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Monitoring by telemetry reveals differences in movement and survival following hatchery or wild rearing of an endangered fish

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Abstract. Species reintroduction is a management strategy used to conserve endemic fish biodiversity. The present study investigated stocking on-grown endangered trout cod (*Maccullochella macquariensis*) in the Murrumbidgee River, Australia. The hypothesis that post-juvenile dispersal underpins the long-term scarcity of adults recorded at fingerling stocking locations was also tested. Radio-tracking was used to quantify dispersal of stocked sub-adults (2-year old hatchery fish, $n = 27$) compared with fish originally stocked as fingerlings (unknown-age wild fish, $n = 31$), but we encountered poor survivorship of the former group (survivorship = 9% and 95%, respectively, at 13 months post release). The hatchery group exhibited both limited dispersal and large-scale dispersal (up to 55 km) downstream from the release site. Wild fish exhibited limited net dispersal, occupying home-ranges within a 13-km reach and occasionally undertook large-scale excursions (10–70 km). It is concluded that (1) re-establishment of cod populations based on release of on-grown fish is not straightforward, and (2) adults of this species have an ability to disperse away from stocking sites. The study demonstrates the benefit of using radio-tracking to monitor the movement and survivorship of stocked threatened fish and indicates a need to consider the effects of hatchery rearing when conducting fish reintroductions.

Additional keywords: dispersal, hatchery, *Maccullochella*, radio-tracking, reintroduction, survivorship.

Introduction

Species reintroduction programs (Wallace 2000), including those for threatened fishes (Brown and Day 2002) should be based on a detailed and transparent platform of experimental research (Fischer and Lindenmayer 2000). Translocation of wild fish and stocking of hatchery-reared fish are common approaches to re-establishing populations of threatened species (Minckley 1995) and enhancing fisheries (Molony *et al*. 2003). Comparison of wild and hatchery-reared fish in the hatchery (Metcalfe *et al*. 2003; Salvanes and Braithwaite 2005) and the wild (Thorstad *et al*. 1998; Dieperink *et al*. 2001; Bettinger and Bettoli 2002) has provided useful insights into the shortcomings of stocking hatchery-reared fish, especially salmonids, in the northern hemisphere. Behavioural changes due to domestication often reduce the survival of stocked fish, resulting in highly variable success among fish stocking programs (Dieperink *et al.* 2001; Bettinger and Bettoli 2002).

Familiarity of wild fish with the river environment is probably a major advantage relative to newly released hatchery fish (Brown and Day 2002). For instance, the movement and dispersal of hatchery and wild-reared fish is likely to differ if wild fish are capable of homing to a territory or home-range that they have occupied previously, whereas hatchery-reared fish are naïve to the new environment. In this regard, studies comparing search behaviour, homing and home-range occupation (e.g. Crook 2004*a*, 2004*b*) of fish offer promise for informing species reintroduction programs. Individuals can disperse immediately following release or later undertake home-range shifts (Crook 2004*a*), leading to emigration and insufficient numbers of adults at the release site to establish a self-sustaining population (Armstrong and Seddon 2008).

In Australia, relative to the northern hemisphere, there has not been a comparable research focus on fish stocking in fresh waters, despite widespread stocking of freshwater fishes including species of the family Percichthyidae (Lintermans *et al*. 2005; Gillanders *et al*. 2006; Lintermans 2006). In temperate mainland Australia, the family Percichthyidae is the most identifiable group of endemic freshwater fishes from the public perspective. This is because the family includes large-bodied species of freshwater cod in the genus *Maccullochella* and the perches of *Macquaria* (Harris and Rowland 1996). These fishes are targeted by recreational anglers and, in several cases, represent conservation listed species (Morris *et al*. 2001; Lintermans and Phillips 2004).

Trout cod *Maccullochella macquariensis* (Cuvier) is a nationally endangered freshwater fish of the family Percichthyidae, endemic to rivers in the south-east of the Murray–Darling Basin, Australia (Ingram and Douglas 1995). The species is

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conservation-listed as endangered in the Australian Capital Territory (ACT) and New South Wales (NSW) and critically endangered in Victoria (Morris *et al*. 2001; DSE 2003; ACT Government 2007). Efforts to recover the species have involved the largest freshwater conservation-stocking program in the country (Lintermans *et al*. 2005; Lintermans 2006). Since 1986, hatchery-produced fingerlings have been stocked into areas where the natural population was locally extinct in NSW, Victoria and the ACT in an effort to re-establish populations (Douglas *et al*. 1994; Gilligan 2005). Large rivers have been the focus of stocking efforts because they were assumed to be the primary habitats of *M. macquariensis*. There has generally been minimal or sporadic monitoring at reintroduction sites, and knowledge of successful survivorship has been mainly from angler reports. Survival and growth of fingerlings through to the age of 2–3 years (juveniles) has been documented at several sites (Faragher *et al*. 1993; Lintermans 1995; Brown 1998; Brown *et al*. 1998; Douglas and Brown 2000; Gilligan 2005; NSW DPI 2006). The number of 3–5-year-old individuals (sub-adult or young adults, Harris and Rowland 1996) captured in monitoring programs is much lower. Reports of large adult individuals have been uncommon. Possible explanations for the scarcity of adults in re-stocked populations are: (1) larger fish (adults) are subject to high mortality including angling pressure and/or natural mortality; (2) larger fish remain at the release site but are undetected by monitoring; and/or (3) juveniles remain at the release site until they reach sub-adulthood at which stage they disperse, becoming difficult to detect.

Generally, fish populations suffer greatest natural mortality in early life-history phases (Jones 1991) and this presumably applies to *M. macquariensis* (Todd *et al*. 2004). It is unlikely that adult fish are subject to high mortality, though an understanding of mortality in this species is a major knowledge gap in recovery of the species (S. Nicol, Department of Sustainability and Environment Victoria, pers. comm.). It is also unlikely that larger fish remain at the site and are not detected by monitoring. Electrofishing has been a commonly employed monitoring technique for *M. macquariensis* and other freshwater cod (Faragher *et al*. 1993; Growns *et al*. 2004; Ebner *et al.* 2008) and has proven successful in detecting a wide range of size classes at a subset of sites (Ebner *et al*. 2006).

The main hypothesis that we tested was that post-juvenile dispersal is the reason for the scarcity of *M. macquariensis* sub-adults and adults recorded at stocking locations. Despite indications that juveniles can be gregarious (Douglas *et al*. 1994), it is possible that as individuals grow and mature they become territorial, leading to dispersal from the release sites, since under hatchery conditions individuals become particularly aggressive towards one another from a very early age (B. Ingram, Department of Primary Industries Victoria, pers. comm.). Therefore, to improve re-establishment of populations of *M. macquariensis*, it is important to determine the movement patterns of sub-adults following stocking in rivers. Hatchery-reared *M. macquariensis* individuals released into upland streams (Ebner *et al*. 2005) and hatchery-reared salmonids released in the northern hemisphere have been reported to disperse predominantly in a downstream direction (e.g. Bettinger and Bettoli 2002). In the context of *M. macquariensis*, limited dispersal has been observed previously in a lowland river (Koehn *et al*. 2008) and percichthyids are known to home following release (Crook 2004*a*, 2004*b*). We tested the hypothesis that hatchery and wild-reared *M. macquariensis* individuals would disperse differently. Additionally, stocking of on-grown fish is also examined as an alternative reintroduction strategy to releasing fingerlings. We also aimed to determine the habitat use of this species to inform river restoration programs in the Murrumbidgee River.

Methods

Site description

The study was done in a lowland reach of the Murrumbidgee River near Narrandera (146°36′E; 34°46′S), between Berembed and Gogeldrie weirs (105 river km) in southern NSW, Australia (Fig. 1). This is one of twelve *M. macquariensis* stocking sites in the Murrumbidgee catchment, with 85 000 fingerlings (~30–50 mm total length (TL)) stocked at this location (Narrandera) between 1996 and 2000 (Gilligan 2005). Good numbers of wild fish captured by subsequent surveys indicate the reach to be the most successful stocking site for the species in NSW (Growns *et al*. 2004; Gilligan 2005). In this reach, water is diverted at Berembed, Yanco and Gogeldrie weirs to meet irrigation requirements between spring and autumn. In-stream flow remains a function of rainfall during winter (Ebsary 1992). The geomorphology includes a transition from lower confined floodplains to open floodplains (Young *et al*. 2001). River red-gum (*Eucalyptus camaldulensis*) is common along much of the riparian edge of the river and channel widths are in the order of 70 m (Growns *et al*. 2004). River depths of 3–5 m are commonly encountered on outside bends. The dominant in-stream habitat comprises structural woody habitat (SWH) consisting of fallen trees or branches, particularly of river red-gum.

Source of fish

Two experimental release groups were used for this study. The first (hatchery) group comprised 29 *M. macquariensis* individuals (2 years of age, mean ± s.e. total length (TL) 394.00 ± 6.71 mm, range 310–429 mm; weight 1159.97 ± 53.16 g, range 513–1567 g) sourced from Snobs Creek Research Station (Department of Primary Industries) in Victoria and transported to the Narrandera Fisheries Centre in NSW. These individuals were bred from wild broodstock (Murray River natural population). Initially, post-larvae were reared in a fertilised earthen pond under semi-natural conditions. After harvesting the pond, fingerlings were transferred to hatchery facilities where they were weaned onto an artificial extruded diet then on-grown in 500-L circular fibreglass tanks that were part of an intensive recirculating aquaculture system. Methods used for fry rearing, weaning and on-growing were similar to those employed for Murray cod (*M. peelii peelii* (Mitchell)), which are described in more detail by Ingram (2004). The second (wild) group, comprised 32 *M. macquariensis* individuals (age unknown, mean ± s.e. TL 451.90 ± 10.58 mm, range 370–635 mm; weight 1258.19 ± 116.50 g, range 599–3704 g) originally stocked as fingerlings and subsequently collected by boat electro-fishing from the Murrumbidgee River at Narrandera before surgery (Ebner *et al*. 2006). These individuals were collected between 10.3 km downstream and 4.7 km upstream

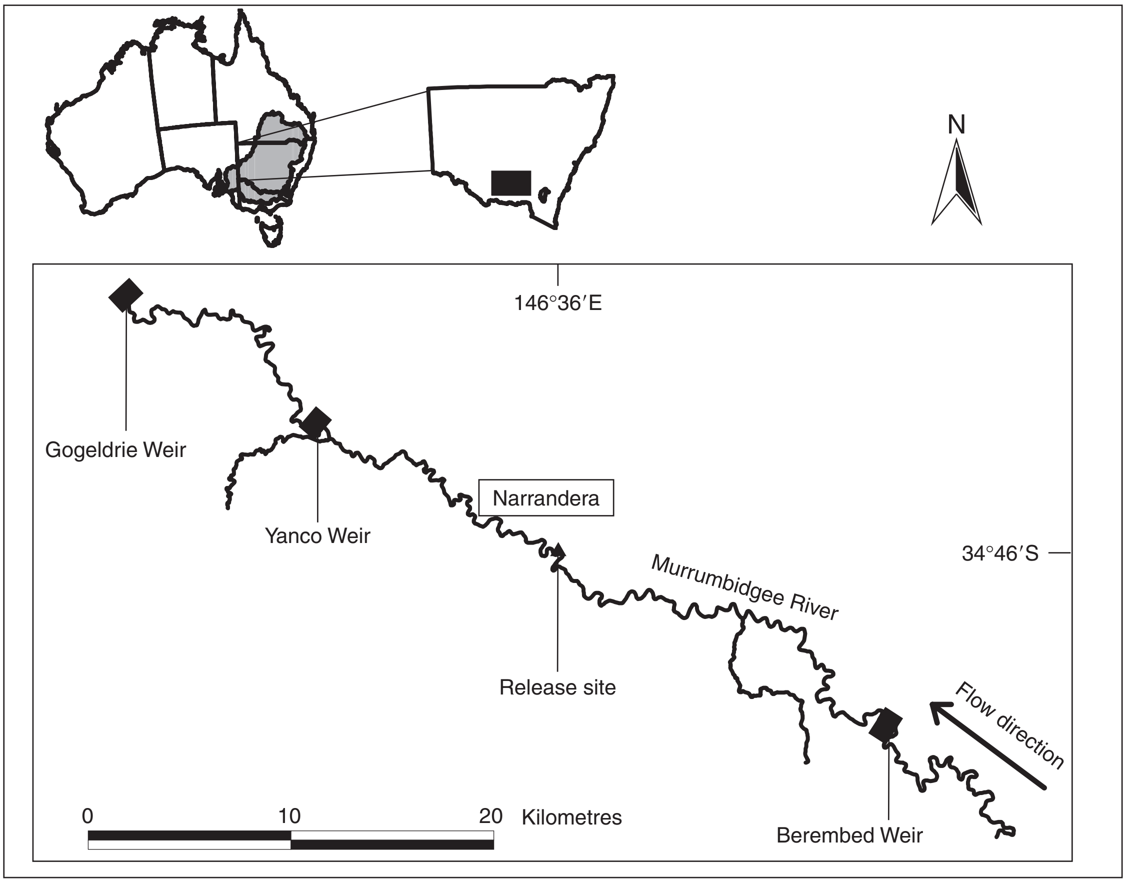

Fig. 1. Location of the study reach along the Murrumbidgee River within New South Wales, Australia.

of their later release site, and a GPS record was obtained at each capture location (Ebner *et al.* 2006). Fulton's condition index (Ricker 1975) was applied to both groups. A two-sample *t*-test identified that hatchery fish were characterised by a higher condition index than the wild group ($t = 18.8$; d.f. $= 48.6$; $P < 0.05$) due to large fat deposits in the peritoneal cavity.

Surgery and release

Radio-tags (F1830, 35, 40 and 50, 11–25 g, Advanced Telemetry Systems (ATS), Isanti, MN, two-stage radio-transmitters, 150–152 MHz, pulse coded, duty cycle of 5 s on and 7 s off) were surgically implanted into hatchery and wild fish from 12–16 September and 16–24 September 2003 respectively. Radio-tag to bodyweight ratios ranged from 1.1 to 2.1% and 0.6 to 2.1% for hatchery and wild fish respectively. The surgery method was similar to that described by Ebner *et al.* (2007), with the exception of incisions being 2–3 cm in the current study. For external identification, individuals were also tagged with a dart tag in the dorsal musculature between the second and third dorsal spines. Individuals initially recovered in a darkened enclosure holding 200 L of aerated water at a Practical Salinity of 5 (based on the Practical Salinity Scale of 1978). On regaining swimming ability, individuals were transferred to large circular concrete enclosures that held between 500 and 1000 L at a Practical Salinity of 5. Hatchery and wild individuals were held in separate enclosures to prevent aggressive interactions. One wild individual died immediately post-surgery and autopsy revealed internal bleeding from a severed artery within the peritoneal cavity.

On 25 September 2003, 21 hatchery individuals implanted with radio-tags were released into the Murrumbidgee River, 5 river kilometres upstream of Narrandera (Fig. 1). On 26 September, 29 wild individuals implanted with radio-tags were released at the same location. Surgery was repeated on a further 10 individuals (two wild and eight hatchery individuals) that showed signs of loose sutures and/or open incisions, with three hatchery individuals rejecting their first radio-tags. On 1 October, two hatchery individuals were euthanased because they had developed severe infection around the incision and showed no sign of healing externally (despite swimming and behaving similarly to other healthy individuals). The remaining six hatchery and two wild individuals had healed incisions and were released on 1 October.

Radio-telemetry

A two-person crew, aboard a 3-m aluminium punt powered by an 8-Hp, two-stroke outboard motor, undertook manual radio-tracking approximately fortnightly for the first 3 months and then monthly up until 13 months post release. Individuals were located during daylight hours using a scanning receiver

(Australis 26k, Titley Electronics, Ballina, Australia or R4100, ATS) and a three-element Yagi antenna (Titley Electronics or ATS). Locations of individuals were recorded by taking three waypoints with a hand-held GPS (Garmin GPSII Plus or Garmin GPS 76 Marine Navigator (Olathe, KS, USA); Figure of merit (F.O.M.) ≤ 5.0 at $\sim$95% of locations, F.O.M. ≤ 7.0 at 100% of locations).

Record was made of the habitat occupied by each individual, including positioning within either a straight, the inside bend or the outside bend of a river channel. Water depth ($\pm$0.1 m) was recorded using a depth sounder (Eagle Strata 128, Catoosa, GA) mounted on the stern of the boat. Distance from the bank was estimated by both crew members and averaged. Structural habitat that each fish was detected was characterised as structural woody habitat, clay bank, macrophytes or an absence of structure (referred to as open-water). Habitat was determined visually and from depth sounder images obtained on repeated passes. Water temperature was collected at half-hourly intervals 5 river kilometres downstream from the tagged fish release site using a Hydrolab MS5 (Loveland, CO, USA) set at 0.5 m below the water surface (Sue Vink, CSIRO Land and Water, unpubl. data) and averaged to provide a daily record. Temperature stratification was unlikely to occur at this site owing to the predominance of summer irrigation flows. River discharge was recorded at daily intervals (NSW DNR 2004).

From 13 November 2003 to 14 November 2004, remote radio-telemetry data loggers (DCCII Model D5041, ATS connected to an ATS R4100 receiver, powered by 12-V power supply) were deployed at Berembed and Yanco weirs, 75 km apart (see Fig. 1). These loggers scanned 60 frequencies sequentially (58 implanted radio-transmitters and two reference transmitters that were retained in the vehicle used to conduct field exercises) every 30 min. The approximate detection range of these loggers was 1 km.

Data analysis

The average of three replicate spatial points recorded at the location of an individual was used to minimise GPS error (except where one of these replicates was clearly an outlier i.e. >10 m from either of the other replicate points in which case the two similar replicates were averaged). Large-scale movement of individuals was quantified from records of the remote telemetry logger stations combined with those arising from manual radio-tracking. Movement distances were calculated using ArcView 3.2 (ESRI, CA, USA) based on maps digitised at the 1 : 25 000 scale. For large-scale movement and dispersal, each spatial location was shifted onto the river mid-line. A polyline was generated based on the sequential locations of each individual using the Animal Movement Extension in ArcView (Hooge and Eichenlaub 1997). This was used to construct a time series of (1) the proximity of individuals to the release point and (2) distance moved between consecutive radio-tracking events. A post hoc power analysis (performed in Statistica version 7: StatSoft, Tulsa, OK, USA) revealed that sample sizes were adequate for detecting differences in dispersal of the wild and hatchery groups.

Dispersal between the two release groups was compared using two-sample *t*-tests of log-transformed data at 1 and 3 months post release. Homing was categorised as return to a location within one home-range, in either an upstream or downstream direction, from where an individual was originally captured (relevant to wild fish only), based on a maximum home-range size of 272 m for a subset of this group (Thiem *et al.* 2008). To determine if homing success was a function of translocation distance from capture sites, a two-sample *t*-test was applied to square-root-transformed data. To determine if translocation direction (upstream or downstream from the release site) affected homing success, a χ^2 analysis was used. Total range was calculated as the distance between the furthest upstream and downstream location attained by each individual in the study. This did not include the capture locations of wild individuals but did incorporate records from the remote telemetry loggers. Home-range was estimated from monthly locations of individuals beginning 8 weeks after release because at this stage, >90% of wild individuals had established fidelity to a site and so any potential biases from the use of a single release site were removed. We tested the hypothesis that following initial dispersal and/or homing, *M. macquariensis* fish undertook comparatively limited movement, based on a two-sample *t*-test to compare total range with home-range of wild individuals. Site fidelity was classified as repeated monthly locations (i.e. a minimum of two locations) <272 m upstream or downstream from a previous location. In general, movements were either contained within this length of river or vastly exceeded this distance. Linear home-range estimates were taken as the minimum direct distance between upstream and downstream extremities where site fidelity was clearly established (inaccuracy of the base-map prevented calculation of linear home-range along the river channel midline). Minimum convex polygons (MCP) were used to estimate home-range area (Hooge and Eichenlaub 1997), where a minimum of 10 monthly fixes was obtained unless otherwise stated.

All statistical analyses were conducted in Statistix for Windows (version 8.1: Analytical Software, Tallahassee, FL, USA). *T*-tests were conducted following *F*-tests for homogeneity of variance. Wilk–Shapiro normality tests were conducted, with data transformed where necessary to achieve approximate normal distribution (Tabachnick and Fidell 1989). The significance level for hypothesis tests was $P = 0.05$.

Results

Dispersal

Dispersal from the release site was characterised by a different scale of movement between the two *M. macquariensis* groups (Fig. 2) and was significantly greater for the hatchery than the wild group at both 1 ($t = 2.45$; d.f. $= 40.8$; $P < 0.05$) and 3 months ($t = 2.14$; d.f. $= 41.8$; $P < 0.05$) post release. Individuals from the wild group remained within 5 km of the release site (upstream or downstream) for the majority of the study, with the exception of a maximum of four individuals on any fortnightly or monthly radio-tracking exercise (Fig. 2). Typically, these exceptions involved movements up to 15 km upstream or downstream from the release site, although one individual was recorded 40 km upstream of the release site over a 4.5-month period (Fig. 2). Conversely, the hatchery group exhibited pronounced modal classes 0–5 km and 5–10 km downstream

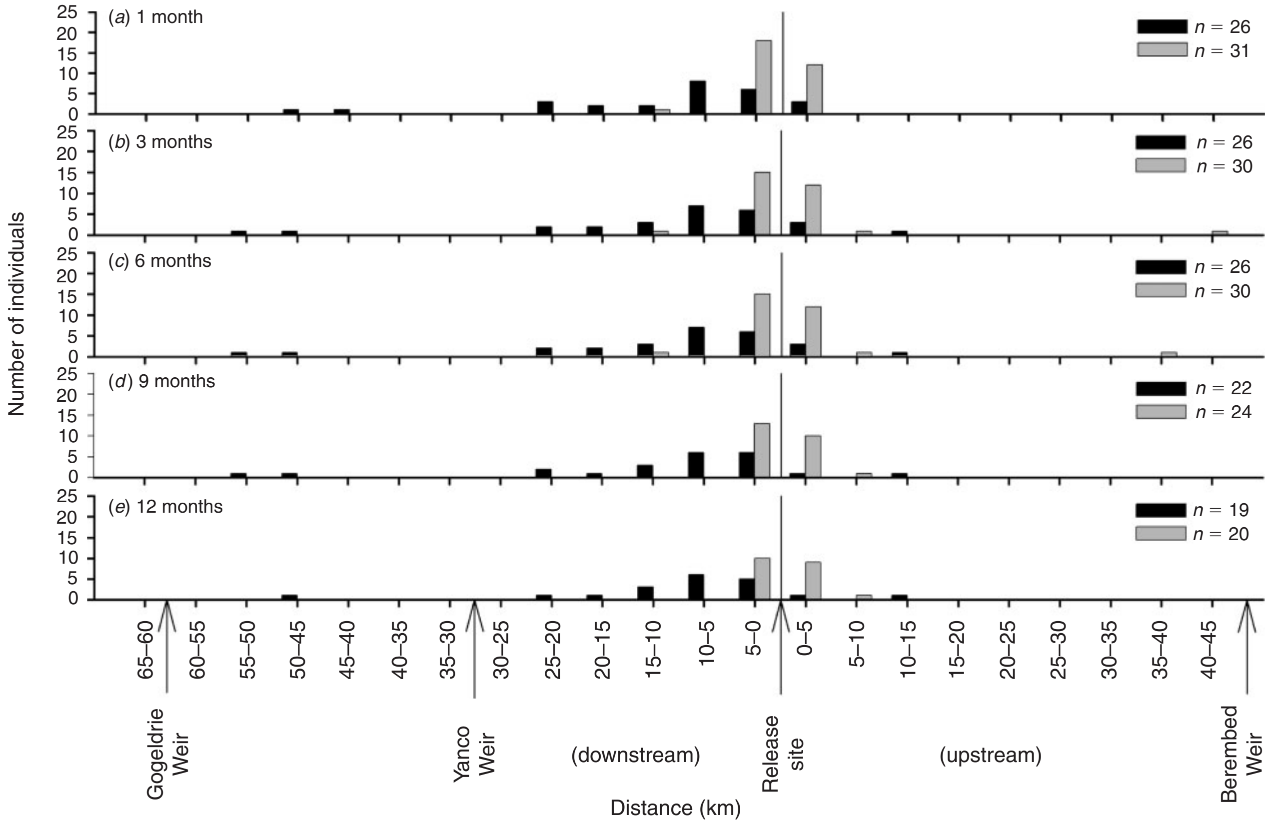

Fig. 2. Dispersal of hatchery (■) and wild (□) *Maccullochella macquariensis* groups in the Murrumbidgee River. Time after release: (*a*) 1 month; (*b*) 3 months; (*c*) 6 months; (*d*) 9 months; and (*e*) 12 months. Distance moved is expressed as upstream and downstream direction in 5-km categories.

of the release site, plus large-scale downstream movement of individuals within 1 month of being released (Fig. 2). Two individuals that had passed through Yanco Weir and were 40–50 km downstream of the release site represented the largest of these downstream movements. At 7–8-weeks post release, the location of individuals from the hatchery group was similar to the previous fortnightly fix and generally remained stable until the completion of the study (Fig. 2). Additionally, a hatchery individual that was undetected at 4-weeks post release was located 10–15 km upstream of the release site 7 weeks post release where it remained for the entire study (Fig. 2).

Up until 5–6 weeks after release, both the hatchery and wild groups remained close to the release site, with the hatchery group also dispersing downstream whereas the wild group moved in either direction (Fig. 3*a*, *b*). After this time, there was minimal movement by hatchery individuals (Fig. 3*b*). Similarly, there was minimal movement by the majority of wild individuals, but a subset of individuals displayed pronounced upstream and/or downstream movement (Fig. 3*a*). These movements were not synchronised, occurring in November and December 2003 and April, May and September 2004 based on monthly radio-tracking exercises (Fig. 3*a*). These movements showed no discernable relationship with changes in discharge, temperature (Fig. 3*c*) or expected spawning period (Koehn and O'Connor 1990; Koehn and Harrington 2006).

In addition to movements detected by monthly and fortnightly radio-tracking, the downstream (Yanco Weir) telemetry logger (set up after two hatchery individuals had passed through the weir (Fig. 2)) detected the presence of five individuals (one hatchery and four wild *M. macquariensis*) encountering Yanco Weir. Interestingly, all five individuals did not stay within detection range of the logger for more than a single logger cycle (~30 min). The hatchery individual was the first record on the logger (November 2003), travelling ~11 km downstream from its normal home-range and then returning to its previous location. This individual displayed the fastest recorded swimming speed, covering 10.9 km in a maximum time of 4 hours. In all four instances of wild individuals encountering Yanco Weir, individuals vacated an established home-range to undertake downstream movements of between 27 and 33 km, followed by return journeys to the vacated home-range. One of these movements occurred in December 2003, two in February 2004 and another in April 2004. All journeys were circular, with fish subsequently located at the previously occupied SWH. Minimum swimming speeds for these individuals varied from 0.04 to 0.32 km h^{-1}.

Confirmed survival of individuals from the two groups, wild and hatchery, differed greatly throughout the course of this study (Fig. 4). In the case of the wild group, 29 individuals were alive 6 months after release (Fig. 4*a*). One individual had a failed

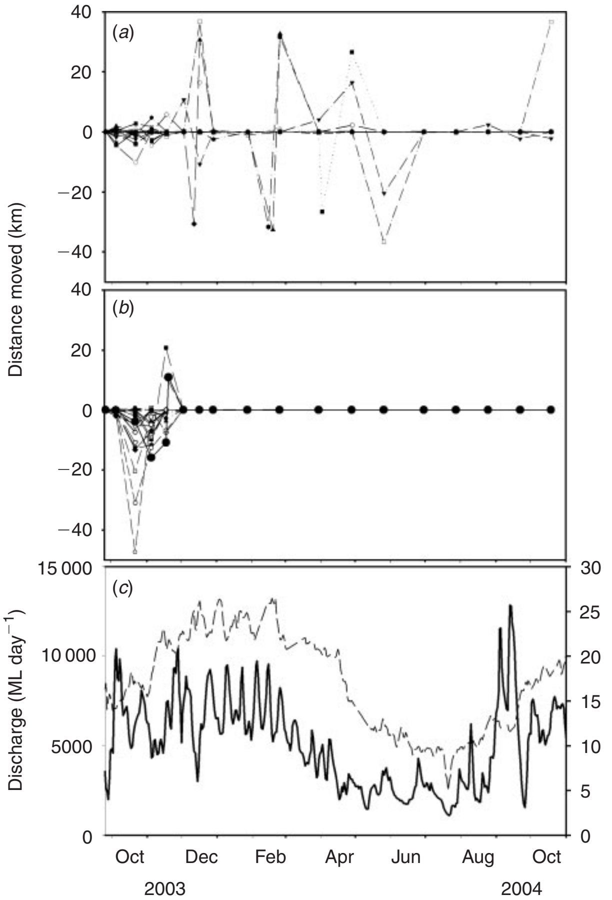

Fig. 3. Minimum distances moved between radio-tracking intervals (as detected by manual radio-tracking and remote telemetry) by all (*a*) wild and (*b*) hatchery trout cod (*Maccullochella macquariensis*) and (*c*) the water discharge (--) and temperature (—) in the Murrumbidgee River at Narrandera. Positive and negative values indicate a direction of movement upstream and downstream, respectively.

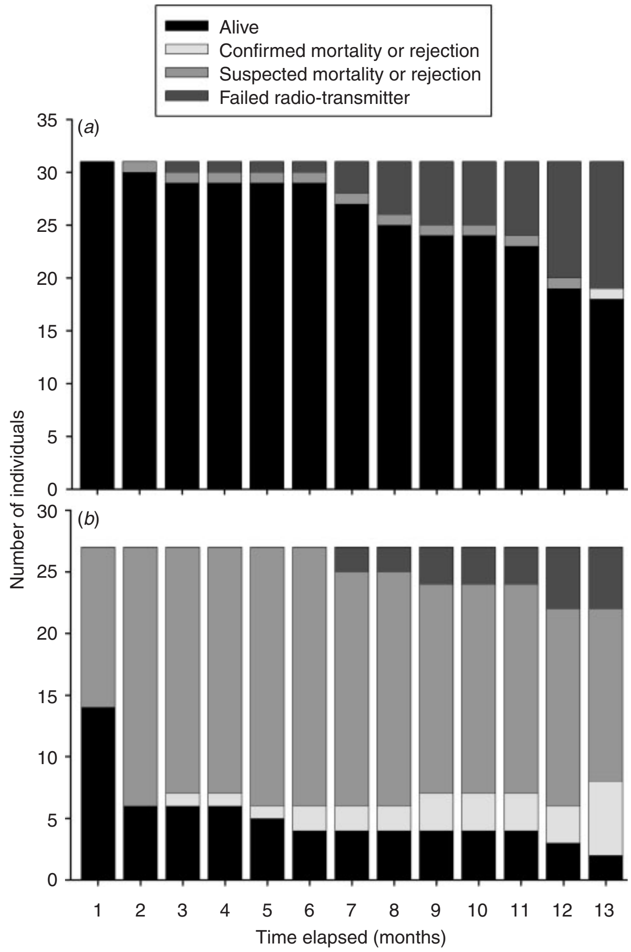

Fig. 4. Fate of radio-tagged (*a*) wild and (*b*) hatchery trout cod (*M. macquariensis*) released into the Murrumbidgee River near Narrandera.

radio-transmitter (heard failing during radio-tracking) and one individual was suspected (and later confirmed) as a mortality or radio-tag rejection. Twelve months after release, 19 individuals were alive and being radio-tracked, with 11 radio-transmitter failures and no further radio-tag rejections or mortality (Fig. 4*a*). A light aircraft was used to search for several of these failed transmitters and verified that they were not operational in the study area or surrounding areas. One individual was reported as an angler capture and subsequent release. This fish was radio-tracked following capture for 3 months until its radio-transmitter failed.

For the hatchery group, survival of individuals declined rapidly, with only 14 individuals alive after 1 month (Fig. 4*b*). This number decreased to six individuals 2 months after release, with three individuals alive after 12 months. Three radio-tags were recovered from shallow water during low-flow events in the river at 3, 6 and 9 months after release. Further, a large number of radio-fixes for hatchery individuals were taken in repeated locations for the duration of the study from 'suspect' locations in either relatively shallow water, or open water devoid of suitable structure, or associated with access points along the river. Three of these radio-tags were verified as radio-tag rejections or mortality through 24-h radio-tracking (i.e. no movement detected), as was one radio-tag from the wild group. In these cases, it could not be determined if rejection of radio-tags or mortality had occurred. In contrast, the majority of wild individuals regularly moved short but detectable distances. As a consequence, further analyses were solely conducted on individuals from the wild group.

Homing in wild fish

Sixteen of 31 wild individuals homed to their original capture location in this study. The majority of individuals originally captured within 3 km either side of the release site (91%) homed to their capture location at some stage during the study. In contrast, individuals captured between 3 and 5 km either side of the release site only homed on 40% of occasions. At capture distances greater than 5 km from the release site, fish did not home back to the original capture site. Homing success was a function of an individual having been captured in close proximity to the release site ($t = -3.66$; d.f. $= 29$, $P < 0.005$). The direction (upstream or downstream of release site) did not effect homing ability ($\chi^2 = 2.00$; $P = 0.1575$).

Typically, homing to a previous capture location was rapid. Ten of sixteen individuals had homed by the second radio-track at 12 days post-release. Five of these individuals homed in less than 7 days to locations within 2 km of the upstream side of the release site. The time required to home was greater for the remaining six individuals, taking between 21 and 67 days.

Individuals exhibiting homing behaviour typically remained at their home site once they had returned, with the proportion of subsequent radio-locations at the home site ranging between 31 and 100%. However, on one occasion, an individual took 12 days to home, stayed in this location for ~8 weeks and then relocated to a different home site.

Total range and home-range of individuals

The total range (mean ± standard error (s.e.)) of wild *M. macquariensis* individuals was 8840 ± 2151 m for the entire study. This was significantly different ($t = 4.16$; d.f. = 43.8; $P < 0.005$) to total range following establishment of home-ranges for 90% of the group (6660 ± 2202 m). This finding is consistent with localised home-range movements following initial dispersal and/or homing.

Twenty-nine of the 31 wild *M. macquariensis* individuals either returned to their pre-capture home-range or established new home-ranges after initial dispersal movements. One individual was not recorded establishing a home-range because its radio-transmitter failed early in the project. A second individual was excluded from home-range analysis because it was verified as a radio-tag rejection or mortality following 24-h radio-tracking. Based on the remaining 29 individuals, the mean linear home-range was 78 ± 13 m and ranged between 8 and 270 m. In the case of three individuals that had undertaken home-range shifts, more than one linear home-range was estimated where at least two radio-tracking fixes were obtained. Each of these estimates was of comparable size to individuals that did not undertake home-range shifts. The home-range area of 19 individuals (with a minimum of 10 monthly radio-tracks) based on minimum convex polygons was between 53 and 4073 m^2, with a mean of 1070 ± 302 m^2. Home-range overlap occurred for a small number of individuals immediately upstream of the release site, including two individuals that inhabited the same log upon establishment of home-ranges for the duration of the study.

Several different types of movement over the 13-month study period were observed following the establishment of home-ranges for 29 wild *M. macquariensis* individuals. These were grouped into three categories of movement that are discussed in turn. Examples of each are provided in Fig. 5. Hatchery fish are not incorporated into this discussion or the subsequent section on habitat use owing to a lack of spatial data resulting from poor survivorship.

(1) Sedentary (occupation of a home-range)

Following home-range establishment, through either homing or dispersal, 18 of 29 *M. macquariensis* individuals exhibited restricted movements for the entire study (Fig. 5*a*). For example, nine of these individuals exhibited homing behaviour to their capture location post dispersal and established tight home-ranges that were seemingly not vacated for the remainder of the study (or until transmitters failed in some cases). This occurred for homing in upstream or downstream directions. The remaining nine individuals also exhibited strong site fidelity and only localised movements were observed following dispersal, but these individuals set up homes in different locations to their capture location, in both upstream and downstream directions from the release site. It should be noted that one of these individuals either took much longer to establish a clear home-range or had a larger home-range than was calculated because it did not exhibit fidelity to a restricted area for consecutive periods of time until 6 months after release. Collectively, this group of 18 individuals comprised 10 females, two males and six individuals of unknown sex (Table 1). Length and weight (mean ± s.e.) of individuals was 443 ± 10 mm and 1147 ± 95 g respectively (Table 1).

(2) Home-range shifts

Five individuals exhibited home-range shift in this study (Fig. 5*b*). This occurred when an established home-range (based on consecutive fixes at repeated locations) was vacated and a new home-range was established. Two *M. macquariensis* females and three of unknown sex exhibited home-range shift behaviour; mean ± s.e. length and weight for these groups was 407 ± 11 mm and 838 ± 71 g respectively (Table 1). For four of these individuals, single home-range shifts were recorded, varying in distance from 863 m to 2.4 km (see example W12, Fig. 5*b*). The fifth individual in this group (W6) exhibited four home-range shifts, at least one of which was to a previous home-range (Fig. 5*b*). These shifts ranged in distance from 1 to 36 km, with the last recorded movement of 36 km to within 5 m of a previous location 5 months earlier (W6, Fig. 5*b*).

(3) Circular journeys

Six individuals exhibited movements not associated with home-range movements or shifts (Fig. 5*c*). Four of these individuals undertook single large-scale return movements and were recorded on the Yanco Weir logger. These movements were characterised by an initial downstream movement of 27 to 33 km, a single record on the downstream logger and a subsequent return of the same distance to a home-range (see W26, Fig. 5*c*). Another individual (W31, Fig. 5*c*) undertook four large-scale movements following the establishment of a home-range. These movements ranged between 2.3 and 20 km and always culminated in a return to a discernible home-range. It should be noted that this individual was detected for 9.5 of the 13 months in a distinct home-range and exhibited fidelity to this location. The remaining individual in this group was located within its home-range on all except for two consecutive radio-tracking occasions. The scale of movement undertaken during these 2 months is unknown. The six *M. macquariensis* individuals in this group were one female, two males and three individuals of unknown sex (Table 1). Length and weight (mean ± s.e.) for this group was 494 ± 20 mm and 1633 ± 223 g respectively (Table 1).

Habitat use

Wild *M. macquariensis* individuals displayed a preference for outside bend habitats (53.3% of locations) within their home-range. The locations of home-range movements were less

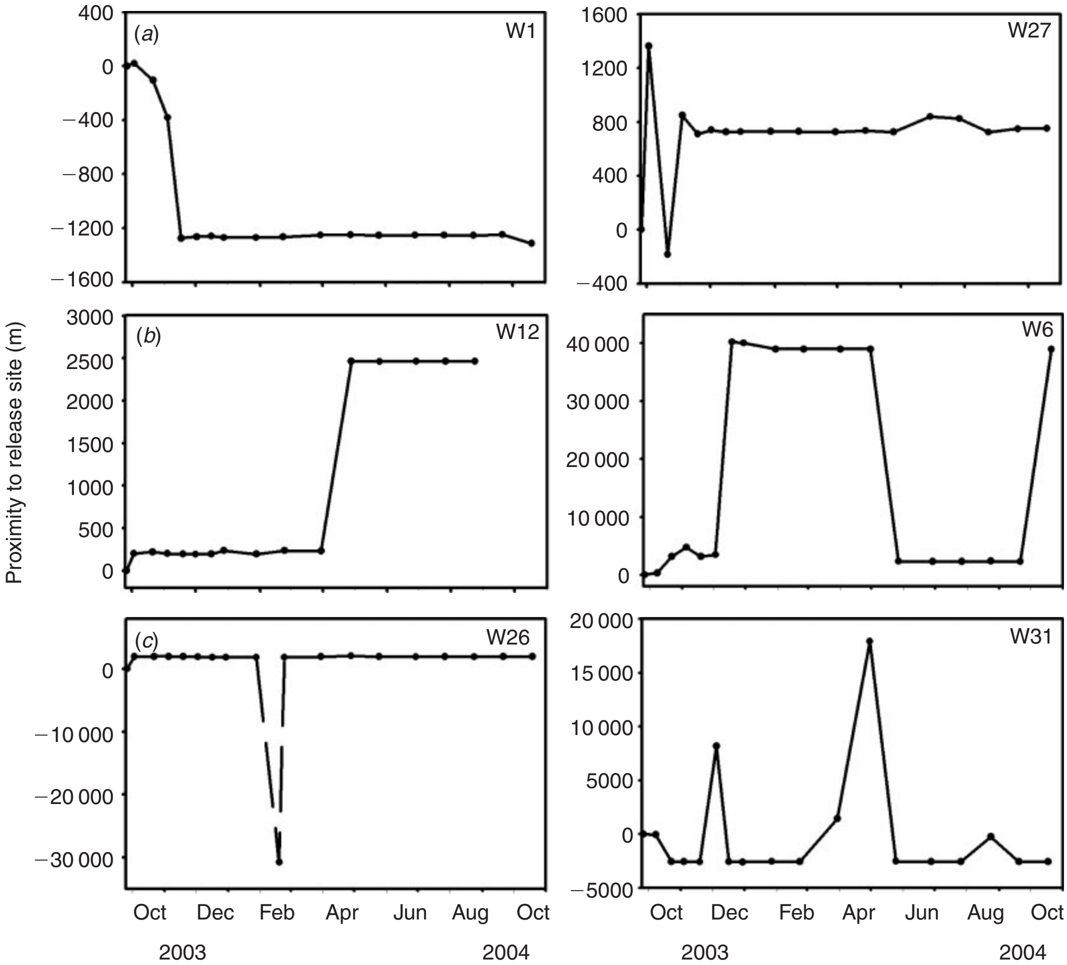

Fig. 5. Typical examples of different types of trout cod (*Maccullochella macquariensis*) movements, representing: (*a*) sedentary home-range behaviour for the entire study, following dispersal, (*b*) home-range shifts that occurred once or multiple times and (*c*) large-scale movements outside of home-ranges that did not result in a home-range shift. The first point in each figure (zero) represents the release location (all fish were released at the same location).

Table 1. Summary statistics for 29 wild trout cod (*Maccullochella macquariensis*) exhibiting different types of movements following the establishment of a home-range

Total length (TL) and weight are expressed as mean ± s.e.

	Sedentary	Shifts	Circular journeys
Number	18	5	6
Sex	10♀, 2♂, 6?	2♀, 3?	1♀, 2♂, 3?
TL (mm)	443 ± 10	407 ± 11	494 ± 20
Weight (g)	1147 ± 95	838 ± 71	1633 ± 223

frequently encountered on straight sections of river channel (23.7%), inside bends (17.3%) and mid-channel (5.7%). *M. macquariensis* individuals also displayed distinct patterns of habitat use within home-ranges. Structural woody habitat was the predominant habitat type used, comprising 83% of fixes. Open water (13%), rock (2%), indeterminate habitat (2%) and undercut banks (<1%) were infrequently used and *M. macquariensis* individuals were not found to use emergent macrophytes.

Discussion

Direction and magnitude of dispersal

The current study represents the first attempt to simultaneously investigate movement of a hatchery and wild *Maccullochella* species. Dispersal patterns of the hatchery and the wild group differed. The wild group exhibited limited dispersal, returning to the reach, 13 km in length, from which they had originally been collected. In comparison, the hatchery group remained near the release site or dispersed in a downstream direction. Similar findings arose from a study of rainbow trout, *Oncorhynchus mykiss* (Walbaum) in the Clinch River, USA (Bettinger and Bettoli 2002). Fish were released immediately below a dam in that study, whereas there was opportunity for upstream dispersal in the current study.

The current study demonstrates that *M. macquariensis* individuals are capable of large-scale dispersal. Previous reports identified that this species operates at smaller scales of less than 10 km (Koehn 1997; Ebner *et al.* 2005, 2007; Nicol *et al.* 2007; Koehn *et al.* 2008; Thiem *et al.* 2008). Our finding may well be a result of the relatively large sample sizes that we used, in addition to the fact that several previous studies have concentrated on aspects of home-range behaviour and habitat use at small spatial or temporal scales (e.g. Nicol *et al*. 2007; Thiem *et al*. 2008). Collectively, these radio-tracking studies of *M. macquariensis* indicate that hatchery-reared individuals are likely to disperse downstream and that individuals stocked as fingerlings or that naturally occur are capable of fidelity to a river reach. The current study indicates that habitat restoration (e.g. Nicol *et al*. 2004) may be maximised by targeting reaches downstream of existing populations or stocking sites for *M. macquariensis*. However, the downstream movement and dispersal observed in the current study poses a paradox for the management of this endangered species. It is widely accepted by river and fisheries managers that weirs pose a major ecological threat to riverine ecosystems and, specifically, migratory fishes within the Murray–Darling Basin (Harris and Mallen-Cooper 1994; Lintermans and Phillips 2004). Conversely, weirs may prove useful initially for concentrating *M. macquariensis* individuals within small reaches in order to establish minimum viable populations (Gilpin and Soulé 1986; Caughley 1994; Ebner *et al*. 2005; Armstrong and Seddon 2008). This approach to stocking would facilitate concentrated research, monitoring and compliance efforts (Ebner *et al*. 2005) and is especially pertinent in view of the low annual hatchery production of this species (Gilligan 2005) relative to that predicted as necessary for establishing wild populations (Todd *et al*. 2004).

Homing

Half of the wild group returned to their original capture location. It is considered that this represents an ability to home. Further, the rapid homing of a substantial number of these individuals, including 30% of the wild group within a fortnight, indicates the effective searching and/or navigational capability of this species. It also represents the first evidence of experimental displacement and subsequent homing in *M. macquariensis* or any of the *Maccullochella* species. Large-scale (10–100s km) return migrations have also been recorded by radio-tracking *M. peelii peelii* (Koehn 1997), *M. peelii mariensis* (Rowland) (Simpson and Mapleston 2002) and *M. ikei* (Rowland) (G. Butler, Southern Cross University, unpubl. data), following release at capture locations. Collectively, these findings indicate that all extant species of *Maccullochella* are capable of homing.

Homing success was a function of an individual having been captured in close proximity to the release site in this study. Similarly, more than half of a sample of *Macquaria ambigua* (Richardson) was found to home following displacements of ~2 km (Crook 2004*a*; $n = 10$) though not following displacement of ~25 km (Crook 2004*b*; $n = 15$). Crook (2004*a*) suggested that several non-homing individuals encountered high-quality habitat not long after release and probably elected not to home. If, in the future, threatened species of *Maccullochella* were to be translocated, it would be informative to have some understanding of the maximum scale at which they home and whether or not unsuccessful homing behaviour will affect the success of translocation.

Individuals were found to have overlapping home-ranges (also see Thiem *et al*. 2008) and, in some cases, individuals exhibited long-term (1 year) co-occupation of SWH in the current study. There is little comparable information of intraspecific interaction in percichthyids. Butler (2001) reported that *M. ikei* individuals foraged in close proximity to one another at the head of a pool in the Nymboida River. Collectively, these observations challenge the idea that Australian freshwater cod are wholly territorial and solitary. Understanding intraspecific interactions that occur in the home-range occupation phase is a necessary step towards re-establishing self-sustaining populations of *Maccullochella*.

Home-range establishment

Much of the movement recorded in this study is comparable with that of Crook (2004*a*, 2004*b*) and is largely in agreement with the revised home-range shift model proposed in the second of these publications. Specifically, three main behaviours, home-range occupation, return movements and home-range shifts, were observed.

However, we also observed behaviour indicating that fish have a detailed spatial knowledge of the riverscape. We are referring to an individual that undertook a return home-range shift in the current study (Fig. 6; also see W6 in Fig. 5). This is an individual returning to occupy a past home-range, though not its most recent home-range. The behaviour typically occurs in a subset of home-range shift cases (Fig. 6). Return home-range shifts have been recorded in studies of other percichthyids including *M. peelii peelii* (Koehn 1997), *M. p. mariensis* (Simpson and Mapleston 2002) and *M. ambigua* (Crook 2004*b*).

The cause of the return movements on a scale of tens of kilometres in the current study is unknown. Crook (2004*b*) considered explorations to be searches for more profitable habitat. Large-scale adult movement has often been ascribed to reproductive activity in percichthyids (Koehn 1997; O'Connor *et al*. 2005). There is also an indication that high flow may be an important factor or a contributing stimulus for percichthyid movement (Koehn 1997; O'Connor *et al*. 2005). The return movements observed in the current study were asynchronous among individuals and occurred outside the known spawning period of the species. In this regard, our findings are similar to that for *M. p. mariensis* (Simpson and Mapleston 2002).

Only large individuals performed return movements in this study. Focussing on a range of size classes and, in particular, large individuals (e.g. >2 kg) may prove useful in future investigations of the movement of this species. Clearly, there is a need for better understanding of the ecological mechanisms underpinning these return movements (Ebner *et al*. 2006). Presumably this will be achieved by complementing the radio-tracking approach with other techniques, including confirmation of reproductive status, manipulation of the dominance hierarchy (if indeed a hierarchy exists) or investigating resource availability.

Within their home-range, wild fish displayed a preference for SWH and outside bends, based on 13 months of monthly radio-tracking 29 individuals in a large river reach (>10 km). The association with SWH is comparable with findings from electrofishing 1 km of the Murrumbidgee River (Growns *et al*. 2004) and radio-tracking studies based on small samples sizes (Koehn 1997; $n = 4$; Nicol *et al*. 2007; $n = 15$; Thiem *et al*. 2008; $n = 10$). Nicol *et al*. (2007) demonstrated that the location of SWH within the channel is also of importance to this species. Specifically,

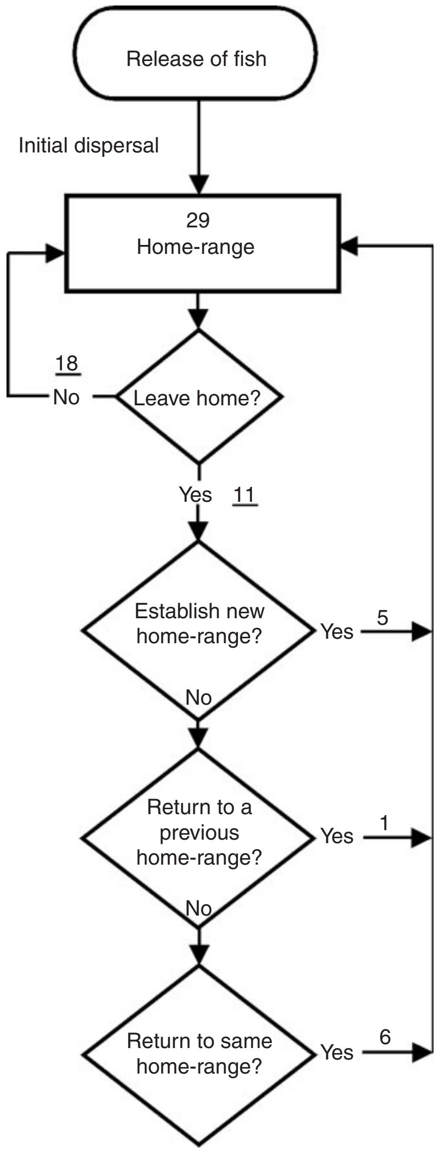

Fig. 6. Categorisation of trout cod (*Maccullochella macquariensis*) ($n = 29$) movement over the 13-month study. The number of individuals exhibiting specific emigration home-range behaviour is shown. The occurrence of each behaviour is scored only once per individual.

Nicol *et al*. (2007) found that association with SWH was greatest in narrow sections and more relaxed in wider sections of the Murray River, and predicted that these results would apply to this species in other river systems. The current study provides a level of validation for this prediction in that *M. macquariensis* individuals were frequently found associated with woody debris in the main channel on outside banks of the Murrumbidgee River.

Possible rejection of radio-tags

It is possible that hatchery fish rejected radio-tags following release into the Murrumbidgee River in the current study. This is indicated by a small number of cases of rejection or signs of unsatisfactory recovery from surgery (e.g. incomplete closing of the incision, tearing of tissue at suture entry points) that occurred within days of implantation before release and contrasts with rapid healing of the incision and complete retention of radio-tags by wild fish (although two individual wild fish showed minor signs of reduced incision closure). The surgical technique was initially validated on hatchery *M. macquariensis* individuals ($n = 9$) that showed complete recovery in an aquaria trial (Ebner *et al*. 2005). The unsatisfactory post-surgery recovery of about one-third of hatchery individuals initially in the current study was probably a function of their notably rotund abdomens relative to the wild fish. However, it is unlikely that radio-tag rejection was widespread following release of the hatchery group since two-thirds of the sample were healing well following initial surgery and the remainder showed signs of healing following re-surgery (with the exception of the two individuals that were euthanased). Radio-tagging of excessively fat hatchery fish should be avoided in future studies. It would also be useful to minimise incision length and radio-tag size, and provide an increased holding period for observation post surgery.

Survivorship

Survivorship of wild and hatchery fish at 13 months post release was 95% and 9% respectively. Poor survivorship of hatchery fish has also been recorded for *M. macquariensis* in releases in the upper Murrumbidgee River catchment (Ebner *et al*. 2005, 2007). Ebner *et al*. (2007) attributed some of the observed mortality to predation by cormorants and the common water rat. Although, collectively, studies of releases of on-grown *M. macquariensis* individuals have revealed poor survivorship (Ebner *et al*. 2005, 2007; this study), the mechanisms for mortality remain largely unexplained. Comparable studies have centred on salmonids (Thorstad *et al.* 1998; Dieperink *et al.* 2001; Bettinger and Bettoli 2002). Of these, higher survival of wild than hatchery fish is reported by both Dieperink *et al*. (2001) and Bettinger and Bettoli (2002). Predation mediated by morphological and behavioural differences was suggested as the explanation for the outcome in those two studies. Similarly, differences in the body shape and dispersal of hatchery and wild groups (Fig. 2) represent possible explanations for higher survival of wild than hatchery groups in the current study. In contrast, Thorstad *et al*. (1998) recorded 77% and 9% survival of hatchery and wild salmon respectively. It was argued that greater energy stores of hatchery fish resulted in their higher survival over winter (Thorstad *et al*. 1998). Better condition of hatchery fish relative to wild fish did not obviously confer a benefit to the former group in the current study. More likely, the familiarity of wild fish with the river environment was critical to their success (Brown and Day 2002).

The causes of mortality were unclear in the current study. Several factors including low visibility, SWH and moderately deep water prevented retrieval of radio-tags or location of fish remains in most instances. In releases of hatchery *M. macquariensis* individuals in upland rivers, the location of radio-tags provided a useful indicator of avian and mammal predation or scavenging (Ebner *et al*. 2007). For instance, radio-tags were found under the roosts of cormorant flocks. Similar reports relate to salmonids overseas (e.g. Dieperink *et al*. 2001). Based on the position of radio-tags in the current study (primarily associated with SWH), a distinction could not be made between radio-tag rejection and predator effects, let alone among broad predator groups (i.e. avian, riparian mammal, fish, anglers) that might have been involved. This highlights a need for improved methods for detecting the timing and cause of mortality of *M. macquariensis* (e.g. Dieperink *et al*. 2001), especially following releases in turbid lowland rivers.

The current study demonstrates the benefit of using radio-tracking to monitor the movement and survivorship of stocked threatened fish to determine if there is fidelity to the release site. Our study also highlights the need to consider the effects of hatchery rearing when conducting fish reintroductions. Similar views have been expressed following poor survivorship or dispersal of other hatchery-reared fishes (e.g. Dieperink *et al*. 2001; Bettinger and Bettoli 2002).

Post-juvenile dispersal

The current study has not clarified if post-juvenile *M. macquariensis* dispersal is the explanation for the apparent disappearance of *M. macquariensis* from fingerling-stocking sites. The complete mortality of the hatchery group partly compromised our study by reducing the total sample size and the number of radio-tagged sub-adults. However, radio-tracking of the wild group revealed that limited emigration occurred in 13 months in the Murrumbidgee River at Narrandera, despite adults exhibiting the capability to move on a scale of tens of kilometres. It may be possible that the wild group comprised individuals that were unlikely to disperse over large distances, since they were collected near their original stocking site (cf. the Restricted Movement Paradigm; Gowan *et al*. 1994).

Observation of five individuals encountering and not passing Yanco Weir in 13 months may also be important considering the possibility that this behaviour may be more common in the population when scaled to the life span of *M. macquariensis*. It highlights a fish passage issue at that weir, and more generally highlights the potential for maintaining a threshold population size. Dispersal away from a release site can lead to insufficient adults to maintain a self-sustaining population, an issue expressed in the small population paradigm (Caughley 1994; Armstrong and Seddon 2008).

To test if post-juvenile *M. macquariensis* dispersal is the explanation for the apparent disappearance of *M. macquariensis* from fingerling-stocking sites, hatchery fish should not be used as a surrogate for examining the dispersal of wild fish in the future. However, the current study has shown the benefit of using radio-tracking to monitor individual movement and estimate survivorship from a sample of stocked threatened fish. Therefore, future efforts to conserve *M. macquariensis* could use this approach to monitor the dispersal and survivorship of large juveniles and sub-adults at sites where reintroductions have been less effective than is the case in the Murrumbidgee River at Narrandera (cf. Gilligan 2005). This study demonstrates the likely benefit of using radio-tracking as the basis for monitoring the fate of widespread stockings of large-bodied percichthyid species in Australia.

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