

RESEARCH ARTICLE

# Sequential fishways reconnect a coastal river reflecting restored migratory pathways for an entire fish community

Meaghan L. Rourke<sup>1,2</sup>, Wayne Robinson<sup>1,3</sup>, Lee J. Baumgartner<sup>3</sup>, Jonathon Doyle<sup>1</sup>, Ivor Grouns<sup>4</sup>, Jason D. Thiem<sup>1,3</sup>

River regulation infrastructure has been implicated in worldwide aquatic biodiversity loss. In-stream barriers such as weirs prevent fish migration and the impact can be particularly severe for diadromous species. Fishways are frequently installed on in-stream barriers to reconnect migratory pathways and rehabilitate diadromous fish populations. Sequential fishways may be necessary in rivers where multiple barriers prevent migration. We monitored a coastal fish community's response to fish passage restoration at 10 predominantly low-level weirs in the freshwater reaches of the Nepean River in southeastern Australia. Few studies have simultaneously assessed fish community passage at successive fishways within a river system. Prior to the installation of the fishways, there was a gradient of reduced species diversity in an upstream direction including the absence of many diadromous species, despite the regular inundation frequency of most weirs. Following the installation of the fishways, species diversity was still greater in the downstream monitoring sites; however, there was evidence of a positive change in fish community structure in middle and upstream sites. Most notably, three diadromous species rapidly expanded their distribution upstream and one amphidromous species expanded its downstream distribution. This study demonstrates appropriately designed successive fishways can successfully reconnect river systems for an entire fish community, encompassing species with a broad range of swimming abilities and diverse life histories.

**Key words:** connectivity, diadromy, fish community passage, restoration, vertical-slot fishway

## Implications for Practice

- Fishways can restore migratory fish populations that have been negatively affected by physical barriers to movement, and sequential fishways may be necessary in rivers where multiple barriers prevent migration.
- Monitoring pre- and postfishway installation is necessary to adequately assess the success of management actions, and historical reference condition of species distributions provides a restoration target.
- Positive changes in fish community responses to restored migratory pathways, such as species-specific range expansions, can occur over short (<5 year) timescales and reflect the successful reconnection of movement pathways.

## Introduction

Landscape fragmentation threatens the loss of biodiversity worldwide (Haddad et al. 2015). River regulation, and the associated construction of dams and weirs, has substantially fragmented aquatic landscapes globally (Dynesius & Nilsson 1994), resulting in biodiversity declines (Malmqvist & Rundle 2002; Dudgeon et al. 2006). Many freshwater fishes undertake migrations ranging from localized movements to extensive long-distance migrations that are often critical to complete

their life cycle (Lucas et al. 2001). Artificial barriers to fish migration not only prevent or impair upstream and downstream migration, but the regulatory structures themselves also cause numerous detrimental impacts through reduced water quality, degraded habitat, and altered frequency and magnitude of flows (McManamay et al. 2015).

Fishways are commonly used to enable fish passage over artificial in-stream barriers to help rehabilitate migratory fish communities. In order to determine effectiveness, a robust

Author contributions: LJB, MLR conceived and designed the research; JD, MLR performed the experiments; WR, MLR analyzed the data; IG contributed analysis tools; MLR, WR, LJB, IG, JDT wrote and edited the paper.

<sup>1</sup>Department of Primary Industries, Narrandera Fisheries Centre, PO Box 182, Narrandera NSW 2700, Australia

<sup>2</sup>Address correspondence to M. L. Rourke, email meaghan.duncan@dpi.nsw.gov.au

<sup>3</sup>Institute for Land, Water and Society, Charles Sturt University, Albury, NSW 2640, Australia

<sup>4</sup>School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

© 2018 NSW Department of Primary Industries. Restoration Ecology published by Wiley Periodicals, Inc. on behalf of Society for Ecological Restoration This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

doi: 10.1111/rec.12886

Supporting information at:

http://onlinelibrary.wiley.com/doi/10.1111/rec.12886/supinfo

monitoring program is needed. However, despite thousands of fishways being constructed worldwide, comparatively few have been assessed for their efficiency (Roscoe & Hinch 2010; Bunt et al. 2012; Hatry et al. 2013). Furthermore, only 4% of North American and 38% of European studies assess whether fishways benefit the entire fish community passing the structure (Roscoe & Hinch 2010). In addition, relatively few studies have assessed fish community passage at successive fishways along a river system. Successive barriers are particularly problematic for diadromous species given that they can prevent access to valuable habitat in the most upstream reaches (Caudill et al. 2007). Installing a single fishway in a river system will not be as beneficial to these species when many barriers need to be negotiated sequentially (O'Hanley & Tomberlin 2005).

In Australia, recent fishway programs have aimed to reinstate fish passage to almost entire river systems, potentially opening up considerable amounts of habitat for diadromous and potamodromous species. Moreover, the fishways have increasingly been designed with the aim of enabling the passage of the migratory fish community (Barrett & Mallen-Cooper 2006; Walsh et al. 2014). For example, 12 vertical-slot fishways have been installed on the Murray River to allow migratory fish to potentially move approximately 2,225 km from the river mouth upstream to Lake Hume (Barrett & Mallen-Cooper 2006). In addition, a series of vertical-slot fishways and a high-level fish lift have been used to allow fish passage from the mouth of the Shoalhaven River to upstream of Tallowa Dam, enabling access to 185 km of previously inaccessible habitat (Walsh et al. 2014; Evan Knoll 2018, personal communication). These fishways were designed and constructed to meet the needs of the entire migratory community comprising both small and large-bodied fish with a range of swimming abilities.

While fishways are designed to address one of the most important problems facing migratory fish—the barriers to upstream passage—they are never 100% efficient at passing the target species. There will always be issues with fish passage efficiency, delays in negotiating a fishway and continued poor ecological conditions due to changes in river hydrology (Mallen-Cooper & Stuart 2007; Bunt et al. 2012; McLaughlin et al. 2013). Nevertheless, it is essential that fish community assessments are carried out pre- and postfishway installation in order to quantify their effectiveness in enabling fish passage and restoring overall fish community composition. Most fishway assessments address fish passage effectiveness for a single species at a single barrier. The aim of this study is to determine whether the long-term disconnection of a diverse eastern Australian coastal fish community by multiple weirs can be reversed over a short timescale through the reinstatement of fish passage. We hypothesized that constructing fishways sequentially, along a longitudinal gradient, will improve the distribution of diadromous fish from downstream to upstream and restore a more natural community structure. We tested this hypothesis by measuring (1) range expansion for individual species and (2) positive changes in fish community assemblages. This study serves as a model

approach that will be useful to inform future watershed-scale restoration efforts for diadromous species obstructed by multiple barriers.

## Methods

### Study Area

The Hawkesbury–Nepean (H–N) river system (hereafter referred to as the Nepean River) of southeastern Australia originates in the Blue Mountains and flows into Sydney Harbor (Fig. 1). Flows in the system are largely regulated by releases from five major dams (all above 56 m high), the Nepean, Avon, Cataract, Cordeaux, and Warragamba (Table S1, Supporting Information; Fig. 1). Downstream of the dams, there are 11 low-level weirs ranging between 0.8 m and 5.6 m high, and one large weir that is 16 m high. These structures are collectively responsible for significant changes to the hydrological regime (Sammut & Erskine 1995) and block upstream fish migration during typical flows (Harris 1984) (Table S1, Fig. 1). Given that most of the weirs are relatively low (<6 m high), it is possible that rainfall events in the upper catchment that lead to short-term river rises (pulses) could drown out barriers and allow fish upstream passage at some of the weirs. However, Hydrologic Engineering Centres River Analysis system (HEC-RAS: [www.hec.usace.army.mil](http://www.hec.usace.army.mil)) modeling has indicated that while the inundation frequency of some weirs is at least annual, others are not expected to be inundated below the one-in-100-years flood level (Table S1). Critically, the second most downstream structure—Wallacia Weir—is not expected to be regularly inundated (Table S1). This has implications for upstream fish migration, particularly for some diadromous species and some short-lived species whose life expectancy is less than the modeled inundation frequency (Katano et al. 2006; Jellyman & Harding 2012).

Fishways were constructed in the Nepean system from 1914 to 1988 (Table S1). However, design and maintenance issues rendered many inefficient or inoperable (Mallen-Cooper 2009). Consequently, from 2009 to 2010, 10 new vertical-slot fishways were installed from Penrith to Douglas Park (Fig. 1) to allow fish passage from the estuary to approximately 250 river kilometers of upstream habitat. These fishways were designed to be compatible with the swimming ability of the entire fish community (35 mm to 1 m in length) and to operate across a wide range of flow conditions experienced in the Nepean River (Mallen-Cooper 2009).

There are at least 41 migratory species of fish recorded in the entire Nepean River (Gehrke 1996) which are classified as anadromous (migrate upstream from the sea to freshwater to spawn), catadromous (migrate downstream to the sea or estuary to spawn, after spawning, adult and juvenile fish migrate upstream to freshwater), amphidromous (spawning occurs in freshwater with larvae drifting to the estuary or ocean, juveniles then migrate upstream; McDowall 2007) and potamodromous (migrate wholly within freshwater).

In the freshwater reaches of the Nepean River downstream from the major dams (the focus of this study), there are 24

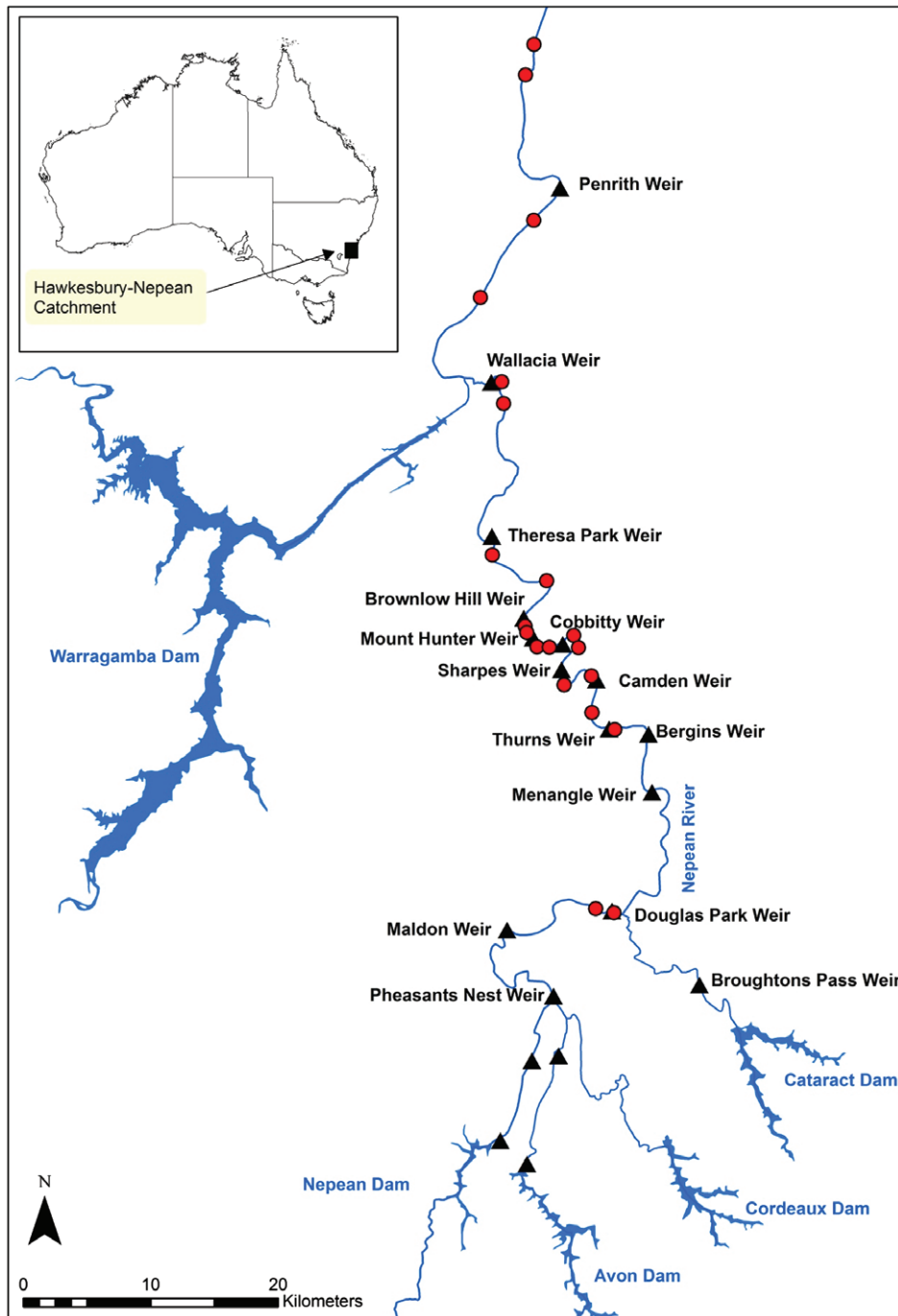


Figure 1. The location of barriers to fish movement (weirs and dams; black triangles) and sampling sites (circles) on the Nepean River system. Sampling sites were used to assess fish community change following installation of multiple fishways.

native, three translocated (native Australian fish but not to the Nepean River), and four alien freshwater fishes recorded (Table S2). Most of these species are diadromous (anadromous, catadromous, or amphidromous). Species distributional modeling and expert opinion suggests that most fishes currently occurring in the system would have occupied all reaches below Maldon Weir before the weirs were installed (Table S2, Fig. 1)

(Grouns et al. 2013; Martin Mallen-Cooper 2014, personal communication). Some of these species may also have been able to occupy sites further upstream, but these were not included in the species distributional modeling. This is in contrast to the contemporary distribution (1975–2009; before completion of the new fishways) (Gehrke & Harris 1996; Baumgartner & Reynoldson 2007; NSW DPI unpublished data). In the

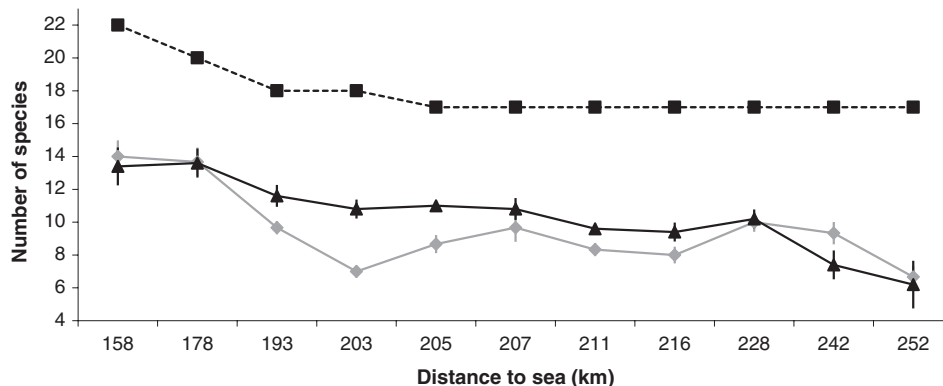


Figure 2. Predicted number of species (dotted line) and mean observed species richness ( $\pm$ SE) before (gray line) and after (solid line) fishway installation for each reach of the Nepean River. Sites are ordered from the most downstream reach on the left (downstream of Wallacia) to the most upstream reach on the right (downstream of Maldon).

most recent study, the only diadromous species recorded as far upstream as Douglas Park (the ninth most upstream weir in the system) were Australian bass (*Percales novemaculeata*), long-finned eel (*Anguilla reinhardtii*), and Cox's gudgeon (*Gobiomorphus coxii*) (Baumgartner & Reynoldson 2007).

#### Sampling Methodology

Twenty monitoring sites were established in 11 sampling reaches between the weirs (Fig. 1) to assess the pre- and post-fishway community assemblage. Thurns Weir and Bergins Weir (Fig. 1) were not considered in this study given the crests are breached and do not impede fish passage.

Standardized boat electrofishing, comprising 12 replicate runs with a total power application time of 90 seconds each, were undertaken at each site during the day (Smith-Root Model 7.5KVa electrofishing units). During each operation, dip nets were used to collect all stunned fish and place them in an aerated live-well. All fish that could not be successfully collected but could be positively identified were recorded as "observed." In addition, 10 unbaited concertina bait-traps (minimum of 2-hour soak during the day) were set to provide an additional method of sampling the small-bodied species in the fish community. At the completion of each electrofishing and bait-trap operation, all fish were identified, counted, and a subset measured (50 individuals per species per method). Each site was sampled on three occasions prefishways (May to December 2009 [winter, and twice in spring]) and five occasions postfishway installation (March 2011 to April 2013 [autumn and spring in 2011 and 2012 and autumn in 2013]).

#### Data Analysis

The historical (pre-weirs) species richness in each of the 11 sampling reaches was quantified using the method described in Grouns et al. (2013). Mean species richness was determined from the pre- and postfishway data (see below) for each reach and displayed on the same plot as that showing mean species richness pre-weirs (Fig. 2).

Permutational analysis of variance (PERMANOVA) was conducted to determine if there was a significant difference in the sampled fish community structure between pre- and post-fishways across all reaches. The analysis used Bray–Curtis similarities calculated using the number of fish caught and observed, standardized (number per 24 hours) and  $\log_e(X + 1)$  transformed. We fitted a factorial PERMANOVA model consisting of four factors; season (Se, random, nested within Year [Yr], four levels: winter, spring, summer, and autumn), Year (random, nested in Before vs. After [BvA], four levels: 2009, 2011, 2012, and 2013), Before/After (fixed, two levels: before and after), and Site (S, fixed, 20 levels). Unfortunately, there is no replication of year nested within the before level of Before/After, thus the analysis assumes homogeneity of inter-annual variance before and after intervention after seasonal effects have been accounted for. Nevertheless, the analysis has adequate permutations and power for the test of interest, which is the fixed factor interaction of Before/After  $\times$  Site which has 18 and 38° of freedom. In this analysis, the 20 sites are treated as independent replicates across the overall system. Significance values were calculated based on 9,999 unrestricted permutations of the raw data. To visualize the differences in the fish community structure pre- and postfishways, multidimensional scaling (MDS) was used to plot the pre- and postfishway similarities between the 20 sites. To avoid a cluttered ordination, only the average fish abundance for each species across the three rounds of the prefishway data and five rounds of postfishway data were used to represent each site. Stress values indicate how well the two-dimensional ordination represents the assemblage structure, where a stress value of less than 0.2 is considered a useful representation of data points within the ordination space (Clarke & Warwick 2001). Species that contributed the most to the dissimilarity between pre- and postfishway groups were calculated using SIMPER.

To complement the overall test for changes in fish assemblage composition, we tested for spatial seriation in the fish communities through the Nepean river pre- and postfishway installation. Seriation is defined as the gradient of change in the fish community from downstream to upstream reaches. In other words, if

the weirs are limiting upstream fish migration, we predicted that adjacent sites will have more similar fish communities than sites that are further apart. In that case, it is expected that seriation will be evident, as either a gradual change in the fish community in an upstream direction or as an abrupt change at one or more fishways. If subsequent installation of the fishways provided sufficient fish passage to alter the fish community composition, it is expected that seriation will decrease during the postfishway period. To test for seriation, a RELATE (Sommerfield et al. 2002) analysis was conducted by comparing the Bray–Curtis similarity matrix to a matrix of the rank order of sites (e.g. Devlin Lane to Penrith downstream = a distance of 1, Devlin Lane to Maldon downstream = a distance of 19) using Spearman's rank correlation method. This analysis was performed separately and the correlation coefficients are reported for each sampling round. Significance values were calculated based on 9,999 permutations of the raw data. All analyses, including PERMANOVA, SIMPER, MDS, and RELATE, were conducted in PRIMER v6 (Clarke & Warwick 2001; Anderson et al. 2008).

Tests for changes in the fish community assemblage pre- and postfishway installation were carried out on each individual weir by comparing the sites immediately upstream and downstream using a four-factor PERMANOVA. The four factors were site location (above or below the weir), timing of sampling (before or after the fishway), year of sampling nested within before or after, and season of sampling (a random factor). The main term of interest was the interaction of the sample site ( $S$  = above or below the fishway) and the time of the sample ( $B \times A$ , before or after the fishway was installed). If a significant result was obtained for the pre- and postfishway interaction with above or below term ( $B \times A \times S$ ), follow-up pair-wise tests were carried out to identify site combinations responsible for the significance. When there were fewer than 100 permutations available, the significance values were obtained using Monte Carlo tests. Where results suggested a significant change in the difference between upstream and downstream sites pre- and postfishway installation, SIMPER analyses were conducted to determine the fishes contributing the most to these changes.

## Results

### Catch Summary

A total of 10,761 fish representing 21 species were recorded (Table S3) before and after fishway construction. Australian bass were the most commonly recorded species (23% of catch) followed by Australian smelt (*Retropinna semoni* 11% of catch). There were four exotic species present in the study area that together contributed 12% of the total catch: common carp (*Cyprinus carpio*; 5% of catch), goldfish (*Carassius auratus*; 5% of catch), eastern gambusia (*Gambusia holbrooki*; 2% of catch), and brown trout (*Salmo trutta*;  $n=2$ ). Three species native to Australian rivers outside the Nepean River were recorded including freshwater catfish (*Tandanus tandanus*), olive perchlet (*Ambassis agassizii*), and silver perch (*Bidyanus bidyanus*). Freshwater catfish were prevalent in the study reach (4% of catch) while olive perchlet were only recorded in the two

most downstream sites ( $n=4$ ) and only a single silver perch was sampled.

### Overall Reach-Wide Assessment

The mean species richness prefishways was lowest at the most upstream reach and remained relatively low throughout the middle reaches, especially at reach four (between Theresa Park and Brownlow Hill weirs) (Fig. 2). Postfishways, mean species richness increased throughout the middle reaches and remained relatively unchanged at the most downstream and upstream reaches (Fig. 2). Mean species richness was considerably lower than the predicted species richness for both time periods (Fig. 2). All native species collected would have been found throughout the study reach prior to the weirs being installed (Table S2).

Potamodromous species were largely found throughout the study reach both pre- and postfishways. In contrast, some diadromous species were not found in the middle and upper reaches prefishways. Only Australian bass and long-finned eel were present throughout the study area (Table S3). Postfishways, three diadromous species—freshwater herring, sea mullet, and freshwater mullet—extended their ranges substantially upstream while Cox's gudgeon extended its downstream distribution (Table S3). Estuary perch (*Percalates colonorum*) (a largely estuarine species) and bullrout (*Notesthes robusta*) were in low abundances and showed no significant change in distribution. Prefishways, the two amphidromous gudgeons (empire gudgeon [*Hypseleotris compressa*] and striped gudgeon [*Gobiomorphus australis*]) were restricted to sites downstream of Wallacia Weir. Postfishways, empire gudgeon did not expand their distribution upstream and only three striped gudgeon were recorded above Wallacia Weir.

There was a significant difference in the fish assemblages in the overall reach pre- and postfishways, but the effect was not consistent across all sites (interaction of  $B \times A \times S$ , Pseudo- $F=1.30$ ,  $df=27, 38$ ,  $p=0.033$ ; Table S4). Prefishways, sites 1–4 were distinct from the upstream sites, while, postfishways, sites 1–6 were distinct from the upstream community (Fig. 3), suggesting the fishways have allowed upstream migration into sites 5 and 6. Species that were primarily responsible for the overall differences in the pre- and postfishway groups were freshwater herring, freshwater mullet, sea mullet, Australian smelt, and goldfish (Table 1). There were significant community differences among seasons within years and among years before and/or years after the fishways were installed [ $Se(Yr(B \times A))$ , Pseudo- $F=3.43$ ,  $df=6, 6$ ,  $p<0.001$ ;  $Yr(B \times A) \times S$ , Pseudo- $F=1.31$ ,  $df=38, 71$ ,  $p=0.011$ ; Table S4].

### Spatial Seriation Assessment

There was an identifiable pattern of fish communities in adjacent sites being more similar than sites that were further apart along the length of the Nepean River both pre- and postfishways (Fig. 3). However, the relationship was consistently stronger in all sampling rounds postfishways than prefishways, indicating that the fish community in adjacent sites became more similar postfishways (Fig. 4).

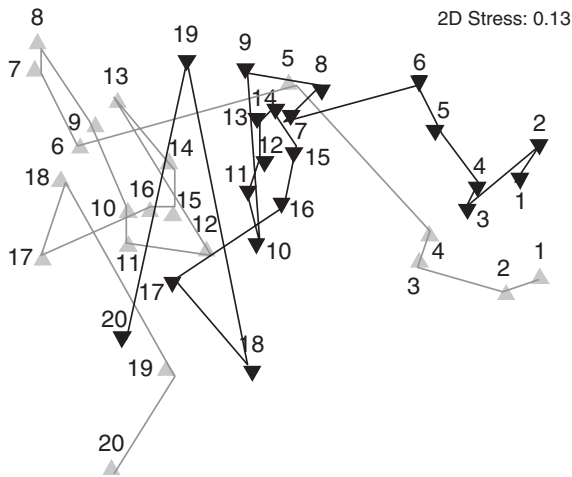


Figure 3. Multidimensional scaling (MDS) ordination showing the dissimilarity of the fish community before (average of three rounds, gray triangles) and after (average of five rounds, black triangles) fishway installation on the Nepean River. Trajectories are overlaid to show site order from downstream of Penrith (1) to downstream of Maldon (20). Note the reduced dissimilarity of sites 5 and 6 to the other most downstream sites postfishway installation.

**Changes in the Fish Community at Individual Fishways**

There were significant differences in the upstream and downstream fish communities at Penrith, Wallacia, and Menangle (BvA × S, Pseudo-F = 3.02, *df* = 1, *p* = 0.020, Pseudo-F = 3.11, *df* = 1, *p* = 0.029, and Pseudo-F = 5.68, *df* = 1, *p* = 0.034, respectively). Follow-up pair-wise PERMANOVA for Penrith revealed that the upstream site (above Penrith Weir) was not different pre- and postfishway (*p* = 0.249) but the downstream site (below Penrith Weir) had a significantly different fish community pre- and postfishway (similarity BvA similarity = 58%, *p* < 0.046). The upstream and downstream sites were an average of 8% more similar postfishway. At Wallacia, there was no significant difference in the fish community at the upstream site (above Wallacia Weir) and downstream site (below Wallacia Weir) prefishway (similarity = 49%, *p* = 0.56) or postfishway (similarity = 64%, *p* = 0.078). In addition, the fish community in the upstream site postfishway was not significantly different to itself prefishway (similarity = 51%, *p* = 0.055), but

was significantly different to the downstream site prefishway (similarity = 58%, *p* = 0.05). The species primarily responsible for the differences pre- and postfishways were freshwater mullet, sea mullet, freshwater herring, Australian smelt, and common carp (data not shown). At Menangle, the upstream (above Menangle Weir) and downstream (below Menangle Weir) site were significantly different pre- and postfishway (similarity = 63%, *p* < 0.05). Postfishways, these two sites were still significantly different, but their similarity had decreased (similarity = 54%).

**Discussion**

The construction of multiple vertical-slot fishways aimed to reconnect fish migration pathways along 250 km of the lower Nepean River to the estuary. The current study revealed there was an increase in species richness and expanded distributions of fishes in the 2 years following the construction of the fishways. While fish passage restoration projects often (but not always) target the broader community, they are rarely assessed to determine if the entire fish assemblage benefitted (but see Barrett & Mallen-Cooper 2006; Thiem et al. 2013; Walsh et al. 2014). Assessment of fish passage success is typically directed at a few key species of recreational or conservation importance (Bellmore et al. 2017). Here we have demonstrated that rapid changes in a fish community toward a more natural structure can be achieved in a river system over a relatively short time period. The successful passage of species encompassing a range of sizes and swimming abilities is unprecedented for a coastal river system anywhere in the world.

Prior to the installation or the retrofitting of existing fishway structures, the Nepean River weirs were a substantial barrier to native fish migration, particularly for diadromous species, consistent with two earlier studies (Gehrke et al. 1996; Baumgartner & Reynoldson 2007). Of the 14 native species collected prefishways, only five species were collected throughout the study reach (i.e. in 90% or more of sites; Australian bass, long-finned eel, Australian smelt, freshwater catfish, and flat-headed gudgeon), despite predictions that most would have occurred throughout the reach prior to weir installation. Further, only two of the 10 diadromous species recorded during the study were found throughout the system prefishways (Australian bass

**Table 1.** Fishes contributing to the mean dissimilarity between fish assemblages before and after fishway installation across the whole study area. Av. Abund is the average abundance (log abundance + 1) of each fish species. Av. Diss is the contribution to pre- and postfishway dissimilarity. \*The contribution to dissimilarity (Contrib%) indicates the proportion of dissimilarity that a species contributes to the overall dissimilarity between pre- and postfishway groups. Diadromous species are in bold.

Species	Before Versus After—Average Dissimilarity = 36.98					
	Av. Abund Before	Av. Abund After	Av. Diss	Diss/SD	Contrib%*	Cum. %
<b>Freshwater herring</b>	0.4	1.6	4.6	1.4	12.5	12.5
<b>Freshwater mullet</b>	0.4	1.4	4.2	1.6	11.3	23.9
<b>Sea mullet</b>	0.6	1.3	4.0	1.5	10.9	34.8
Australian smelt	1.7	1.8	3.8	1.3	10.2	45.0
Goldfish	1.5	1.1	3.0	1.4	8.1	53.0

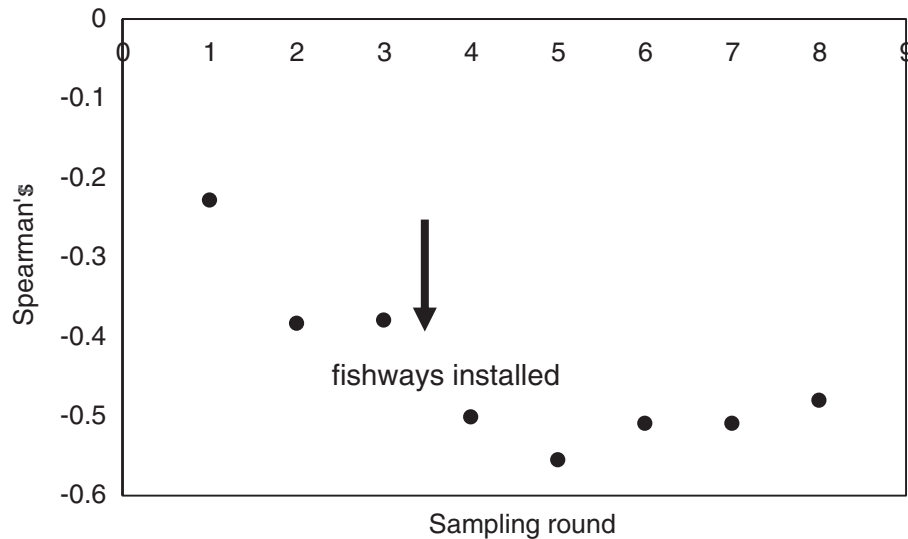


Figure 4. Rank correlation between Bray–Curtis similarities of fish communities and distance between sites in the Nepean River (all  $p$ -values are  $<0.0002$ ). Stronger negative correlations indicate adjacent sites are more similar in species composition than more distant sites.

and long-finned eel). Australian bass have been stocked in Penrith Lakes, downstream of the Penrith weir, though there are no recent records of legal stocking in the upper reaches of the river reaches of the Nepean River (<http://www.dpi.nsw.gov.au/fishing/recreational/resources/stocking>). Given that this species migrates downstream to the estuary for spawning, it is probable that it was successfully able to negotiate the old fishways, was successfully restocked or negotiated barriers during major flooding events. Similarly, long-finned eel are capable climbers and for this reason were probably also able to negotiate the weirs. Thus the evidence is clear that the low-level Nepean River weirs impact species' distribution despite the regular drown-out frequency of most weirs. These results contribute to the limited but growing number of studies that have assessed the effects of low-level dams, weirs, and road crossings and demonstrate that they significantly affect the composition of the fish assemblage (Cumming 2004; Tiemann et al. 2004; Gillette et al. 2005; Katano et al. 2006; Poulet 2007; Nislow et al. 2011; Rolls 2011). Collectively, these studies have major implications for waterways worldwide that are regulated with low-level barriers given that it cannot be assumed that drown-outs will negate the impact of the barrier.

Fish community assemblages upstream and downstream of weirs were more similar following restoration of migratory pathways. Further, we identified an increase in the distribution of several diadromous species including sea mullet, freshwater herring, freshwater mullet, and Cox's gudgeon. All of these species are catadromous (with the exception of the amphidromous Cox's gudgeon). However, some diadromous species did not expand their distributions upstream. For example, the distribution of bullrout, empire gudgeon, and striped gudgeon was almost unchanged in the Nepean River postfishways, despite fish trapping data indicating they can navigate vertical-slot fishways in the Nepean River and a fish lift at Tallowa Dam in the neighboring Shoalhaven catchment (Walsh et al. 2014; Duncan

& Robinson 2016). Assuming that the species distributional modeling is accurate and that these species would have utilized the entire study reach prior to the installation of the weirs, it is likely that other remedial actions are required to alleviate the effects of river regulation, given fishways do not solve all the problems associated with river regulation (Winter & Van Densen 2001).

All of the diadromous species that expanded their distributions did so in an upstream direction, with the exception of Cox's gudgeon. This species substantially increased its downstream distribution. Cox's gudgeon are "marginally" amphidromous, that is spawning occurs in freshwater and larvae are washed downstream into areas of low salinity within the tidal freshwater–estuary interface (Miles et al. 2009). Prefishways, Cox's gudgeon were found in low numbers at the three most upstream sites. Postfishways, Cox's gudgeon were detected at nearly every site and thousands were recorded moving through Penrith, Theresa Park, and Douglas Park fishways (Duncan & Robinson 2016). Therefore, the new fishways have allowed juveniles in the lower reaches to move upstream in much higher numbers than before. The presence of small numbers of Cox's gudgeon upstream prefishways is most likely due to a few individuals that successfully climbed over all of the weirs (Bishop & Bell 1978). Other studies have identified that this species is more abundant in unregulated lowland rivers (Gehrke 1997a) and unregulated slope reaches (Gehrke 1997b; Gehrke & Harris 2001; Rolls 2011). It is evident that the fishway installation facilitated a distribution expansion throughout the Nepean River. The downstream expansion of a fish species' range following barrier remediation has not been reported before to our knowledge and this may also be important for other species.

While the overall results of the current study are encouraging, it is clear that there is still a decline in species richness in an upstream direction and a number of diadromous species were not detected anywhere in the study area. There are three possible

explanations; firstly, it may be possible that this is attributed to individual species' environmental preferences, which is a possibility for estuarine vagrants. Secondly, sufficient time may not have elapsed since the fishways were installed to allow the full benefits to the fish community to be realized. This is a strong possibility given only 2 years of postfishway data was collected. It would be useful to repeat the electrofishing surveys again 5 years after the last surveys to document continued improvements. Finally, there may be a cumulative effect of the fishways in shaping upstream distribution of individual species where some individuals successfully pass through all fishways, while other individuals take much more time or fail to pass altogether (Caudill et al. 2007). A study on Chinook salmon and steelhead in the Colombia River demonstrated that while most adult fish successfully negotiated fishways at eight dams, 32% of Chinook salmon took more than 5 days to pass while others did not pass at all (Caudill et al. 2007). Similarly, a study of fish passage at a multispecies fishway on the Richelieu River demonstrated a broad range in passage times within species (Thiem et al. 2013). Variable fish passage success within a species can be due to a range of factors such as environmental conditions, physical condition, and individual behavior (Caudill et al. 2007). Historically, the lowland reach of the Nepean River was relatively slow-flowing and the only physical challenge to migrating fish was a gorge between Wallacia and Theresa Park that would have experienced high velocities during periods of high flow. In order to pass upstream, fish now need to negotiate multiple fishways and this can result in high energy demands (Hinch & Bratty 2000; Gowans et al. 2003; Keefer et al. 2004; Thiem et al. 2016).

The global reliance on dams and weirs has not yet reached its peak, particularly in developing countries. Current estimates indicate 43% of the world's river volume is moderately to severely impacted by dams or fragmentation (or both), and that this figure is likely to rise to a staggering 93% if all currently proposed dams proceed (Günther et al. 2015). For example, three of the largest river systems in the world, the Congo, Amazon, and Mekong are slated for a further 450 new dams alone (Winemiller et al. 2016). Consequently, it is inevitable that fish passage will become a more pressing concern in the near future, and unless steps are taken to ameliorate this, the cumulative effects along entire river systems will result in a substantial loss of biodiversity. The results of our study have shown that low-level dams can be just as significant a barrier as high-level dams to some species. Low-level dams are frequently exempt from conforming to environmental impact protocols (Winemiller et al. 2016). This is clearly a threat to the fish community and we recommend that proposed low-level barriers are subjected to a more stringent approval process and be equipped with appropriate fish passage facilities.

### Acknowledgments

This study was funded by WaterNSW and overall project guidance was provided by T. Paull. We are grateful to J. Hutchison, J. Stuart, F. Corey, M. Hill, A. Bruce, D. Galt, J. Simpson,

M. Rodgers, C. Smith, D. McLay, T. McGarry, J. McPherson, and R. Rehwinkel who assisted with field work. We thank J. Rehwinkel and C. Walsh for their advice and/or assistance with data analyses and report writing and T. McGarry for generating the map. We also thank M. Mallen-Cooper for assistance in sampling design, data analysis, and for comments on a draft version of this manuscript. T. Paull, D. Galt, C. Walsh, B. Creese, and D. Gilligan reviewed draft versions of this manuscript. This work was conducted under the NSW DPI ACEC permit 09/02 and a Section 37 research permit in accordance with the Fisheries Management Act 1994.

### LITERATURE CITED

- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E: Plymouth, United Kingdom
- Barrett J, Mallen-Cooper M (2006) The Murray River's "Sea to Hume Dam" fish passage program: progress to date and lessons learned. *Ecological Management and Restoration* 7:173–183
- Baumgartner L, Reynoldson N (2007) Fish communities of the Nepean River in the vicinity of Pheasants Nest Weir. NSW Department of Primary Industries, Cronulla, Australia
- Bellmore RJ, Duda JJ, Craig LS, Greene SL, Torgersen CE, Collins MJ, Vittum K (2017) Status and trends of dam removal research in the United States. *WIREs Water* 4:1–13
- Bishop KA, Bell JD (1978) Observations on the fish fauna below Tallowa Dam (Shoalhaven River, New South Wales) during river flow stoppages. *Marine and Freshwater Research* 29:543–549
- Bunt CM, Castro-Santos T, Haro A (2012) Performance of fish passage structures at upstream barriers to migration. *River Research and Applications* 28:457–478
- Caudill CC, Daigle WR, Keefer ML, Boggs CT, Jepson MA, Burke BJ, Zabel RW, Bjornn TC, Peery CA (2007) Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences* 64:979–995
- Clarke KR, Warwick RM (2001) Change in marine communities. PRIMER-E Ltd, Plymouth, United Kingdom
- Cumming GS (2004) The impact of low-head dams on fish species richness in Wisconsin, U.S.A. *Ecological Applications* 14:1495–1506
- Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182
- Duncan M, Robinson W (2016) Improved fish passage along the Nepean River as a result of retrofitting weirs with vertical-slot fishways. NSW Department of Primary Industries, Nelson Bay, Australia
- Dynesius M, Nilsson C (1994) Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266:753–762
- Gehrke PC (1996) Native, introduced and alien species. NSW Fisheries Research Institute and Cooperative Research Centre for Freshwater Ecology, Cronulla, Australia
- Gehrke PC (1997a) Differences in composition and structure of fish communities associated with flow regulation in New South Wales rivers. NSW Fisheries Office of Conservation and Cooperative Research Centre for Freshwater Ecology, Cronulla, Australia
- Gehrke PC (1997b) Species richness and composition of freshwater fish communities in New South Wales rivers. NSW Fisheries Office of Conservation and Cooperative Research Centre for Freshwater Ecology, Cronulla, Australia
- Gehrke PC, Harris JH (1996) Fisheries of the Hawkesbury-Nepean River System. Final Report to the Sydney Water Corporation, NSW Fisheries Research Institute and Cooperative Research Centre for Freshwater Ecology, Cronulla, Australia



- Gehrke PC, Harris JH (2001) Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. *Regulated Rivers: Research and Management* 17:369–391
- Gehrke PC, Astles KL, Harris JH (1996) Comparison of present day and historical fish communities in the Hawkesbury–Nepean River. NSW Fisheries Research Institute and Cooperative Research Centre for Freshwater Ecology, Cronulla, Australia
- Gillette DP, Tiemann JS, Edds DR, Wildhaber ML (2005) Spatiotemporal patterns of fish assemblage structure in a river impounded by low-head dams. *Copeia* 2005:539–549
- Gowans ARD, Armstrong JD, Priede IG, Mckelvey S (2003) Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish* 12:177–189
- Growns I, Rourke M, Gilligan D (2013) Toward river health assessment using species distributional modeling. *Ecological Indicators* 29:138–144
- Günther G, Bernhard L, Alexander EL, Graham KM, Christiane Z, Catherine Reidy L (2015) An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environmental Research Letters* 10:015001
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:e1500052
- Harris JH (1984) Impoundment of coastal drainages of south-eastern Australia, and a review of its relevance to fish migrations. *Australian Zoologist* 21:235–250
- Hatry C, Binder TR, Thiem JD, Hasler CT, Smokorowski KE, Clarke KD, Katopodis C, Cooke SJ (2013) The status of fishways in Canada: trends identified using the national CanFishPass database. *Reviews in Fish Biology and Fisheries* 23:271–281
- Hinch SG, Bratty J (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions of the American Fisheries Society* 129:598–606
- Jellyman PG, Harding JS (2012) The role of dams in altering freshwater fish communities in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 46:475–489
- Katano O, Nakamura T, Abe S, Yamamoto S, Baba Y (2006) Comparison of fish communities between above- and below-dam sections of small streams; barrier effect to diadromous fishes. *Journal of Fish Biology* 68:767–782
- Keefer ML, Peery CA, Bjornn TC, Jepson MA, Stuehrenberg LC (2004) Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. *Transactions of the American Fisheries Society* 133:1413–1439
- Lucas M, Baras E, Thom TJ, Duncan A, Slavik O (2001) Migration of freshwater fishes. Blackwell Science, Oxford, United Kingdom
- Mallen-Cooper M (2009) Environmental flows for the Upper-Hawkesbury–Nepean River: Nepean River fish passage design report, St Ives, Australia
- Mallen-Cooper M, Stuart IG (2007) Optimising Denil fishways for passage of small and large fishes. *Fisheries Management and Ecology* 14:61–71
- Malmqvist B, Rundle S (2002) Threats to the running water ecosystems of the world. *Environmental Conservation* 29:134–153
- McDowall RM (2007) On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries* 8:1–13
- McLaughlin RL, Smyth ERB, Castro-Santos T, Jones ML, Koops MA, Pratt TC, Vélez-Espino L-A (2013) Unintended consequences and trade-offs of fish passage. *Fish and Fisheries* 14:580–604
- McManamay RA, Peoples BK, Orth DJ, Dolloff CA, Matthews DC (2015) Isolating causal pathways between flow and fish in the regulated river hierarchy. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1731–1748
- Miles NG, West RJ, Norman MD (2009) Does otolith chemistry indicate diadromous lifecycles for five Australian riverine fishes? *Marine and Freshwater Research* 60:904–911
- Nislow KH, Hudy M, Letcher BH, Smith EP (2011) Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology* 56:2135–2144
- O'Hanley JR, Tomberlin D (2005) Optimizing the removal of small fish passage barriers. *Environmental Modeling & Assessment* 10:85–98
- Poulet N (2007) Impact of weirs on fish communities in a piedmont stream. *River Research and Applications* 23:1038–1047
- Rolls RJ (2011) The role of life-history and location of barriers to migration in the spatial distribution and conservation of fish assemblages in a coastal river system. *Biological Conservation* 144:339–349
- Roscoe DW, Hinch SG (2010) Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries* 11:12–33
- Sammut J, Erskine WD (1995) Hydrological impacts of flow regulation associated with the Upper Nepean water supply scheme, NSW. *Australian Geographer* 26:71–86
- Somerfield PJ, Clarke KR, Olsford F (2002) A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. *Journal of Animal Ecology* 71:581–593
- Thiem JD, Binder TR, Dumont P, Hatry C, Katopodis C, Stamplecoskie KM, Cooke SJ (2013) Multispecies fish passage behaviour in a vertical slot fishway on the Richelieu River, Quebec, Canada. *River Research and Applications* 29:582–592
- Thiem JD, Dawson JW, Hatry D, Danylchuk AJ, Dumont P, Gleiss AC, Wilson RP, Cooke SJ (2016) Swimming activity and energetic costs of adult lake sturgeon during fishway passage. *The Journal of Experimental Biology* 219:2534–2544
- Tiemann JS, Gillette DP, Wildhaber ML, Edds DR (2004) Effects of lowhead dams on riffle-dwelling fishes and macroinvertebrates in a Mid-western river. *Transactions of the American Fisheries Society* 133:705–717
- Walsh C, Rodgers M, Robinson W, Gilligan D (2014) Evaluation of the effectiveness of the Tallowa Dam Fishway. NSW Department of Primary Industries Fisheries Final Report Series No. 143, NSW Department of Primary Industries, Batemans Bay
- Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T, Nam S, et al. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351:128–129
- Winter HV, Van Densen WLT (2001) Assessing the opportunities for upstream migration of non-salmonid fishes in the weir-regulated River Vecht. *Fisheries Management and Ecology* 8:513–532

## Supporting Information

The following information may be found in the online version of this article:

**Table S1.** Year of construction of weirs, dams and fishways on the Hawkesbury–Nepean river system.

**Table S2.** Predicted distributions of fishes in the study reaches (downstream to upstream order) of the Nepean River.

**Table S3.** Total catch from standardized effort sampling for each site before (year 1, 2009) and after (years 2–4, 2011–2013) fishway commissioning.

**Table S4.** PERMANOVA analysis testing for differences in the fish assemblages pre- and postfishways.

Coordinating Editor: John Isanhart

Received: 30 April, 2018; First decision: 15 June, 2018; Revised: 3 September, 2018; Accepted: 4 September, 2018; First published online: 8 October, 2018