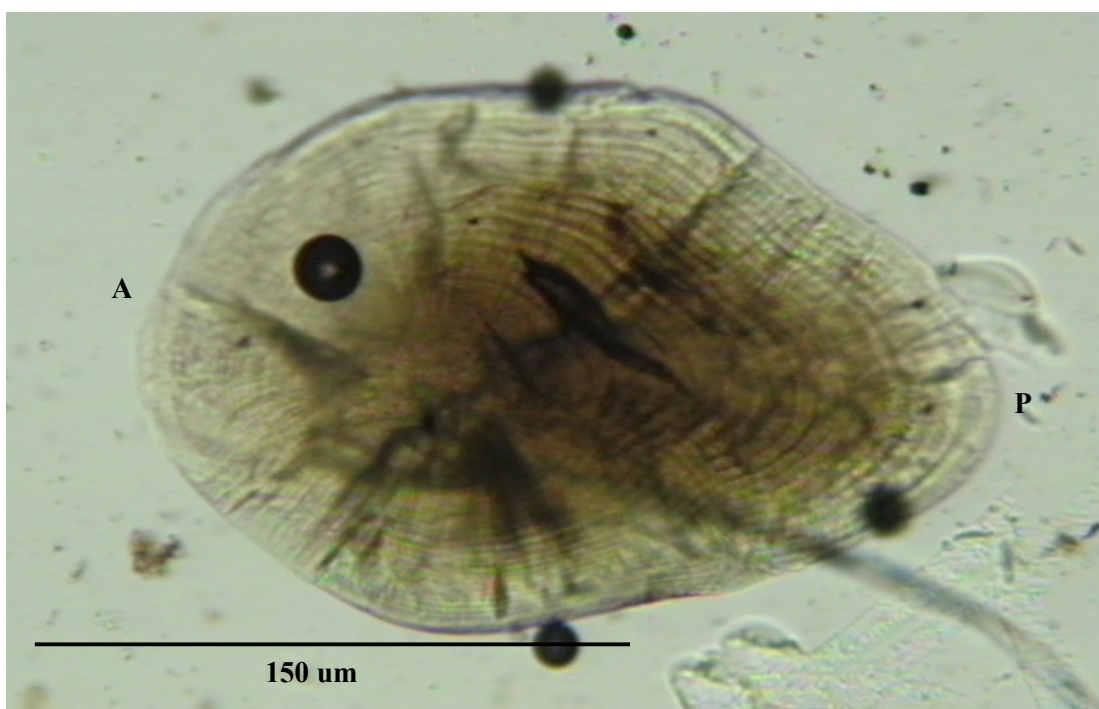


Figure 2. Ground carp lapilli, fish number 5 (Batch 115), indicating anterior (A) and posterior (P) sectors. Length 29mm estimated age 30 days.

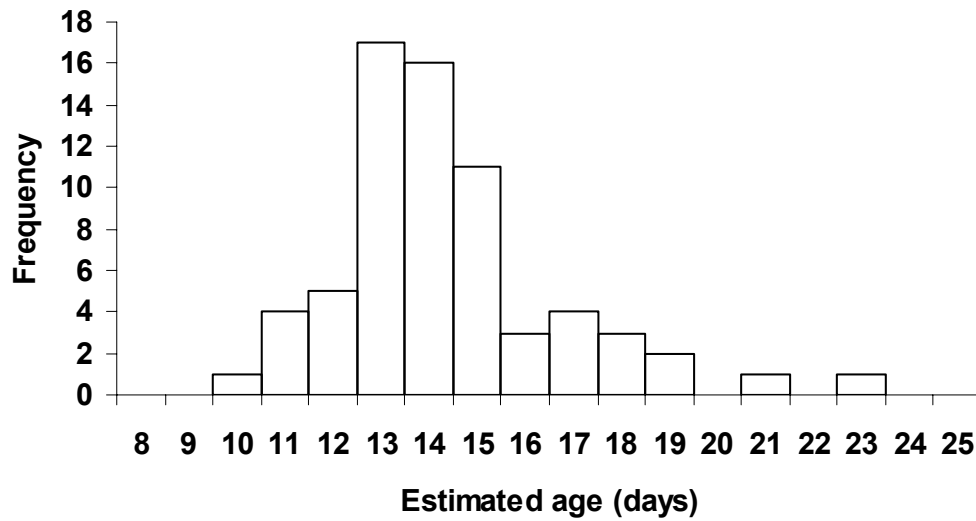


Figure 3. Frequency distribution of aged samples of juvenile Murray Cod.

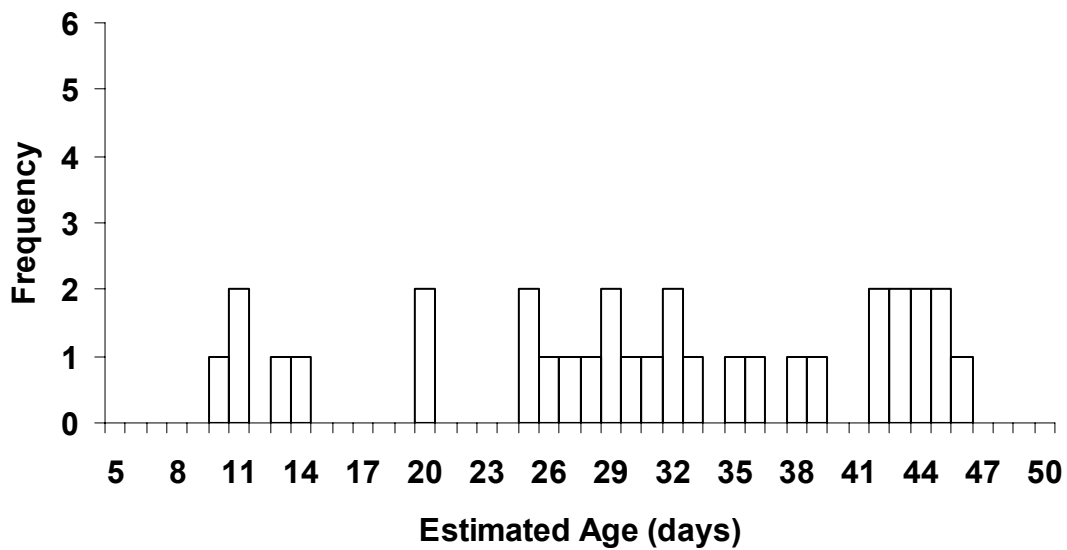


Figure 4. Frequency distribution of aged samples of juvenile Carp.

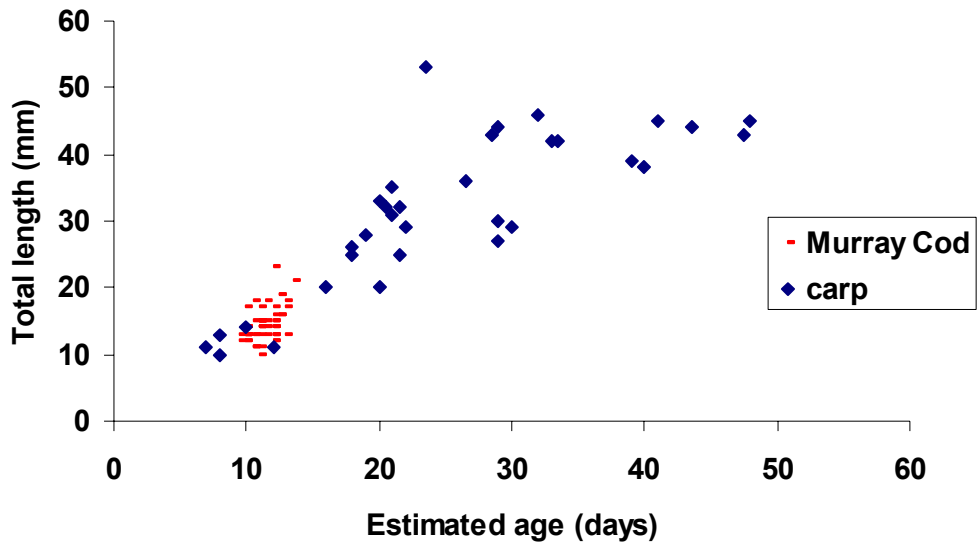


Figure 5. Length versus estimated age for juvenile Murray Cod and Carp.

Species	Batch Number	Specimen	Total Length (mm)	NSW Fish Reference	Date of Capture	Age (days)	Readability
Murray Cod	50	1	9	C1	97/98	13	4
Murray Cod	50	2	11	C2	97/98	15	3
Murray Cod	50	3	11	C3	97/98	15	3
Murray Cod	50	4	10	C4	97/98	13	3
Murray Cod	50	5	11	C5	97/98	15	2
Murray Cod	50	6	11	C6	97/98		5
Murray Cod	50	7	12	C7	97/98	16	3
Murray Cod	50	8	11	C8	97/98	14	2
Murray Cod	50	9	10	C9	97/98	13	3
Murray Cod	50	10	11	C10	97/98		5
Murray Cod	50	11	11	C11	97/98	15	4
Murray Cod	50	12	10	C12	97/98	13	3
Murray Cod	50	13	10	C13	97/98	14	3
Murray Cod	50	14	10	C14	97/98	14	3
Murray Cod	50	15	10	C15	97/98	13	1
Murray Cod	50	16	12	C16 Mk 2	97/98	14	4
Murray Cod	50	17	12	C17	97/98	13	3
Murray Cod	50	18	12	C18	97/98	17	4
Murray Cod	50	19	13	C19	97/98	21	2
Murray Cod	50	20	12	C20	97/98		5
Murray Cod	50	21	11	C21	97/98	18	3
Murray Cod	50	22	12	C22	97/98	16	2
Murray Cod	50	23	11	C23	97/98	13	4
Murray Cod	50	24	12	C24	97/98	12	5
Murray Cod	50	25	10	C25	97/98	12	4
Murray Cod	50	26	11	C26	97/98		5
Murray Cod	50	27	12	C27	97/98		5
Murray Cod	50	28	10	C28	97/98	13	4
Murray Cod	50	29	10	C29	97/98	13	3
Murray Cod	51	1	10	101	98/99	14	2
Murray Cod	51	2	10	102	98/99	11	3
Murray Cod	51	3	10	103	98/99	13	3
Murray Cod	51	4	10	104	98/99	13	2
Murray Cod	51	5	10	105	98/99	12	3
Murray Cod	51	6	10	106	98/99	11	2
Murray Cod	51	7	12	107	98/99	13	2
Murray Cod	51	8	12	108	98/99		5
Murray Cod	51	9	11	109	98/99	14	3
Murray Cod	51	10	10	110	98/99	13	3
Murray Cod	51	11	11	111	98/99	13	4
Murray Cod	51	12	12	112	98/99	13	2
Murray Cod	51	13	9	113	98/99		5
Murray Cod	51	14	10	114	98/99		5
Murray Cod	51	15	13	115	98/99	18	3
Murray Cod	51	16	11	116	98/99	11	4
Murray Cod	51	17	9	117	98/99	12	2
Murray Cod	51	18	11	118	98/99	10	4
Murray Cod	51	19	13	119	98/99	13	2
Murray Cod	51	20	12	120	98/99	19	2
Murray Cod	51	21	12	121	98/99	19	3
Murray Cod	51	22	12	122	98/99	13	2
Murray Cod	51	23	12	123	98/99	14	3
Murray Cod	51	24	10	124	98/99	11	4
Murray Cod	52	1	11	M1	97/98	14	1
Murray Cod	52	2	11	M2	97/98	14	2
Murray Cod	52	3	11	M3	97/98	14	2
Murray Cod	52	4	11	M4	97/98	15	3
Murray Cod	52	5	12	M5	97/98	15	4
Murray Cod	52	6	12	M6	97/98	14	2
Murray Cod	52	7	11	M7	97/98	15	1
Murray Cod	52	8	12	M8	97/98	23	3
Murray Cod	52	9	12	M9	97/98	12	4
Murray Cod	52	10	12	M10	97/98	14	3
Murray Cod	52	11	10	M11	97/98	15	4
Murray Cod	52	12	11	M12	97/98	14	4
Murray Cod	52	13	10	M13	97/98		5
Murray Cod	52	14	10	M14	97/98	17	3
Murray Cod	52	15	11	M15	97/98	17	4
Murray Cod	52	16	11	M16	97/98	15	3
Murray Cod	52	17	12	M17	97/98	15	3
Murray Cod	52	18	10	M18	97/98	18	3
Murray Cod	52	19	11	M19	97/98	15	3

Species	Batch Number	Specimen	Total Length (mm)	NSW Fish Reference	Date of Capture	Age (days)	Readability
Carp	114	1	10	5		14	2
Carp	114	2	7	6		11	4
Carp	114	3	22	7		29	3
Carp	114	4	29	8		27	5
Carp	114	5	16	9		20	3
Carp	114	6	22	10			5
Carp	114	7	11	11			5
Carp	114	8	8	12		10	3
Carp	114	9	8	13		13	4
Carp	115	1	20	F1	97/98	32	4
Carp	115	2	21	F2	97/98	25	3
Carp	115	3	21	F3	97/98	31	2
Carp	115	4	18	F4	97/98	26	3
Carp	115	5	29	F5	97/98	30	4
Carp	115	6	19	F6	97/98	28	3
Carp	115	7	30	F7	97/98	29	3
Carp	115	8	29	F8	97/98		5
Carp	115	9	26	F9	97/98	36	4
Carp	115	10	12	F10	97/98	11	3
Carp	115	11	34	F11	97/98		5
Carp	115	12	11	F12	97/98		5
Carp	115	13	12	F13	97/98		5
Carp	115	14	11	F14	97/98		5
Carp	115	15	29	F15	97/98		5
Carp	115	16	20	F16	97/98	20	3
Carp	116	1	9	1	98/99		5
Carp	116	2	10	2	98/99		5
Carp	116	3	10	3	98/99		5
Carp	116	4	10	4	98/99		5
Carp	116	5	10	5	98/99		5
Carp	116	6	21	6	98/99	35	4
Carp	116	7	21	7	98/99	32	4
Carp	116	8	18	8	98/99	25	4
Carp	116	9	23	9	98/99	53	4
Carp	116	10	20	10	98/99	33	4
Carp	116	11	33	11	98/99	42	4
Carp	116	12	28	12	98/99	43	4
Carp	116	13	32	13	98/99	46	3
Carp	116	14	29	14	98/99	44	4
Carp	116	15	33	15	98/99	42	3
Carp	116	16	41	16	98/99	45	4
Carp	116	17	48	17	98/99	45	3
Carp	116	18	40	18	98/99	38	3
Carp	116	19	43	19	98/99	44	3
Carp	116	20	39	20	98/99	39	2
Carp	116	21	47	21	98/99	43	2

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